THE ROYAL
SOCIETY

doi 10.1098/rspb.2001.1730

Buoyant balaenids: the ups and downs of buoyancy in right whales

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A variety of marine mammal species have been shown to conserve energy by using negative buoyancy to power prolonged descent glides during dives. A new non-invasive tag attached to North Atlantic right whales recorded swim stroke from changes in pitch angle derived from a three-axis accelerometer. These results show that right whales are positively buoyant near the surface, a finding that has significant implications for both energetics and management. Some of the most powerful fluke strokes observed in tagged right whales occur as they counteract this buoyancy as they start a dive. By contrast, right whales use positive buoyancy to power glides during ascent. Right whales appear to use their positive buoyancy for more efficient swimming and diving. However, this buoyancy may pose added risks of vessel collision. Such collisions are the primary source of anthropogenic mortality for North Atlantic right whales, whose population is critically endangered and declining. Buoyancy may impede diving responses to oncoming vessels and right whales may have a reduced ability to manoeuvre during free ascents. These risk factors can inform efforts to avoid collisions.

Keywords: *Eubalaena glacialis*; buoyancy; tagging; diving behaviour; conservation

1. INTRODUCTION

When a marine mammal dives it is under strong constraints to conserve energy since aerobic metabolism is contingent upon stored oxygen. Most marine mammals stroke continuously as they descend from the surface, but as their lungs collapse, causing a volume decrease, many species use their increasingly negative buoyancy to produce passive glides in the later stages of descent (Williams *et al.* 2000). Experimental manipulation of the buoyancy of elephant seals causes them to modify their dive behaviour (Webb *et al.* 1998). We decided to study dive behaviour in a balaenid whale that is known historically to be positively buoyant at the surface, to test the hypothesis that gliding during descent is employed by other cetacean and pinniped taxa.

This study focused on the North Atlantic right whale, *Eubalaena glacialis*. Whalers termed this species the ‘right’ whale to kill because their carcasses were more likely than those of other whales to float (Scammon 1874; Starbuck 1878). The historic overexploitation of these whales devastated their populations (Mitchell 1977; Reeves & Mitchell 1986*a*,*b*; Waring *et al.* 1999). While some populations of balaenids (right and bowhead whales) appear to be recovering from whaling (Hill & DeMaster 1999; Best *et al.* 2001), the North Atlantic right whale numbers fewer than 300 individuals and appears to be in decline (Caswell *et al.* 1999). Indeed, this is one of the most endangered of all the large whales and is under significant threat of extinction if current conditions persist (Caswell *et al.* 1999; Clapham *et al.* 1999). Although northern right whales have not been hunted since 1914 (except for isolated exceptions), other human activities have greatly increased their mortality rate. Collisions with vessels are a serious cause of human-induced injury and mortality. Between 1970 and 1999, ship strikes were responsible for 16 out of 18 deaths attributed to human activity. These strikes accounted for more than one-third of the 45 known right whale fatalities (Laist *et al.* 2001); given that many carcasses were not examined, the true total is almost certainly higher. Reducing anthropogenic mortality is essential if this population is to remain viable (Caswell *et al.* 1999). A significant obstacle to developing targeted measures for mitigating ship strikes is our ignorance of the precise behavioural and acoustic conditions that lead to a collision.

2. METHODS

We attached a new digital acoustic recording tag (DTAG) to North Atlantic right whales to study their diving behaviour. Data on the motor and acoustic behaviour of submerged marine mammals have traditionally been difficult to obtain. When an animal is submerged, these data are available only to observers working in clear-water locations or with specialized techniques (Connor *et al.* 1992; Davis *et al.* 1999; Nowacek *et al.* 2001). Even under these circumstances observations are limited by light penetration into and through the water. Electronic tags have been effectively used to record dive times, depths, locations, and some swimming movements of wild marine mammals (Davis *et al.* 1999; Fletcher *et al.* 1996; Read & Westgate 1997; Westgate *et al.* 1995). The small size and capabilities of the DTAG, however, provide novel data in a robust package: sensors include a three-axis accelerometer, compass, water temperature and

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Received 5 March 2001 *Accepted* 4 May 2001

