

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

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22 **Abstract**

23

24 Protracted entanglement in fishing gear often leads to emaciation through reduced

25 mobility and foraging ability, and energy budget depletion from the added drag of towing

26 gear for months or years. We examined changes in kinematics of a tagged entangled

27 North Atlantic right whale (Eg 3911), before, during and after disentanglement on 15 Jan

28 2011. To calculate the additional drag forces and energetic demand associated with

29 various gear configurations, we towed three sets of gear attached to a load-cell

30 tensiometer at multiple speeds. Tag analyses revealed significant increases in dive depth

31 and duration; ascent, descent and fluke stroke rates; and decreases in root mean square

32 fluke amplitude (a proxy for thrust) following disentanglement. Conservative drag

33 coefficients while entangled in all gear configurations (mean $\pm$ SD  $C_{d,e,go} = 3.4 \times 10^{-3} \pm$ 34  $0.0003$ ,  $C_{d,e,gb} = 3.7 \times 10^{-3} \pm 0.0003$ ,  $C_{d,e,sl} = 3.8 \times 10^{-3} \pm 0.0004$ ) were significantly greater35 than in the nonentangled case ( $C_{d,n} = 3.2 \times 10^{-3} \pm 0.0003$ ;  $P = 0.0156, 0.0312, 0.0078$ 

36 respectively). Increases in total power input (including standard metabolism) over the

37 nonentangled condition ranged 1.6%-120.9% for all gear configurations tested;

38 locomotory power requirements increased 60.0%-164.6%. These results highlight

39 significant alteration to swimming patterns, and the magnitude of energy depletion in a

40 chronically entangled whale.

41

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

44

**45 Introduction**

46 Entanglement in fishing gear is the leading cause of detected mortalities of large  
47 whales in the Northwest Atlantic (van der Hoop *et al.* 2012). Upon initial entanglement, a  
48 number of outcomes are possible: individuals may die anchored in gear, or may break  
49 free, either cleanly or carrying all or a portion of the entangling gear (Clapham *et al.*  
50 1999). Chronic effects of entanglement in free-swimming individuals include systemic  
51 infection and debilitation from extensive tissue damage (Cassoff *et al.* 2011). More  
52 common in protracted cases is severe emaciation due to the inability to cope with a  
53 negative energy budget, driven by the combined effects of reduced mobility and foraging  
54 ability, and increased energetic demand imposed by towing accessory gear for months to  
55 years (Moore *et al.* 2006, Moore and van der Hoop 2012).

56 Whereas disentanglement efforts were first developed to release large whales  
57 entangled and anchored in fixed fishing gear (Ledwell *et al.* 2010), techniques have been  
58 adapted to address the issue in free-swimming individuals (Moore *et al.* 2010).  
59 Disentanglement response efforts are coordinated by multiple agencies with the primary  
60 goal of removing all entangling gear. During a disentanglement procedure, buoys or  
61 floats are often added to trailing gear to increase a whale's drag through the water and  
62 slow its movement (Moore *et al.* 2010). To further reduce boat aversion and allow for  
63 close approaches necessary for successful disentanglement, methods have been  
64 developed to lightly sedate large whales at sea (Moore *et al.* 2010).

65 No data exist for large whales on the behavioral impacts of sedation and  
66 disentanglement or on the energetic cost of entanglement in fishing gear due to drag.  
67 Through detailed spatial and behavioral monitoring by means of a biologging tag (Dtag)

68 (Johnson and Tyack 2003), we examined changes in dive behavior and kinematics of a  
69 tagged entangled North Atlantic right whale (North Atlantic Right Whale Catalog  
70 (Hamilton *et al.* 2007) No. 3911, hereafter Eg 3911), before, during, and after  
71 disentanglement procedures on 15 Jan 2011. Further, we estimate drag forces experienced  
72 by the whale based on its body proportions, and the additional drag forces and energetic  
73 demand experienced while entangled in various gear configurations.

74

## 75 **Methods**

76 Eg 3911, born in 2009 (NARWC Database, 2011), was first sighted entangled and  
77 displaying consequent emaciation on 25 Dec 2010 by an aerial survey team offshore  
78 Ponte Vedra Beach near Jacksonville, FL, USA. The entanglement involved attachment  
79 at a minimum of six sites around the mouth, wraps around both pectoral fins, and  
80 approximately 30 m of line trailing aft of the flukes (Moore *et al.* 2012) (Fig. 1). We  
81 conducted disentanglement attempts on 29 and 30 Dec 2010, though the whale remained  
82 entangled and was tracked by a satellite telemetry buoy. A third and final multiagency  
83 disentanglement effort took place 15 Jan 2011 near Melbourne, FL, during which we  
84 tagged Eg 3911 with a biologging device (Dtag). Subsequently, we sedated, partially  
85 disentangled to the extent possible, administered antibiotics, and tracked the whale for six  
86 days via satellite with a Low Impact Minimally-Percutaneous External-electronics  
87 Transmitter (LIMPET) (Andrews *et al.* 2008) (Fig. 2). We observed Eg 3911 dead at sea  
88 by an aerial survey team on 1 Feb 2011, and towed her ashore for necropsy performed on  
89 3 Feb 2011. The ultimate cause of death was pre-mortem shark predation, though the  
90 proximate cause was chronic constrictive deep rope lacerations and severe emaciation

91 (Moore *et al.* 2010, McLellan and Costidis unpublished necropsy report<sup>1</sup>). Upon necropsy,  
92 we systematically removed, photographed, and described the remaining entangling gear.  
93 In total, the entanglement involved approximately 132 m of 1.12 cm diameter floating  
94 synthetic line, including six gangions and two fragments of vinyl coated trap mesh. This  
95 gear was consistent with that used in fixed trap/pot fisheries, though the target species  
96 could not be identified (Morin and Kenney 2011). We used a portion of the entangling  
97 gear in the experiments, below.

