Corrigendum

Pregnancy is a drag: hydrodynamics, kinematics and performance in pre- and post-parturition bottlenose dolphins (*Tursiops truncatus*)

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There was an error published in *J. Exp. Biol.* **214**, 4151-4159.

In the Abstract, the value for the mean increase in frontal surface during pregnancy should have read 56±13% (not 51±14%). This is the only place that this error occurred; the values reported for the increase in frontal surface area for each individual dolphin are correct as reported in the Results section.

The authors apologise for any inconvenience that this error may have caused but assure readers that it does not affect the data, results, interpretations or conclusions of the paper.

RESEARCH ARTICLE

Pregnancy is a drag: hydrodynamics, kinematics and performance in pre- and post-parturition bottlenose dolphins (*Tursiops truncatus*)

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SUMMARY

Constraints on locomotion could be an important component of the cost of reproduction as carrying an increased load associated with eggs or developing fetuses may contribute to decreased locomotor performance for females across taxa and environments. Diminished performance could increase susceptibility to predation, yet the mechanism(s) by which gravidity and pregnancy affect locomotion remains largely unexplored. Here we demonstrate that morphology, hydrodynamics and kinematics were altered during pregnancy, providing a mechanism for diminished locomotor performance in two near-term pregnant (10 days pre-parturition) bottlenose dolphins (*Tursiops truncatus*). Near-term pregnancy resulted in a 51±14% increase in frontal surface area, coinciding with dramatic increases in drag forces while gliding. For example, pregnant females encountered 80 N of drag at 1.7 m s^{-1} whereas that magnitude of drag was not encountered until speed doubled for females 18 months post-parturition. Indeed, drag coefficients based on frontal surface area were significantly greater during pregnancy ($C_{d,F}$=0.22±0.04) than at 18 months post-parturition ($C_{d,F}$=0.09±0.01). Pregnancy also induced a gait change as stroke amplitude and distance per stroke were reduced by 13 and 14%, respectively, compared with non-pregnant periods (1–24 months post-parturition). This was concomitant with a 62 and 44% reduction in mean and maximum swim speeds, respectively, during the pregnancy period. Interestingly, attack speeds of known predators of dolphins surpass maximum speeds for the pregnant dolphins in this study. Thus, pregnant dolphins may be more susceptible to predation. This study demonstrates unequivocally that changes in morphology, hydrodynamics and kinematics are associated with diminished performance during pregnancy in dolphins.

Key words: cetacean, drag coefficient, locomotion, mechanics, morphology, odontocete, speed, stroke amplitude, stroke frequency, swimming.

INTRODUCTION

Numerous studies across taxa have described diminished locomotor performance for gravid and pregnant animals inhabiting aquatic, terrestrial and aerial environments. It was hypothesized that the decreased maternal locomotor ability was due to carrying an extra load associated with gravidity or pregnancy for crustaceans (Winfield and Townsend, 1983; Berglund and Rosenquist, 1986), fish (Plaut, 2002; Svendsen et al., 2009), scorpions (Shaffer and Formanowicz, 1996), insects (Isaacs and Byrne, 1998; Gu and Danthanarayana, 2000), reptiles (Shine, 1980; Seigel et al., 1987; Cooper et al., 1990), birds (Lee et al., 1996; Veasey et al., 2001) and mammals (McLean and Speakman, 2000). Prelaying common eiders (*Somateria mollissima*) are even rendered flightless (Guillemette and Ouellet, 2005). In addition to lowered performance, pregnant animals also exhibit increased sedentary periods, as evident in numerous primates (Miller et al., 2006), sea lions (*Zalophus californianus*) (Williams et al., 2007) and bats (*Glossophaga soricina*) (Voigt, 2003). The reduced locomotor performance of these reproductive females has profound implications for predator avoidance, particularly for animals that live in open, seemingly featureless habitats that rely on speed to avoid predators (i.e. pelagic dolphins and African ungulates). Indeed, it has been hypothesized that relatively immobile brooding squid (*Gonatus onyx*) could provide an easy target for predators (Seibel et al., 2005). Yet the

mechanism(s) by which the increased load of gravidity and pregnancy diminishes locomotor performance is virtually unknown (Svendsen et al., 2009).