Figure 1. The DTAG encased in a moulded polyethylene fairing attached to a North Atlantic right whale in the Bay of Fundy, August 2000. The inset shows a detailed view of the tag package.

pressure sensors, and a hydrophone. The DTAG continuously records the orientation, heading and depth of the tagged animal in complete synchrony with sounds sensed by the hydrophone. The sensor sampling rate (23 Hz) and accuracy are sufficient to track both subtle and fast movements, while the audio bandwidth (8 kHz) covers the vocalization frequency range of right whales (Clark 1982). By recording behaviour and sound synchronously, the DTAG can unambiguously capture behaviour that is not observable from the surface.

The tags, housed in a polyethylene fairing, were attached to free-swimming right whales in the Bay of Fundy, Canada, with three suction cups, two forward and one aft (figure 1). The hydrophone was either potted in the aft suction cup (1999) or enclosed in the fairing (2000). Also enclosed in the fairing were batteries, syntactic foam floatation, and a radio transmitter for tracking and package recovery. An anodic corrosive wire embedded within the attachment hardware was designed to release the package from the whale. One package released via this mechanism, the others due to skin sloughing, contact with another whale, or some other force that caused the suction to release. Tags remained attached to whales for up to 21 hours, although attachments of *ca.* 5 hours were more typical. Sensor and acoustic data were stored simultaneously, which provided exact synchronization that is typically difficult to achieve with multi-package integration (Skrovan *et al.* 1999; Williams *et al.* 2000). From the accelerometers we calculated the whales' pitch and roll angles, while the magnetometers gave heading. The tag was attached dorsally and approximately midway between the blowholes and the caudal peduncle. In this position, the pitch angle of the animal contains a significant signal due to oscillations of the body during swimming and so can provide an indication of when the animal is stroking as well as the stroke rate (Skrovan *et al.* 1999). The high-speed sampling capabilities of the DTAG permit fine resolution of sampled data. A single fluke stroke, for example, that occurs at *ca.* 0.2 Hz can be analysed with over 100 data points in exact synchrony with all other recorded data.

3. RESULTS

(a) *Diving behaviour*

Swimming and dive data recorded by the DTAG from eight right whales during 95 dives in 1999 and 2000 indicate that the tagged whales were positively buoyant at depths greater than Williams *et al.* (2000) report for seals, dolphins and blue whales. Williams *et al.* (2000) suggest that all marine mammals glide on descent to conserve energy, but the positive buoyancy of right whales allows them to conserve energy while gliding on ascent. All dives from these tagged whales were interpreted to be foraging dives based on their flat-bottomed shape (figure 2; Le Boeuf *et al.* 1988). The extent of active swimming during descent versus ascent and their overall pitch angle demonstrate the positive buoyancy of these right whales (figure 3). While descending, the whales had to propel themselves at steep angles to the bottom of their dives (table 1; figure 3*b*,*c*). During ascent, however, they glided at relatively shallow angles for 15–60% of the total ascent time (table 1; figure 3*d*,*e*). Despite these differences in swimming behaviour between ascent and descent, their rate of ascent was equal to or greater than their descent rate (table 1).

The depth at which a whale begins to glide is also an indication of its buoyancy, since buoyancy decreases upon