#### 98 Sedation

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

105 We administered sedative via injection (Moore *et al.* 2010) of 14 mL (0.1 mg kg<sup>-1</sup>  
106 body weight) each of 50 mg mL<sup>-1</sup> Butorphanol and Midazolam (ZooPharm Inc., Windsor,  
107 CO, USA), and sedative reversal via 7 mL (0.05 mg kg<sup>-1</sup>) of 50 mg mL<sup>-1</sup> Naloxone and  
108 49 mL of 0.1 mg mL<sup>-1</sup> Flumazenil. The reversal needle inserted fully, but on recovery it  
109 was discovered that the syringe had malfunctioned and the dose remained in the syringe  
110 barrel and was not administered. We also administered two doses of antibiotics (56 mL  
111 each; total 17.6 g of 220 mg mL<sup>-1</sup> Ceftiofur; Pfizer Inc, Madison, NJ, USA). Injections  
112 occurred via a ballistic syringe system (Paxarms, Timaru, New Zealand; (Moore *et al.*

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113 2010); Fig. 3), with the syringe attached to a stainless steel leader tied to 20 m of 80 kg  
114 test line spooled at the projector barrel tip, and then tied to a custom float. The float is  
115 designed to extract the needle and provide a visual marker for retrieval (Moore *et al.*  
116 2010).

117

### 118 Tagging and Behavior

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

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

### 128 *Dive Parameters*

129 We defined dives as depths >5 m, representing the top 29%-38% of the water  
130 column where Eg 3911 was tagged. We estimated bottom depth from bathymetric charts  
131 with coordinates of pursuit and disentanglement operations. Tidal range for 15 Jan 2011  
132 was only 30 to 70 cm above chart datum for Cape Canaveral, FL. We calculated  
133 proportional depth as the amount of the water column explored relative to available  
134 (depth of dive/approximate depth of dive location). We manually detected descent and  
135 ascent periods of each dive, reflecting periods of sustained motion to depth and to the

136 surface, respectively. Dive profiles appeared in randomized order for the manual  
 137 determination of descent and ascent periods to reduce potential bias. We calculated  
 138 descent and ascent rates as the distance traveled from the surface to the depth at which  
 139 the descent period ends (or from depth to surface for ascents), over the duration of that  
 140 period.

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

#### 147 *Dive Area Ratio (DAR)*

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

$$154 \quad DAR = \frac{A_a}{DT} = \frac{\sum_{i=2}^n \frac{(d_{d,i} + d_{d,i-1})}{2} \times \left(\frac{1}{fs}\right)}{DT}, \quad (1)$$

155 where  $A_a$  = integrated actual dive area,  $d_d$  = tag-derived depth (m) at  $n$  intervals during  
156 dive,  $D$  = maximum depth of dive (m),  $fs$  = tag sampling rate (Hz), and  $T$  = total dive  
157 duration (s).

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

#### 165 *Respiration*

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

#### 169 *Proxies for Thrust*

170         The Dtag captures individual fluke strokes as cyclic oscillations in the deviation  
171 of the pitch angle (degrees) from mean orientation. We considered three tag-obtained  
172 measures of thrust production: (1) fluke stroke rate, the inverse of the time between peaks  
173 in pitch angle averaged over 30 s bins (fluke strokes per second, Hz) (Johnson and Tyack  
174 2003), which is a relative indicator of thrusting intensity; (2) the root mean square (RMS)  
175 energy of fluke amplitude, a measure of signal average and variability and is proportional  
176 to power (Semmlow 2012), measured only within dives to discount large changes in pitch  
177 associated with surfacing events; and (3) glides, characterized by periods where no fluke

178 oscillation occurs in the pitch rate signal. We identified glides as segments where the  
179 absolute value of the Hilbert transform of the pitch rate signal was  $<0.05$  (Woodward *et*  
180 *al.* 2006a), and visually checked these sequences. Based on previously described gliding  
181 behaviors in right whales (Nowacek *et al.* 2001, Woodward *et al.* 2006a), we defined the  
182 minimum glide duration as 5 s.

### 183 *Overall Dynamic Body Acceleration (ODBA)*

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

### 192 *Phase Definitions and Statistical Analyses*

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

199       To determine the behavioral effects of sedation on an entangled whale, we used  
200 Wilcoxon rank sum tests to compare dive parameters and respiration rates within the

201 Sedation/Entangled phase, between the 21 min prior to and the 50 min following sedative  
202 injection, but prior to removal of the gear and buoys. We used Three-sample Kruskal-  
203 Wallis single factor analysis of variance tests with tied ranks and *posthoc* Bonferroni-  
204 corrected ( $\alpha = 0.05/3 = 0.0167$ ) Wilcoxon rank sum tests to compare the distributions of  
205 various dive parameters between Sedation/Entangled, Disentangled and Recovery phases.  
206 To compare the observed *vs.* expected ratio of time spent above and below the wave drag  
207 limit between phases, we used Chi-square contingency tables.