Only a few studies have attempted to investigate the mechanism by which gravidity and pregnancy lower maternal locomotor ability. A few investigators examined gait (Taves et al., 1982; Golomer et al., 1991; Foti et al., 2000; Plaut, 2002), yet surprisingly, all of these studies indicated that there were no differences in gait between the gravid and non-gravid or pregnant and non-pregnant states. For example, investigations of female mosquitofish (*Gambusia affinis*) showed no change in stroke amplitude and stroke frequency across reproductive states (Plaut, 2002) and the stride length and step frequency of humans seemed to be unaltered by pregnancy (Taves et al., 1982; Foti et al., 2000). Yet Golomer et al. (Golomer et al., 1991) suggested that by the eighth month of pregnancy, humans seem to have decreased stride length with a concomitant increase in step frequency, even though quantitatively these differences were deemed insignificant. Wu et al. (Wu et al., 2004) maintained that gait in humans is affected by pregnancy but this effect is masked by the large inter-individual differences in postural adaptations to pregnancy across women. Overall there is a paucity of information on the effect of pregnancy on locomotor kinematics in comparative systems.

Dolphins are an ideal model with which to investigate how pregnancy might alter locomotion. First, pregnancy results in
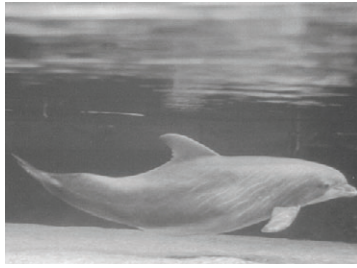
Pre-parturition   Post-parturition

Fig. 1. Photographs of a bottlenose dolphin (*Tursiops truncatus*) before parturition and at 8 months post-parturition. Note the white stretch marks in the thoracic-abdominal area on the pregnant dolphin, which indicate that the animal had undergone a rapid increase in body girth during the pregnancy period. Photo credit: Dolphin Quest.

marked changes in streamlining (S.R.N., personal observation) (Fig. 1) that could increase opposing forces to locomotion (drag). Second, the stretching of the abdominal muscles (due to the presence of the fetus) could decrease the ability to generate thrust. This is because dolphins generate thrust exclusively with their tail flukes (Fish and Hui, 1991). Third, dolphins have a relatively stiff upper vertebral column (cervical vertebrae fused for streamlining) (Long et al., 1997), which could preclude the issue of postural adjustments to pregnancy. The morphology and swimming kinematics of dolphins are characteristic of the thunniform mode, which is typical of some of the fastest marine vertebrates, including scombrid fishes, laminid sharks and cetaceans (Lighthill, 1969). As with other thunniform swimmers, dolphins generate thrust exclusively with a high-aspect-ratio caudal hydrofoil (tail flukes) (Fish and Hui, 1991). Thus, kinematic analyses provide a quantitative assessment of gait by considering both tail movement amplitude and beat frequency. A qualitative assessment of effort may also be obtained because higher amplitudes and frequencies are associated with greater energy expenditure (Kooyman and Ponganis, 1998). Kinematic analyses also allow for quantification of performance (swim speed) while hydrodynamic analyses provide a means of assessing forces opposing locomotion (drag).

In this study, we demonstrate how pregnancy affects the morphology of bottlenose dolphins (*Tursiops truncatus*) and we used hydrodynamic and kinematic analyses to quantify how drag, gait and performance change between pre-parturition and post-parturition periods. Specifically, we measured morphology (body length, maximum girth, body mass and frontal surface area), gliding drag (drag, drag coefficient and Reynolds number), swimming kinematics (stroke amplitude, stroke frequency and stroke frequency normalized for speed), swimming effectiveness (distance per stroke and Strouhal number) and swim performance (mean and maximum swim speeds) of two female bottlenose dolphins at ≤10 days pre-parturition and at 1–24 months post-parturition (Fig. 1). Ultimately, this study elucidated mechanisms by which the physical alterations of pregnancy can diminish locomotor performance in a marine mammal.