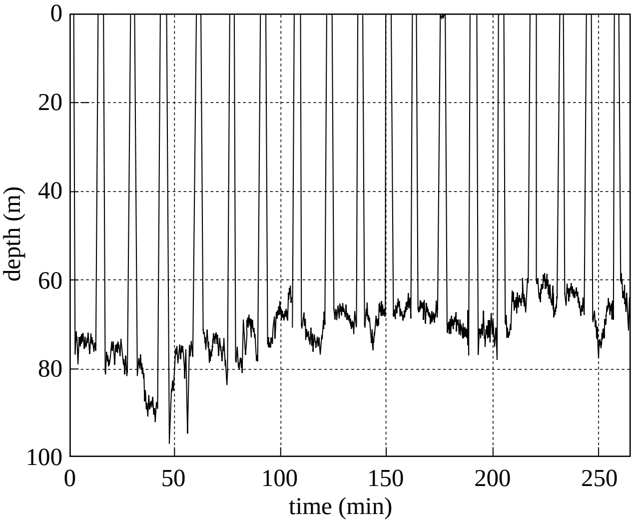

Figure 2. Dive profiles, i.e. depth of dive, for the entire tag record for whale 1309. The 'U-shape' of the dives is interpreted as indicating that these are foraging dives based on previous work with pinnipeds (Le Boeuf *et al.* 1988). Current research focused on the prey fields present in the area of diving right whales is providing more detail about foraging behaviour. Although the dive patterns show significant regularity, gradual changes and pronounced excursions may indicate, respectively, a whale following or searching for a prey patch.

collapse of the lungs with depth (Ridgway *et al.* 1969; Skrovan *et al.* 1999). At a depth of approximately 10 m, for example, the ambient pressure is twice as great as it is at the surface, and it doubles with every doubling of depth thereafter. The volume of air-filled compartments is correspondingly reduced by half with each doubling of pressure, and the air-filled cavities of diving marine mammals are subject to these forces. This decrease in volume without a change in mass results in decreased buoyancy. All right whales began ascent glides at depths significantly deeper than the 18 m at which a blue whale became negatively buoyant (table 1; Williams *et al.* 2000).

(b) *At-depth swimming behaviour*

Beyond the energetic savings of prolonged ascent glides, all tagged whales swimming at depth displayed two additional energy-conserving strategies that are not unique to positively buoyant whales: consistent fluke stroke rate and burst-and-glide swimming. Once they arrived at their target depth many whales swam horizontally, presumably feeding. To exploit maximally a prey patch that occurs at depth a right whale must efficiently maintain forward velocity to filter-feed, which probably causes a significant increase in drag (Kenney *et al.* 1986). During the flat-bottom portion of these feeding dives, the tagged animals displayed a burst-and-glide swimming pattern with a constant fluke rate in each short burst of fluking (figure 3*e*). Locomotor connective tissues of some cetaceans approximate a resonant spring system (Pabst 1996; Pabst *et al.* 1999), and mechanical models suggest that cetaceans swim at their resonant frequency (Pabst 1996). Burst-and-glide swimming is used by other species as an effective energy conservation mechanism (Blake 1983; Weihs 1974), and while the right whales' glide portions were short (*ca.* 8 s), whales often glided for a total of more than a minute while swimming at depth. These short glides save energy and oxygen not only through reduced muscular activity but probably also by reducing pressure drag and boundary layer separation experienced by swimming animals (Webb 1975; Daniel 1984; Fish *et al.* 1988).

4. DISCUSSION

The buoyancy of right whales is not only affected by the volume of gas-filled cavities, but also by the proportion of positively buoyant tissues such as blubber and negatively buoyant tissues such as bone. Gas-filled cavities change in volume with water pressure, creating a dynamic component of buoyancy that varies with depth. Other tissues are less compressible, creating a static component of buoyancy that is largely depth invariant. Variability in the buoyancy of tagged right whales is suggested by the different depths at which they began to glide (table 1). This is similar to female elephant seals, in which changes in body fat percentage over the course of a foraging season closely tracked changes in their buoyancy (Crocker *et al.* 1997). Tissue buoyancy may therefore be an important yet variable factor in the overall buoyancy of right whales. By analysing the vertical acceleration as a function of depth during glides, the DTAG data may provide a method for assessing the relative contribution of these dynamic versus static buoyant forces when combined with an analysis of other forces acting on a whale (e.g. drag). *In situ* measurements of blubber layer thickness in individual right whales are being made to assess the body condition of these animals (Moore *et al.* 2001), which is important with respect to reproductive capacity (Frisch 1984) and may have implications for their swimming and diving behaviour as we have observed.

While some marine animals can regulate their buoyancy to maintain depth (Alexander 1990), marine mammals must surface frequently and inevitably will swim against buoyant forces at some part of the dive cycle. Marine mammals exploit these buoyant forces for efficient locomotion during diving. Right whales emphasize glides on ascent, while other species that become negatively buoyant when their lungs collapse during a dive conserve energy by gliding during descent (Skrovan *et al.* 1999; Williams *et al.* 2000). Our tag data show that right whales are positively buoyant even under hydrostatic pressures that must certainly have collapsed their air-filled cavities to a fraction of their normal volume. This means that right whales must counteract this buoyancy as they dive but can use it to assist ascent.