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

#### 214 Gear Towing

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

221 To measure drag force, we used an MLP-100 load cell tensiometer (Transducer  
222 Techniques, Temecula, CA, USA) between two eyebolts threaded into opposite sides of  
223 the cell. One eyebolt suspended the load cell parallel to a vertical spar on the side of the

224 Skiff. The second eyebolt attached to a leader running through the pulley at the base of  
225 the spar, then immediately attached to the gear (*i.e.*, the leader produced drag that was  
226 negligible compared to the gear). We held the base of the spar at the surface and at 2 m  
227 depth, consistent with the animal's body depth of 2.20 m.

228 We modified the drag force signal from the load cell as in Cavatorta *et al.* (2005)  
229 and recorded it through the serial port on a laptop, sampled at 250 ms. We calculated  
230 mean ( $\pm$ SD) drag forces from the data record for a given gear configuration (gear-only,  
231 gear-and-buoys, or sinkline), anchor point (surface or 2 m depth), and boat speed (0.772 –  
232 2.98 m s<sup>-1</sup>). We measured boat speed via a handheld GPS unit and used this speed as a  
233 relative indicator of the effect of whale swimming speed. These speeds are biologically  
234 relevant, as right whales are known to swim in the range of 0.52 (Mayo and Marx 1990)  
235 to 2.05 m s<sup>-1</sup> (Baumgartner and Mate 2003) and maximum speeds for balaenids have been  
236 recorded between 4 - 4.5 m s<sup>-1</sup> (Hamner *et al.* 1988). Tide was less than 0.5 knot.

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

243 To mimic the configuration on the animal, we attached the buoys added during  
244 disentanglement (Configuration 2; 'gear-and-buoys'), an A3 Polyform buoy (42.5 cm  
245 diameter) and an NB60 Scanmarin buoy (45.4 cm diameter) to the aft-most figure-eight  
246 knots on the removed gear (*i.e.*, Configuration 1). We connected each buoy to its

247 respective figure-8 knot by an 11.4 cm karabiner and an approximately 1 m long lanyard  
 248 of 0.95 cm diameter polysteel. The buoys and karabiners used in the tow deployments  
 249 were identical to those used in the disentanglement procedure; however, during the  
 250 disentanglement, we attached buoys to the fore-most and aft-most knots. We assume this  
 251 difference in the gear configuration does not change the results materially.

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

#### 254 Energetic Requirements

255 We applied the following calculations to determine the forces acting on Eg 3911.  
 256 The Reynolds number,  $Re$ , describes the relative importance of viscous and inertial forces  
 257 acting on a body, calculated as

$$258 \quad Re = lU/\nu \quad (2)$$

259 where  $l$  is the length of the body (m),  $U$  is the velocity or swimming speed ( $\text{m s}^{-1}$ ) and  $\nu$  is  
 260 the kinematic viscosity of the surrounding medium ( $1 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$  for seawater). Reynolds  
 261 numbers  $> 5 \times 10^6$ , as calculated here and is the case for other large whales, indicate a  
 262 turbulent boundary layer.

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

$$265 \quad D_f = \frac{1}{2} \rho U^2 A_w C_f, \quad (3)$$

266 where  $\rho$  is the density of the surrounding medium (here seawater,  $1025 \text{ kg m}^{-3}$ ),  $A_w$  is the  
 267 total wetted surface area ( $\text{m}^2$ ; Alexander 1990) calculated from body mass  $M$  (kg) as  $A_w =$   
 268  $0.08M^{0.65}$  (Fish 1993).  $C_f$  is a frictional drag coefficient, which depends on boundary

269 layer flow characteristics (*e.g.*, Blake 1983). For a turbulent boundary condition, as  
 270 calculated above,

$$271 \quad C_f = 0.072(Re^{-1/5}). \quad (4)$$

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

$$275 \quad C_{D0} = C_f + C_p = C_f \left[ 1 + 1.5 \left( \frac{d}{l} \right)^{3/2} + 7 \left( \frac{d}{l} \right)^3 \right], \quad (5)$$

276  
 277 where  $d$  is the maximum width of the body (or diameter; m) estimated from photographs  
 278 using width-to-length ratios of the widest point of the body.