MATERIALS AND METHODS
Experimental animals
Two adult female bottlenose dolphins [*Tursiops truncatus* (Montagu 1821)] were studied in a large, oblong natural lagoon at Dolphin Quest Hawaii (high tide dimensions: 43×53×7 m deep, low tide dimensions: 37×46×5 m deep). Studies occurred from October 2003 to November 2005, which corresponded to the time when the dolphins were ≤10 days pre-parturition and 1–24 months post-parturition. Data were collected during the last 10 days of pregnancy and throughout 1 week intervals for each of the postpartum periods (1, 10, 13, 18 and 24 months postpartum). Water temperature during this period ranged from 24.0 to 26.7°C (mean=25.3±0.4°C). These

animals had been held at the facility for several years, thus the animals were acclimated to their environment. Animals were fed a mixed fish diet of capelin, herring and squid supplemented with vitamins.

Morphological measurements
Body length (beak tip to fluke notch) and maximum girth (taken at the anterior insertion of the dorsal fin) measurements followed standard protocols for dolphins and were measured at 2 weeks pre-parturition and 18 months post-parturition. Dolphins were also weighed at 18 months post-parturition by beaching onto a digital scale. Weighing was precluded for the pregnant dolphins because of the positioning of the fetus, thus the masses of the pregnant dolphins were estimated using a dolphin-specific morphometric calculator (Messinger et al., 1999). This calculator was designed specifically for bottlenose dolphins and utilizes gender, age, total body length and maximum girth of the dolphin to estimate body mass. Data used to parameterize the equation were acquired from dolphins at four facilities including Dolphin Quest. Although this equation was not derived from pregnant animals, obese animals were included in the sample. We utilized their equation specific for obese (girth ≥152.4 cm) female dolphins ≥11 years old to account for the shift in body mass associated with pregnancy. Body mass (M_b; kg) is estimated by:

$$M_b = 0.8L + 0.0066G_{max}^2 - 131, \qquad (1)$$

where L is body length (cm) and G_{max} is maximum girth (cm) (Messinger et al., 1999). The percent error between the estimated and predicted mass for the two individual dolphins at 18 months post-parturition were only 0.02 and 1.21%; consequently, we felt that the use of this equation was a valid approach for estimating the mass of the pregnant animals. It was assumed that the frontal surface area of a dolphin is best represented by a circle; the measured maximum girth served as the diameter of the circle and the surface area of the circle was calculated using a standard geometric equation.

Swimming trials
During each data collection interval, the swimming motions of the animals were recorded daily throughout daylight hours. A submerged SCUBA diver, sitting stationary on a wide ledge on one side of the enclosure, used a digital video camcorder (Sony Hi-8, Sony, Oradell, NJ, USA) housed in an underwater housing (Amphibico Dive Buddy, Amphibico, Montreal, QC, Canada) to film the dolphins as they passed by. The SCUBA diver kept the video camera stationary such that the dolphins were only filmed when they were in the field of view of the camcorder. The animals swam approximately 1–3 m below the surface of the water and swam in a straight-line path within 7–8 m parallel to the SCUBA diver. Experimental swim sessions included both opportunistic trials (no reward) and directional trials between two trainers (reward based).

For opportunistic trials, the SCUBA diver was positioned in an area of the lagoon where the animals passed in a stereotypic straight-line path. For directional trials, the trainers were positioned across the lagoon from each other in a way that forced the dolphins to swim a straight-line path. Rewards (tactile stimulation, toys and food) were based on the intensity of the swimming provided. Standard operant conditioning was used to train the directional swimming. Only video clips showing dolphins swimming alone (>1 m in all directions from any other dolphin) were included in the analyses.