The buoyancy in North Atlantic right whales reported here might have implications in the risk of a ship strike. If a right whale at the surface dives to avoid an oncoming vessel, its buoyancy may slow this vertical avoidance response. Buoyancy may also pose risks during ascent from a dive. After whales begin the passive component of their ascent, their ability to manoeuvre is likely to be reduced relative to when they are under power. We know relatively little about the use of control surfaces in cetaceans, but active propulsion and manoeuvrability are related. Mysticete whales can turn more effectively while under power and have reduced turning performance due

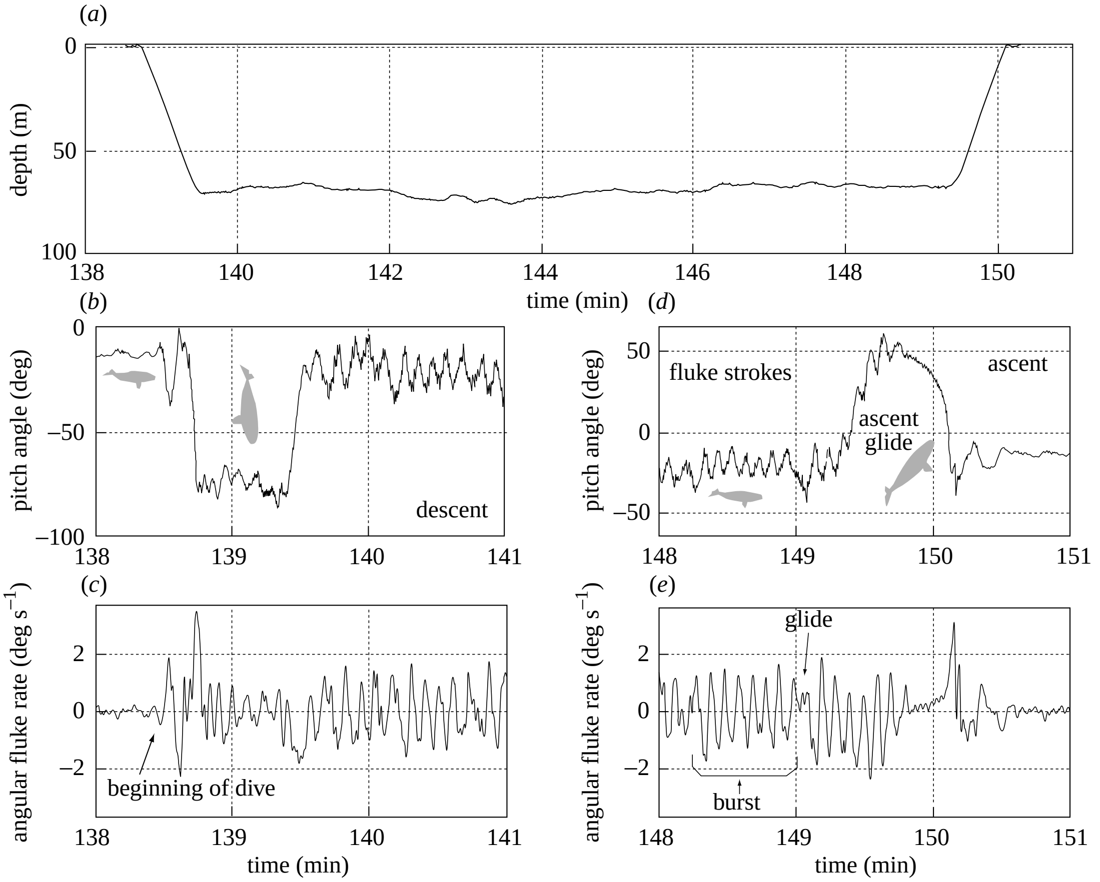

Figure 3. Continuous swimming and diving data recorded by the DTAG from whale 1309. (*a*) The depth of dive profile, calculated from water pressure, for a representative dive recorded by the tag. (*b*) The whale's pitch during the descent of the dive shown in (*a*). Fluke strokes can be seen as relatively fast, small amplitude oscillations of the overall pitch record, i.e. compare the pitch angle record at minute 138 with minute 140 when the whale is actively swimming at depth. The fluke strokes recorded by the accelerometers (pitch) correspond directly with increased flow noise recorded on the hydrophone as the whale accelerates during a fluke stroke. The correspondence of these two quantities provides an unequivocal ground truth for the fluke stroke measurements. The 'baseline' negative pitch angle results from the angle of attachment of the tag (figure 1), which is done purposely in an effort to use the water flow to force the tag down onto the animal. We have corrected for this inherent negative pitch angle in all data reported in table 1. In (*c*) the angular fluke rate in degrees per second is shown. This method of analysis shows the rate of change in the fluke stroke, i.e. during passive gliding the angular fluke rate is zero. The continuous fluking during the descent is shown in this plot. (*d*) The pitch record for the ascent portion of the dive shown in (*a*); note the difference in scale of the ordinate axis as compared with (*b*). During the latter part of the ascent the fluke stroke oscillations disappear from the pitch record, indicating that the whale is gliding. The glide is confirmed by the angular fluke rate (*e*). The angular rate spike just after minute 150 corresponds to the whale breaking the surface at an angle and falling back to the horizontal. Tracking the angular rate of change also clearly shows the burst-and-glide 'packets' as the whale swam (*e*).