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

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

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

$$300 D_w = \frac{1}{2} \rho U^2 S_w C_{D0} \gamma k g . \quad (6)$$

301 Line lying flush with the body surface produces a surface protuberance that may  
 302 disrupt fluid flow over the body, affecting body drag. The total drag of the system is not  
 303 simply the sum of the drag on the body and on the element, but also the interference  
 304 between the elements (interference drag) (Blake 1983). The magnitude of interference  
 305 drag varies non-linearly with the position (% of  $l$ ) and height of the protuberance ( $p$ , m)  
 306 compared to the length of the body ( $l$ , m) (Jacobs 1934, Blake 1983). As protuberance  
 307 height is increased from  $p = 0$  to  $p = 0.001l$  (e.g., from 0 to 1.25 cm diameter line)  
 308 interference drag is comparatively small, on the order of 10% of the drag of the element.  
 309 Increases in drag over this height scale are slow due to the protuberance being in the  
 310 body's boundary layer ( $\delta$ ); however, they should not be considered negligible (Jacobs  
 311 1934). For this height scale, the interference drag coefficient of a protuberance  $j$  ( $C_{DI,j}$ ) is

$$312 \quad C_{DI,j} = \left( \frac{p_j}{\delta_j} \right)^{(1/3)}, \quad (7)$$

313 where we calculated boundary layer thickness ( $\delta$ , m) at the location of protuberance  $j$   
 314 (distance from leading edge,  $l_{x,j}$ ; m) based on the ratio between the maximum diameter  
 315 and the diameter at the location of protuberance  $j$  ( $d_{x,j}$ ) as

$$316 \quad \delta_j = \left( \frac{d}{d_{x,j}} \right) 0.02 l_{x,j}. \quad (8)$$

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

$$319 \quad D_I = \sum_{j=1}^n D_{I,j} = \sum_{j=1}^n \frac{1}{2} \rho U^2 A_{1p,j} C_{DI,j}. \quad (9)$$

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

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

$$328 \quad D_T = D_w + a(D_b + D_l) + D_I, \quad (10)$$

329 where  $D_b$  is the drag on tethered buoys or other accessory gear,  $D_l$  is the drag on the  
 330 attached line,  $D_I$  is the interference drag, and  $a$  is the shielding factor, based on the  
 331 spacing distance,  $x$ , between the body and the towed gear where if  $x/d$  is less than 2,  $a =$   
 332 0.75, and if  $x/d$  is greater than 1,  $a = 1$ . In this study, we empirically measured ( $D_b + D_l$ ).

333 We derive the total power input ( $P_{I,T}$ ; W) required for propulsion at a certain  
 334 speed under any calculated drag condition (generic  $D$ ) as

$$335 \quad P_{I,T} = P_L + P_{I,B} = (DU/\eta) + P_{I,B}, \quad (11)$$

336 where  $P_L$  is locomotory power, and  $P_{I,B}$  is power input for standard metabolism, both in  
 337 W, and  $\eta$  is an efficiency coefficient of 0.15 (Fish 1993, Hind and Gurney 1997). Given  
 338 the uncertainties in appropriate metabolic rate estimation for cetaceans (Gallivan 1992),  
 339 we estimated minimum and maximum standard metabolism (W) using Kleiber ( $3.4M^{0.75}$ ;  
 340 where  $M$  is body mass in kg), and  $3 \times$  Kleiber.

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

$$346 \quad U_{red} = \left[ \frac{P_L \eta U^2}{D_T} \right]^{(1/3)}. \quad (12)$$

347 To determine the additional power demands experienced by Eg 3911 while  
 348 entangled, we compared  $P_{I,T}$  for the drag conditions of a nonentangled whale, with  
 349 surface drag factor  $\gamma$  following disentanglement (*i.e.*,  $\gamma = 1.0$ ), to the conditions of an  
 350 entangled whale, towing three gear configurations tested in this experiment, with surface  
 351 drag factor  $\gamma$  calculated for the mean  $\pm$  SD dive depth prior to disentanglement (*i.e.*,  $\gamma =$   
 352 1.6).

353

## 354 **Results**

### 355 Tagging and Behavior

356 *Dive Parameters*

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

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

363 Dive depth increased significantly with every phase ( $\chi^2 = 26.66$ ,  $P < 0.0001$ ; Fig.  
 364 6). Median dive depth was significantly (138%) shallower in Sedation/Entangled  
 365 compared to Disentangled ( $Z = -6.121$ ;  $P < 0.0001$ ). Significant increases in dive depth  
 366 occurred between Disentangled and Recovery ( $Z = 4.607$ ;  $P < 0.0001$ ), though only by  
 367 19%. Even when considering increases in approximate regional water column depth with  
 368 time, proportional dive depth was significantly shallower in Sedation/Entangled (by 95%)  
 369 compared to following the removal of gear and buoys (*i.e.*, in Disentangled;  $Z = -5.216$ ;  $P$   
 370  $< 0.0001$ ; Fig. 6). Further, we observed no significant difference in proportional dive  
 371 depth between Disentangled and Recovery phases ( $Z = -0.679$ ;  $P = 0.497$ ).

372 Descent rates ( $\text{m s}^{-1}$ ) during dives differed significantly between phases ( $\chi^2 =$   
 373  $49.87$ ;  $P < 0.0001$ ; Fig. 6), where descents during Sedation/Entanglement were 57%  
 374 slower than in Disentangled ( $Z = -6.287$ ;  $P < 0.0001$ ). There was no significant difference  
 375 between the descent rates in Disentangled and Recovery ( $Z = 0.535$ ;  $P = 0.5927$ ).

376 Ascent rates ( $\text{m s}^{-1}$ ) during dives also differed significantly between phases ( $\chi^2 =$   
 377  $46.22$ ;  $P < 0.0001$ ; Fig. 6), with significantly slower ascents (31%) during  
 378 Sedation/Entanglement compared to in Disentanglement ( $Z = -5.948$ ;  $P < 0.0001$ ). Similar

379 to descent rate, ascent rate did not differ between Disentanglement and Recovery ( $Z =$   
 380  $0.090$ ;  $P = 0.9285$ ).