Video analysis

Short 2–6 s video clips of the dolphins swimming were extracted from the videotapes using digital video software (Pinnacle Studio 8, Pinnacle Systems, Inc., Mountain View, CA, USA). Anatomical points of interest were digitized at a rate of 60 fields s^{-1} of video using a motion-analysis system (Peak Motus 6.1; Peak Performance Technologies, Inc., Englewood, CO, USA) following methods similar to those of Skrovan et al. (Skrovan et al., 1999) and Noren et al. (Noren et al., 2006). For clips of dolphins gliding continuously with no body movement, the cranial insertion of the dorsal fin was digitized to assess drag. For clips of dolphins stroking continuously, distinct morphological features including the rostrum tip, cranial insertion of the dorsal fin, and the fluke tip were digitized to assess kinematics and performance according to Noren et al. (Noren et al., 2006). To correct for any slight deviations in the dolphins' vertical angle in the water column, all coordinates were transformed so that the starting position of the cranial insertion of the dorsal fin (digitized point closest to the center of mass) represented the zero position on the *y*-axis. The measured body length (*L*) of each study animal, which did not change during the study interval because the females had already attained mature body length, provided a scalar so that the system could calculate instantaneous transformed coordinates, velocity and acceleration for each digitized point. Only video clips where dolphins swam steadily, maintained a parallel path to the camera lens, and had no qualitatively apparent acceleration were included in the analyses. In addition, a rock within the field of view of the camcorder was also digitized to ensure that the camera was held steady throughout the entire pass of the animal. Digitized video clips that indicated that the reference point moved were excluded from the analyses.

Drag and Reynolds number calculations

Only video clips of dolphins gliding continuously with no body movements and submerged a minimum of three times the maximum body diameter below the water's surface were used in the analyses. In addition, only trials obtained at ≤10 days pre-parturition and at 18 months post-parturition were used in these analyses to correspond with the interval for which morphological measurements were taken. Deceleration (*a*; m s^{-2}) was calculated every 60 frames (this is equivalent to 1 s intervals) to provide semi-instantaneous deceleration values. This approach is better than simply using a beginning and end point for calculating deceleration because it provides for changes in velocity during the glide, smoothes small fluctuations in the rate of deceleration, and compensates for errors in measuring and plotting during the digitizing process. The resulting calculated deceleration for each video clip ($\bar{a}$) was the mean of the *a*-values over the entire clip. Drag (*D*; N) was then determined following standard methods for marine mammals (Williams and Kooyman, 1985):

$$D = (M_{b} + M_{a})\bar{a}, \qquad (2)$$

where M_{a} is the added mass of the animal (kg) [approximately $0.2M_{b}$ (Weihs, 2002)] (Webb, 1975). The added mass is the mass added to a system because of the fact that a decelerating (or accelerating) body must move some volume of surrounding fluid with it as it moves. The added mass force opposes motion so it must be factored into the system (for a review, see Webb, 1975). The drag coefficient based on the dolphins' frontal surface area was calculated according to:

$$C_{d,F} = 2D \, (\rho F V^{2})^{-1}, \qquad (3)$$

where ρ is water density (assumed to be the mean density of water at the sea surface; 1025 kg m^{-3}), *F* is frontal surface area (m^{2}) and *V* is the mean of the instantaneous velocities (m s^{-1}) during the glide. This methodology for calculating drag coefficient is in accordance with those used previously for marine mammals by Williams and Kooyman (Williams and Kooyman, 1985) and Feldkamp (Feldkamp, 1987). In addition, Reynolds number (*Re*) was calculated according to:

$$Re = LV / \nu, \qquad (4)$$

where ν is the kinematic viscosity of seawater, estimated at $1.044 \times 10^{6} \, m^{2} \, s^{-1}$ for the temperature and salinity of our study site. This calculation of *Re* for dolphins follows the approach of Fish (Fish, 1998).

Swimming kinematics and Strouhal number calculations

A quantitative assessment of gait was obtained by calculating peak-to-peak fluke stroke amplitude (*A*; m) and tailbeat oscillation frequency (*f*; strokes s^{-1}) from the data. Multiple sequential strokes were used to calculate the mean stroke amplitude and tailbeat oscillation frequency for each video clip. Normalized tailbeat frequency (ratio of tailbeat frequency to swim speed) (Rohr and Fish, 2004) and distance per stroke were also calculated so that any differences in tailbeat frequency between reproductive state could be detected without the compounding effect of swim speed, because tailbeat frequency increases significantly with swim speed in odontocetes (Fish, 1993; Fish, 1998; Skrovan et al., 1999; Fish et al., 2003; Noren et al., 2006). Stroke amplitude was not normalized for swim speed because odontocetes do not modulate swim speed by changing stroke amplitude (Fish, 1993; Skrovan et al., 1999; Fish et al., 2003; Noren et al., 2006). The principal wake parameter, a dimensionless number called the Strouhal number (*St*), was also calculated according to Triantafyllou et al. (Triantafyllou et al., 1993):

$$St = fA / V, \qquad (5)$$

and *V* is the mean of the instantaneous velocities during the glide.