Table 1. Detailed dive behaviour of tagged right whales.

(The four whales tagged in 1999 are listed first, and identifications, sexes and ages are from the central right whale catalogue (Hamilton & Martin 1999). One whale tagged in 2000 has not yet been photo-identified, and is distinguished by an abbreviation for the species (*Eubalaena glacialis*) and the Julian day on which the individual was tagged. Standard errors for depths are shown in parentheses.)

whale	dives recorded	ratio of ascent rate to descent rate	ratio of maximum pitch angle during ascent to descent	depth at start of ascent glide (m)
1909 (10 yrs, ♀)	21	1.13	0.77	79.1 (0.8)
2209 (7 yrs, ♂)	6	1.17	0.88	52.9 (1.4)
1607 (13 yrs, ♂)	15	1.16	1.0	57.8 (1.8)
1307 (16 yrs, ♂)	20	1.20	0.83	83.8 (2)
1309 (adult ♂)	18	1	0.80	41 (1.5)
2760 (11 yrs)	5	0.96	0.65	65.7 (7.4)
*Eg*2000_222b	3	0.75	1.06	37.4 (3.9)
1238 (> 19 yrs, ♂)	7	1.05	0.77	30.6 (1.6)

to their large size and proportionately small control surfaces (Fish 1997, 1999). Thus, even if a whale correctly perceives a ship as a threat, a passive ascent may increase the risk of collision by compromising the animal's ability to execute an effective evasive manoeuvre. The hydrodynamic forces induced by large ships that draw submerged objects into the hull (Knowlton *et al.* 1995, 1998) compound the risk of collision both on ascent and descent. Together these phenomena may partly explain why this species is so vulnerable to ship strikes. Continuing experiments with this new tool, tracking whales' acoustic and motor behaviour in the presence of ships (i.e. the circumstances surrounding collisions), will hopefully provide useful information for the design of effective ship strike mitigation measures.

We thank the field crew from Woods Hole, the International Fund for Animal Welfare, especially the crew of their vessel *Song of the Whale*, Michael Moore and his crew on the *Hannah T*, and the New England Aquarium Right Whale research team. This research was conducted under US permit NMFS no. 1014 and Canadian permit DFO no. 2000-489. This work was supported by the Office of Naval Research (grant no. N00014-99-10831), the National Marine Fisheries Service/Cooperative Institute for Climate and Ocean Research (CICOR grant no. NA87RJ0445), the Massachusetts Environmental Trust, the International Fund for Animal Welfare, and a Cecil and Ida Green Technology Award. This is contribution no. 10463 from the Woods Hole Oceanographic Institution.

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