381 For Eg 3911 ( $h = 1$  m,  $d = 2.20$  m), wave drag is maximal within 0.1 m of the  
 382 surface, and becomes negligible below 5.58 m depth ( $h = 6.58$  m). The ratio of time spent  
 383 above vs. below the wave drag limit (5.58 m) over the entire deployment was 1.06,  
 384 meaning Eg 3911 spent almost equal amounts of time above and below the threshold.  
 385 However, significantly more time was spent in surface waters where energy requirements  
 386 are higher before (7.02:1) vs. following sedative injection (2.47:1;  $\chi^2 = 141$ ;  $P < 0.0001$ ;  
 387 Table 3), and while entangled (*i.e.*, during Sedation/Entangled; 2.87:1) vs. during  
 388 Disentangled (0.6656:1) and Recovery phases (0.4405:1;  $\chi^2 = 3220$ ;  $P < 0.0001$ ).

389 Dive duration (s) differed significantly between phases ( $\chi^2 = 26.67$ ;  $P < 0.0001$ ;  
 390 Fig. 6), where dives during Sedation/Entangled were 56% shorter than in  
 391 Disentanglement ( $Z = -3.151$ ;  $P < 0.0016$ ). Dive duration also increased significantly, by  
 392 30%, from Disentanglement to Recovery ( $Z = 3.4218$ ;  $P = 0.0006$ ).

### 393 *Dive Shape*

394 Dive shape, as measured by the DAR, differed significantly between phases ( $\chi^2 =$   
 395  $19.1083$ ;  $P = 0.0001$ ; Fig. 7), with significantly lower DAR during Sedation/Entangled  
 396 than in Disentangled or Recovery phases ( $Z = -3.1615, 4.3410$ ;  $P = 0.0016, < 0.0001$   
 397 respectively). There was no significant difference in the DAR between Disentangled and  
 398 Recovery phases ( $Z = 0.9443, P = 0.3450$ ).

### 399 *Respiration*

400 Respiration rate per 5-minute interval did not change following sedative delivery  
 401 ( $P = 0.4312$ ; Table 3). We detected no significant difference between respiration rate

402 before (5.00 (2.00) /5 min) and after (5.00 (1.75) /5 min) buoy and gear removal ( $P =$   
 403 0.1679).

#### 404 *Proxies for Thrust*

405 Fluke stroke rate increased significantly following sedative injection ( $Z = -8.417,$   
 406  $P < 0.0001$ ; Table 3). Fluke stroke rate within dives differed significantly between phases  
 407 ( $\chi^2 = 18.7179$ ;  $P = 0.0001$ ; Fig. 8), being significantly lower during Sedation/Entangled  
 408 compared to the Disentangled phase ( $Z = -3.928$ ;  $P < 0.0001$ ). Fluke stroke rate did not  
 409 differ in Disentangled and Recovery phases ( $Z = -0.0323$ ,  $P = 0.9742$ ).

410 Following sedative injection, RMS energy within dives increased significantly, by  
 411 28% ( $Z = -3.0832$ ;  $P = 0.0020$ ; Table 3). RMS energy was 12% lower after gear and buoy  
 412 removal ( $Z = 3.1943$ ;  $P = 0.0014$ ). From Disentangled to Recovery phases, RMS energy  
 413 within dives significantly decreased ( $Z = -2.5960$ ;  $P = 0.0094$ ).

414 Glide duration did not differ significantly before and after sedative injection ( $P =$   
 415 0.1993), or before and after the removal of the gear and buoys ( $Z = 0.334$ ;  $P = 0.9734$ ).

416 While glides occurred in all phases, the portion of the dive cycle in which gliding  
 417 occurred differed between phases. When entangled ( $n = 18$ ), 50% of glides occurred  
 418 during the bottom period, 33% during descent and 17% on ascent. However, following  
 419 disentanglement ( $n = 41$ ), 85% of glides were performed during the bottom period, and  
 420 15% during ascent. No glides were performed during descent following disentanglement.

#### 421 *ODBA*

422 Within dives, ODBA did not differ significantly between phases ( $\chi^2 = 5.4288$ ;  $P =$   
 423 0.0662). During dive descents, ODBA differed significantly between phases ( $\chi^2 =$   
 424 8.2055;  $P = 0.0165$ ), being significantly (10%) lower during Sedation/Entangled than in

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

#### 429 Gear Towing

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

#### 436 Energetic Requirements

437 The mean theoretical drag coefficient of a nonentangled right whale ( $C_{d,n}$ ) of Eg  
 438 3911's dimensions, swimming at  $0.75 - 2.9 \text{ m s}^{-1}$  ranged from  $3.7 \times 10^{-3}$  to  $2.9 \times 10^{-3}$   
 439 respectively (mean $\pm$ SD;  $C_{d,n} = 3.2 \times 10^{-3} \pm 0.0003$ ; Fig. 10). The drag coefficient for each  
 440 entangled gear scenario was calculated by applying Equation 6 ( $C_d = D_T / (1/2) \rho U^2 A_w \gamma k$   
 441  $g$ ). Though drag coefficients for Eg 3911 entangled in all gear configurations differed  
 442 based on the value of  $k$  (Fig. 9), the most conservative estimates with  $k = 3$  ( $C_{d,e,go} =$   
 443  $3.4 \times 10^{-3} \pm 0.0003$ ,  $C_{d,e,gb} = 3.7 \times 10^{-3} \pm 0.0003$ ,  $C_{d,e,sl} = 3.8 \times 10^{-3} \pm 0.0004$ ) were  
 444 significantly greater than in the nonentangled case (Wilcoxon signed rank,  $P = 0.0156$ ,  
 445  $0.0312$ ,  $0.0078$  respectively).