Statistics

This is the first study to examine the effect of near-term pregnancy on swimming in dolphins, thus our primary interest was to quantify differences in kinematics and hydrodynamics between pregnant and non-pregnant periods. Although data were collected at several points post-parturition, the purpose of this study was not to address any changes that may occur in swimming kinematics with recovery after pregnancy. Although we collected data from two individuals, the purpose of this study was not to examine individual variation in kinematics. Because the inclusion of postpartum and individual variation can only serve to weaken any resulting relationships, this analytical approach reinforces the robustness of the conclusions from the pooled data. Each data point was obtained from a unique trial (a complete pass of the animal past the video camera), and each

trial was of a slightly different swim speed; therefore, measurements were considered to be independent and not repeated. One trial represented one sample. This approach enabled us to pool the data and to have a large enough sample size for statistical analyses. This methodology has been utilized by other studies of the swimming kinematics of dolphins (Fish, 1993; Skrovan et al., 1999; Fish et al., 2003; Noren et al., 2006; Noren et al., 2008; Noren, 2008; Noren and Edwards, 2011). Nonetheless, because the calculated drag coefficient is related to morphology, we compared the drag coefficients between the two dolphins using a Student's *t*-test to ensure that they were not significantly different before pooling this data. We also used analyses of covariance (ANCOVAs) to test the effect of individual on the relationships for stroke amplitude with swim speed and tailbeat frequency with swim speed for each reproductive state (pre-parturition and post-parturition) before pooling this data.

For the data extracted from the video clips of gliding dolphins, non-linear regression analyses were used to determine the relationship between swim speed and drag and the significance of these regressions was determined using *F*-tests. Differences in drag coefficient, swim speed and Reynolds number between reproductive categories (pre-parturition and post-parturition) were determined using Student's *t*-test or Mann–Whitney rank sum test when normality failed. For the data extracted from video clips of stroking dolphins, Pearson correlation coefficient analyses were used to determine correlations between swim speed and swimming kinematics (peak-to-peak stroke amplitude, tailbeat oscillation frequency, and the product of peak-to-peak stroke amplitude and tailbeat oscillation frequency) for each reproductive state. Least squares linear regression analyses were used to determine the relationships for those variables that were deemed correlated and the significance of these regressions was determined using *F*-tests. In cases where the swimming kinematic was significantly correlated with speed, the slopes and intercepts across reproductive state (pre- and post-parturition) were compared by Student's *t*-tests according to Zar (Zar, 1984). Differences in stroke amplitude, normalized tailbeat frequency, distance per stroke, Strouhal number and swim speed between reproductive categories were determined using Student's *t*-test or the Mann–Whitney rank sum test when normality failed. Normality was determined using the Kolmogorov–Smirnov

test. These standard statistical analyses were performed using Sigma Stat 2.03 (Systat Software, Inc., Point Richmond, CA, USA). All means are denoted ±1 s.e.m. and α=0.05.

RESULTS

Our results showed that near-term pregnant females experienced a marked alteration in morphology (Fig. 1) that corresponded with changes in drag forces, swimming kinematics and swimming performance. Body length did not change, which was expected because these females had already reached mature body length; however, there was a marked increase in maximum body girth (16 and 26% increase for the two individual dolphins) from the 18 month post-parturition to the pre-parturition (pregnancy) period. As a result, there was a large increase in frontal surface area (43 and 69% increase for the two individual dolphins) during pregnancy, which effectively increased the gliding drag of these animals compared with 18 months post-parturition. For example, 80 N of drag were experienced by pregnant dolphins gliding at $1.7\,\mathrm{m\,s^{-1}}$ whereas dolphins measured at 18 months post-parturition did not experience this magnitude of drag until they were gliding at twice the speed ($3.4\,\mathrm{m\,s^{-1}}$; see Fig. 2 for the velocity and drag relationships for each reproductive state). Indeed, the calculated drag coefficient based on frontal surface area was significantly greater for the dolphins prior to parturition ($C_{d,F}$=0.22±0.04, N=6) compared with 18 months post-parturition ($C_{d,F}$=0.09±0.01, N=19; t=4.470, d.f.=23, P<0.001); the drag coefficients of the two individual dolphins were combined because they were not different between the animals prior to parturition (T=5.00, N=2, 4, P=0.533) nor at 18-months post-parturition (t=–0.202, d.f.=17, P=0.842). Meanwhile, speed was significantly greater for the gliding periods at 18 months post-parturition ($3.69\pm0.15\,\mathrm{m\,s^{-1}}$) compared with pre-parturition ($1.41\pm0.12\,\mathrm{m\,s^{-1}}$; t=–7.980, d.f.=23, P<0.001), as were Reynolds numbers (18 months post-parturition: $8.63\pm0.34\times10^6$; pre-parturition: $3.29\pm0.31\times10^6$; t=–8.405, d.f.=23, P<0.001).

For either reproductive state, individual did not significantly influence the relationships between stroke amplitude and swim speed (pre-parturition: F=0.109, P=0.743, N=59; post-parturition: F=0.163, P=0.688, N=92) or tailbeat frequency and swim speed (pre-parturition: F=0.004, P=0.953, N=59; post-parturition: F=0.461, P=0.499, N=92), thus these data were pooled across individuals for

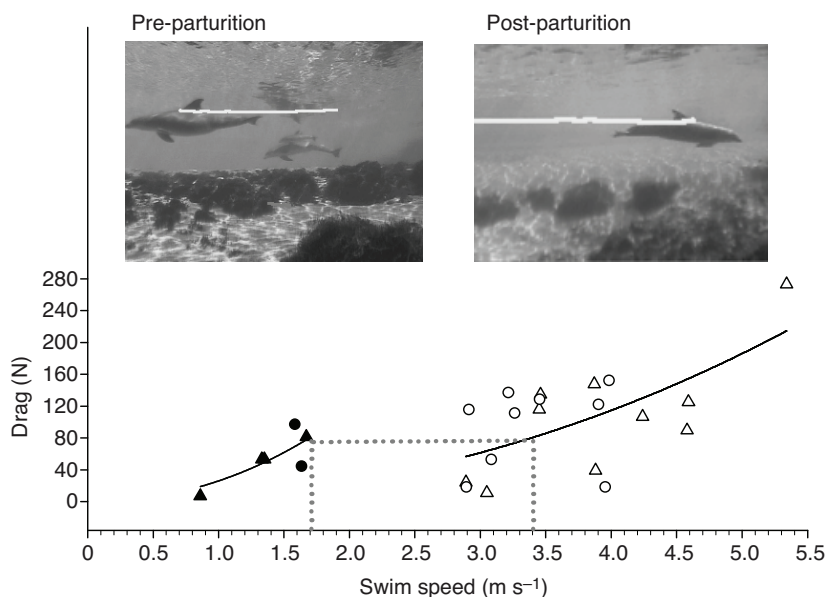Pre-parturition   Post-parturition

Fig. 2. Drag forces encountered by two dolphins were greater during near-term pregnancy compared with that encountered at 18 months post-parturition. The relationships for swim speed *versus* drag during pre-parturition (black) and post-parturition (white) periods are described according to the following equations: pre-parturition: D=26.14$U^{2.13}$ (r=0.78, F=6.32, P=0.066, N=6); post-parturition: D=5.69$U^{2.17}$ (r=0.61, F=10.33, P=0.005, N=19), where D is drag (N) and U is swim speed ($\mathrm{m\,s^{-1}}$). The dotted gray box shows that 80 N of drag were experienced by pregnant dolphins gliding at $1.7\,\mathrm{m\,s^{-1}}$ whereas dolphins at 18 months post-parturition did not experience this magnitude of drag until they were gliding at twice the speed ($3.4\,\mathrm{m\,s^{-1}}$). A different symbol (circle and triangle) was used for each of the two individual dolphins. Digitized video clips for an individual dolphin in the pregnant and non-pregnant state are also shown; a distinctive trace represents the movement of the cranial insertion of the dorsal fin (distinct morphological feature closest to the dolphin's center of mass).