446 Having made low (Kleiber) and high ( $3 \times$  Kleiber) estimates of BMR, and using  
 447 two values of  $k$  (1 and 3), we present drag and power requirements as the lower ( $k = 1$ ,

448 BMR = Kleiber) and upper ( $k = 3$ , BMR =  $3 \times$  Kleiber) bounds of the model results. Drag  
449 forces on Eg 3911 while not entangled ranged from 37.2 N to 1263 N at  $0.75 - 2.9 \text{ m s}^{-1}$ .  
450 The associated total power requirements in the nonentangled condition (Eq. 11) ranged  
451 from 2791 W – 16140 W (Fig 10). Locomotory power requirements ranged from 191 –  
452 25021 W.

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

458 Locomotory power requirements increased on average 70.5% (SD 9.5) for the gear-only  
459 configuration, 91.0% (22.5) for the sinkline configuration, and 101.9% (31.9) for the  
460 gear-and-buoy configuration (total range 60.0%-164.6%). Alternatively, to maintain the  
461 same power output over the range of swimming speeds, an individual entangled in gear-  
462 only, sinkline, and gear-and-buoy configurations would need to decrease swimming  
463 speed by 16.2% (SD 1.5), 19.2% (3.0), or 20.5% (3.9), respectively (total range 14.5%-  
464 27.7%).

465

## 466 **Discussion**

467 We describe the effect of sedation and near-complete disentanglement of a free-  
468 swimming entangled right whale, Eg 3911. Tag data show major changes in locomotion  
469 before and after disentanglement. Modeling the drag forces of the removed gear, we show  
470 that entangled whales can have significantly increased energetic demand.

471 Sedative injection had little to no effect on dive parameters or respiration rate. It is  
472 likely that in this condition, behavior is dominated by the effect of entangling gear rather  
473 than of a light sedative. At the dosage level ( $0.1 \text{ mg kg}^{-1}$ ), Midazolam has not been found  
474 to cause cardiovascular, respiratory, or airway reflex changes in humans (Reves *et al.*  
475 1985), though a previous study reports increased respiration rates following sedation in  
476 right whales (Moore *et al.* 2010).

477 After sedation, Eg 3911 spent a greater proportion of time below the wave-drag  
478 threshold (5.58 m), though showed no difference in maximum dive depth. This increased  
479 submergence time may be linked to the lethargy associated with sedation. Moore *et al.*  
480 (2010) describe less forceful surfacing events in sedated right whales. However,  
481 increased fluke rate and RMS energy post sedation may suggest the drugs had an  
482 analgesic effect in reducing entanglement-associated pain, and therefore freeing the  
483 animal to locomote more strongly.

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

490 Changes in kinematics and dive parameters indicate the whale altered its behavior  
491 immediately following disentanglement. Previous studies suggest that propulsive forces  
492 are increased in response to changes in resistive forces, where elephant seals adjust stroke  
493 intensity when buoyancy is experimentally altered (Aoki *et al.* 2011). Animals may also

494 actively alter swimming dynamics or posture to compensate for an added load. As  
495 suggested by Watson and Granger (1998), animals facing an increase in drag may either  
496 (1) maintain characteristic velocity, exponentially increasing energy expenditure; or (2)  
497 reduce swimming speed in an attempt to reduce the cost of locomotion. Fluke stroke rate,  
498 which has been shown to correlate with speed in dolphins (Fish 1993) and other  
499 cetaceans (Fish 1998), increased significantly following disentanglement. Further, Eg  
500 3911 showed descent and ascent speeds 57% and 31% faster (respectively) after  
501 disentanglement, greater than the expected 14.5% – 27.7% as calculated above. While  
502 changes in swimming speed were likely due to a combination of factors rather than  
503 energy conservation alone (*e.g.*, sedation, pursuit by a vessel), this case suggests that  
504 entanglement significantly alters swimming modes.

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

514         Given that the added buoys were further from the whale than the water column  
515 was deep, the buoys should have never been submerged to provide an upwards buoyant  
516 force that Eg 3911 could take advantage of to conserve energy in diving (Nowacek *et al.*

517 2001). Glides occurred in all phases of the dive cycle, indicating that passive swimming  
518 was not timed to take advantage of changes in buoyancy by gliding on ascent while  
519 entangled. The emaciated condition of Eg 3911 may have led to negative buoyancy, as  
520 has been found in emaciated bottlenose dolphins (Dunkin *et al.* 2010), and dive depths  
521 were much shallower than the predicted depth of lung collapse in cetaceans (30 – 235 m)  
522 (Fahlman 2008). It is thus likely that glides were employed to conserve energy (Videler  
523 and Weihs 1982, Williams 2001) rather than to optimize the benefits of buoyancy.