subsequent analyses. For both pregnant and non-pregnant periods, swim speed was not correlated with stroke amplitude (pre-parturition: $r=-0.232$, $P=0.077$, $N=59$; post-parturition: $r=-0.00494$, $P=0.963$, $N=92$; Fig. 3A) but it was strongly correlated with tailbeat frequency (pre-parturition: $r=0.882$, $P<0.001$, $N=59$; post-parturition: $r=0.908$, $P<0.001$, $N=92$; see Fig. 3B for the linear regression equations for tailbeat frequency *versus* swim speed). Interestingly, between reproductive categories the *y*-intercepts of the relationships for tailbeat frequency *versus* swim speed were not different ($t=0.0534$, d.f.=149, $P=0.957$) whereas the slopes of these relationships were different ($t=-2.886$, d.f.=149, $P=0.004$). The greater slope for the non-pregnant periods implies that dolphins have faster rates of increase in speed per a given tailbeat frequency compared with pregnant periods. Meanwhile, analyses of the product of tailbeat frequency and stroke amplitude in relation to speed for both pre-parturition ($r=0.714$, $P<0.001$, $N=59$) and post-parturition ($r=0.764$, $P<0.001$, $N=92$) revealed that the inclusion of stroke amplitude did not improve the predictive power for speed, but rather the inclusion of stroke amplitude lowered the correlation value (r) due to increased scatter.

Closer examination revealed that locomotor gait was adjusted in response to the state of pregnancy. From kinematic analyses (Fig. 4), it was evident that the stroke amplitude of the dolphins was decreased by 13% during pregnancy compared with the stroke amplitude during 1–24 months post-parturition (pregnant female mean=0.61±0.02 m, median=0.62 m, $N=59$; non-pregnant female mean=0.70±0.01 m, median=0.69 m, $N=92$; $T=3303.5$, $P\leq0.001$; Fig. 4B). The pregnant dolphins appeared to compensate for this by increasing tailbeat frequency per a given speed; the normalized tailbeat frequency (ratio of tailbeat frequency to swim speed) (Rohr and Fish, 2004) for pregnant females ($N=59$) was significantly greater ($T=6206.5$, $P\leq0.001$) than that during 1–24 months post-parturition ($N=92$). This in turn decreased distance covered per stroke during the pregnancy period (pregnant mean distance per stroke: 1.80±0.04 m stroke^{-1}, $N=59$; non-pregnant mean distance per stroke: 2.09±0.02 m stroke^{-1}, $N=92$; $t=-7.596$, d.f.=149, $P\leq0.001$; Fig. 4C). In one stroke, pregnant females achieved only 86% of the distance covered by non-pregnant females. Interestingly, the Strouhal number for swimming dolphins during the pregnancy period (mean=0.34±0.01, median=0.35, $N=59$) was not significantly different from that during 1–24 months post-parturition (mean=0.34±0.01, median=0.34; $T=4649.5$, $P=0.529$, $N=92$).