524 ODBA has shown to be a reliable estimator for activity and metabolic rate in free-  
525 swimming animals (Fahlman *et al.* 2008). It was thus expected that ODBA be greater  
526 under the entangled condition; however, ODBA was often lower while entangled,  
527 compared to after disentanglement. We suggest that restraint by the drag and buoyancy of  
528 the gear may have reduced Eg 3911's ability to make large dynamic movements.

529 Accelerometer measurements determine only the movement of the animal (*i.e.*, net  
530 movement) and those forces associated, but not the forces required to move against any  
531 materials that may be restraining movement (*i.e.*, total exertion). Consider a running  
532 parachute: the runner expends considerably more energy with the parachute, though their  
533 motion is more limited and is slower than without the apparatus. The application of  
534 ODBA to free-swimming and restrained cases likely requires separate metabolic  
535 calibrations for each condition, which are not available for entangled large whales at this  
536 time.

537 Together, the effects of added buoyancy, added drag, and reduced swimming  
538 speed due to towing accessory gear pose many threats to entangled whales. If buoyancy  
539 overwhelms an animal's ability to descend to the depth of its preferred prey, its foraging

540 ability may be significantly compromised, accelerating the transition to a negative energy  
541 balance. Increased time spent in surface waters results in greater overall drag, due to  
542 surface effects (Hoerner 1965, Hertel 1969), and places individuals at greater ship strike  
543 risk (Nowacek *et al.* 2001, Parks *et al.* 2012). Reduced swimming speed will lead to  
544 increases in travel time, potentially delaying an entangled individual's arrival to feeding  
545 or breeding grounds in the case of migratory species (Watson and Granger 1998, Jones *et*  
546 *al.* 2011).

547         Most significant, however, is the energy drain associated with added drag. The  
548 drag experienced by an animal is significantly affected by the size of the animal relative  
549 to the entangling gear, and its configuration, position of attachment, placement in the  
550 animal's wake, and surface area (Feldkamp 1985). The addition of buoys to entangling  
551 gear during disentanglement procedures to increase surface area, buoyancy, and  
552 turbulence does significantly increase drag forces; however, this method has been used  
553 successfully to disentangle whales that have survived to breed (Robbins and Knowlton  
554 2012, Robbins and Landry 2012). Therefore, we suggest that current practice be  
555 continued in adding buoys only for short-term operations, such as a single  
556 disentanglement attempt. The benefits of partial or full gear-removal likely outweigh the  
557 short-term energetic impact buoy-addition may incur.

558         Since not all entanglements can be resolved during a single attempt, a 36 cm  
559 diameter satellite/VHF telemetry buoy is the current method of tracking entangled  
560 individuals for later re-sighting and disentanglement. In eight cases, these buoys have  
561 also provided sufficient drag to allow whales to remove some or all remaining gear (S.

562 Landry pers. comm.<sup>3</sup>). Since the current telemetry buoy does create drag force (*ca.* 76 N  
563 at  $1.3 \text{ m s}^{-1}$ , (Woodward *et al.* 2006b)) entanglement responders should continue to make  
564 every effort to: use telemetry on a case-by-case basis, strategically place the telemetry  
565 buoy to minimize impacts, remove as much of the original trailing gear to minimize  
566 additional drag force and reduce the duration of buoy placement. Longer-duration, lower  
567 drag telemetry buoy designs should continue to be developed for tracking entangled  
568 individuals for later disentanglement.

569         To reduce locomotory costs, marine mammals have adapted low drag coefficients.  
570 Drag has been estimated from Dtag records (Miller *et al.* 2004, Simon *et al.* 2009,  
571 McGregor 2010), though this method requires a measure of speed, which cannot be  
572 obtained from this tagging event due to boat noise and low pitch angles. Still, the  
573 theoretical coefficient we estimated for Eg 3911 ( $3.7 \times 10^{-3}$  to  $2.8 \times 10^{-3}$  over a range of  
574 speeds) falls well within the range of previously estimated drag coefficients for large  
575 whales ( $5.2 \times 10^{-3}$  –  $1.4 \times 10^{-2}$ ) (Miller *et al.* 2004, McGregor 2010). Significant increases  
576 (2.3%-69.2%) in the drag coefficient occur in the entangled scenario, leading to 60.0%-  
577 164.6% increases in locomotory power output.

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

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<sup>3</sup> Scott Landry, Provincetown Center for Coastal Studies Marine Animal Entanglement Response, 5 Holway Ave, Provincetown MA 02657 USA

583 in a severely entangled right whale (Hunt *et al.* 2006), the relationships between  
584 entanglement stress and metabolic rate are too complex to be considered here.

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

595 A simple calculation can illustrate both the effects of increased drag, and of  
596 reduced swimming speed (Watson and Granger 1998, Jones *et al.* 2011). Using our most  
597 conservative estimate, a nonentangled right whale swimming 2,900 km, at an average  
598 speed of  $1.5 \text{ m s}^{-1}$  could complete a one-way migration in 22 d, expending  $7.3 \times 10^9 \text{ J}$  of  
599 energy. Entangled in the gear-only configuration, an individual could migrate at the same  
600 speed, arriving on time and expending  $9.3 \times 10^9 \text{ J}$  of energy (a 27% increase) or could  
601 swim at a reduced speed to arrive 5 d late, expending  $9.6 \times 10^9 \text{ J}$  (a 31% increase). If this  
602 same calculation is made with a more energetically costly entanglement scenario (*e.g.*,  
603 gear-and-buoys), the entangled individual could arrive on-time, expending  $1.0 \times 10^{10} \text{ J}$  (a  
604 37% increase), or 5 days late expending essentially the same  $1.0 \times 10^{10} \text{ J}$ . Under both  
605 entanglement and speed maintenance or reduction scenarios, the energy store budgeted

606 for a nonentangled one-way migration ( $7.3 \times 10^9$  J) would be exhausted between 71%-78%  
 607 of the distance to the destination.

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

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615

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626

### 627 Tables

628

629 **Table 1. List of symbols**

Symbol	Units	Definition
$\delta$	m	Boundary layer thickness
$\gamma$		Surface drag augmentation factor
$\eta$		Propulsive efficiency
$\rho$	$\text{kg m}^{-3}$	Density of surrounding medium
$a$		Shielding factor
$A_a$		Integrated actual dive area
$A_w$	$\text{m}^2$	Total wetted surface area
$A_{\perp p}$	$\text{m}^2$	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
$f_s$	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
$U$	$\text{m s}^{-1}$	Velocity (swimming speed)
$U_{red}$	$\text{m s}^{-1}$	Reduced velocity due to increased drag condition
$\nu$	$\text{m}^2 \text{s}^{-1}$	Kinematic viscosity of surrounding medium
$x$	m	Spacing distance between whale and (first) towed body

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**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 <i>Cabretta</i> left scene; Vessel <i>Orion</i> following at 50-300 m distance.
	22268	16:15:00	Tag off

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**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

639

640 **Table 4.** Mean (SD) drag forces (N and kg) exerted by (1) 33.63m of fishing gear and (2)  
 641 gear and buoy configurations removed from Eg 3911, and (3) 160m of sinkline at surface  
 642 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)

643 **Table 5.** Total drag forces (N) on, and power output (W) required by, Eg 3911 swimming  
 644 entangled in various configurations (Gear Only, Gear and Buoys, and Sinkline) of fishing  
 645 gear, and the percentage increase in power, or percent decrease in swimming velocity due  
 646 to increased drag over the normal (nontangled) condition. Ranges represent the lower  
 647 and upper bounds of values of k (profile drag augmentation factor) and metabolic rate  
 648 (see text).  
 649

	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 Buoy	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

650

651

652 **Figure Titles**

653

654 **Figure 1.** Aerial photograph of right whale Eg 3911 on 30 Dec 2010, showing complex  
655 entanglement in the head and pectoral fins. Photo under NOAA Fisheries Permit #594-  
656 1759

657

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

663

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

669

670 **Figure 4.** Fishing gear removed from right whale Eg 3911 on 15 Jan 2011. The total  
671 length of the configuration is approximately 24.93 m, with a combined line length of  
672 33.63 m. A tape measure (left) is drawn to 1 m for spatial reference.

673

674 **Figure 5.** Dive profile of right whale Eg 3911 over the course of a 6:11 (hr:min) Dtag  
675 attachment. Estimated bottom depth (m; horizontal black line) and event markers are  
676 plotted for reference.

677

678 **Figure 6.** Boxplots of dive parameters of right whale Eg 3911 separated into phases (1)  
679 Sedation/Entangled, (2) Disentangled, and (3) Recovery in the DTAG record of right  
680 whale Eg 3911. Brackets denote significant differences between two phases. Asterisks  
681 indicate outliers.

682

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

689

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

695

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

700

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

705

706

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872

### 873 **Supplemental Information**

874

875 We used four methods to estimate body weight from length. (1) Age-weight and  
 876 length-weight functions (Moore *et al.* 2004) approximated the weight of a two year old or  
 877 950 cm right whale to 6,717 and 6,396 kg respectively, though the paucity of the data at  
 878 these age values suggests a more plausible range of 8,000 – 10,000 kg. (2) An additional  
 879 age-dependent length-weight function (Fortune 2012) estimated 10,551 kg. (3) To  
 880 address the degree of emaciation of the individual and its effect on the above weight  
 881 estimates, we estimated width-to-total body length ratios at intervals of 10% of the body  
 882 length from the tip of the rostrum and compared to width-to-length ratios measured using  
 883 vertical aerial photogrammetry of 10 adult female right whales (Miller *et al.* 2012) (Table  
 884 S1). This comparison suggests Eg 3911 was on average 20% thinner than other adult  
 885 female right whales, allowing for a weight estimation of between 6,400 – 8,440 kg. (4)  
 886 We reduced other scaling factors for gray whales (Sumich 1986) and generic cetaceans  
 887 (Geraci and Lounsbury 2005) by 20% to account for emaciation to obtain estimates of  
 888 7,048 kg and 7,200 kg respectively.

889

890 **Table S1.** Width-to-total body length ratios at intervals of 10% of the body for 10  
 891 mesomorphic right whales and Eg 3911.

	Width to Total Body Length Ratio							
	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

892