The increased drag and change in gait for pregnant females was associated with lowered swim performance. Mean and maximum swim speeds for the dolphins were lower during pregnancy than during 1–24 months post-parturition. Mean swim speed for pregnant females (mean=1.55±0.07 m s^{-1}, median=1.39 m s^{-1}, $N=59$) was only 38% of that achieved during the non-pregnant state (mean=4.13±0.09 m s^{-1}, median=4.14 m s^{-1}, $N=92$; $T=1833$, $P\leq0.001$; Fig. 4D) and maximum swim speed for the pregnant females (3.54 m s^{-1}) was only 56% of that attained during the non-pregnant state (6.32 m s^{-1}). Although these speeds were measured in a large natural lagoon, it is evident that our experimental design adequately captured the performance capabilities of dolphins. The mean and maximum swim speeds of non-pregnant females were greater than the minimum cost of transport speed (2.1 m s^{-1}) (Williams et al., 1993) and observed sustainable swim speeds (3.1 m s^{-1}) (Lang, 1975) of non-pregnant adult bottlenose dolphins participating in open-water swim trials. In addition, the maximum swim performance of the non-pregnant dolphins in this study exceeded the maximum performance of non-pregnant wild bottlenose dolphins (5.7 m s^{-1}) (Rohr, 2002).
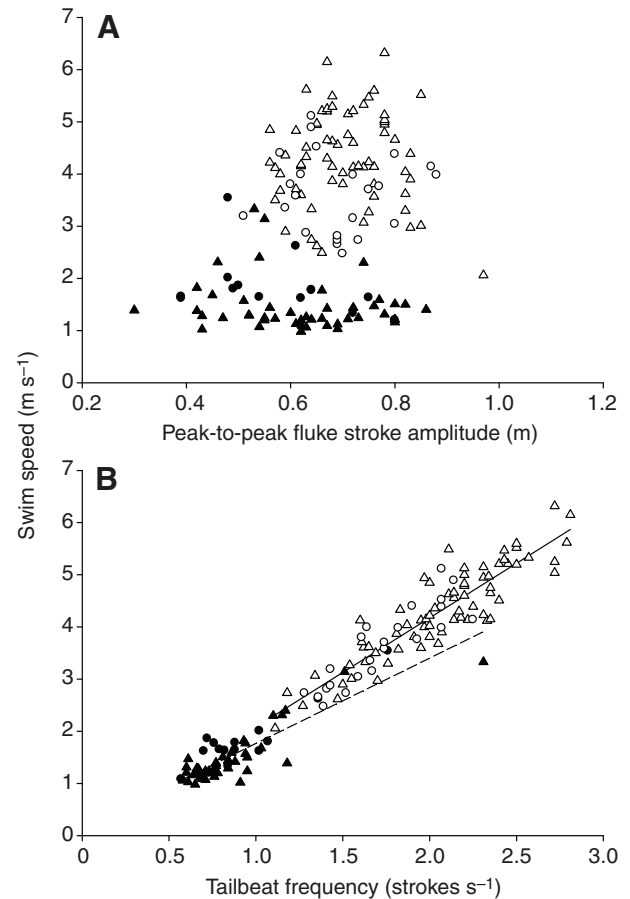

Fig. 3. Swimming kinematics in relation to swimming speed for pre-parturition and post-parturition periods of two bottlenose dolphins. Peak-to-peak fluke stroke amplitude (A) was not correlated with swim speed for pregnant (black symbols) and non-pregnant (white symbols) females (see Results for statistics). In contrast, tailbeat frequency (B) was significantly correlated with swim speed for pregnant (black symbols) and non-pregnant (white symbols) females (see Results for statistics). Given the strong linear correlation between swim speed (U) and tailbeat frequency (f), linear regressions are provided for pregnant ($U=1.64f+0.13$; $r^2=0.778$, $F=200.044$, $P<0.001$, $N=59$, dashed line) and non-pregnant ($U=2.09f-0.01$; $r^2=0.824$, $F=421.525$, $P<0.001$, $N=92$, solid line) females. A different symbol (circle and triangle) was used for each of the two individual dolphins.

Unfortunately, there are no published values on the swimming capabilities of near-term pregnant dolphins for comparison with those of the pregnant dolphins in this study.

DISCUSSION

This study demonstrates the influence that pregnancy can have on morphology, hydrodynamics, swimming kinematics and swimming performance in a marine mammal. Pregnant dolphins appear to be disadvantaged by their marked change in morphology (Fig. 1), which affected streamlining and potentially impacted the ability of their locomotor muscles to generate tension. These alterations in turn lowered swim performance, as might be expected given that the ability to sustain performance is dependent on the magnitude of the resistant forces and the characteristics of the muscles (Fish and Rohr, 1999). Furthermore, physiological changes that can occur during pregnancy (i.e. reduced lung volume and changes in blood flow away from working muscle) may have acted synergistically to lower swim performance because steady-state locomotor performance is
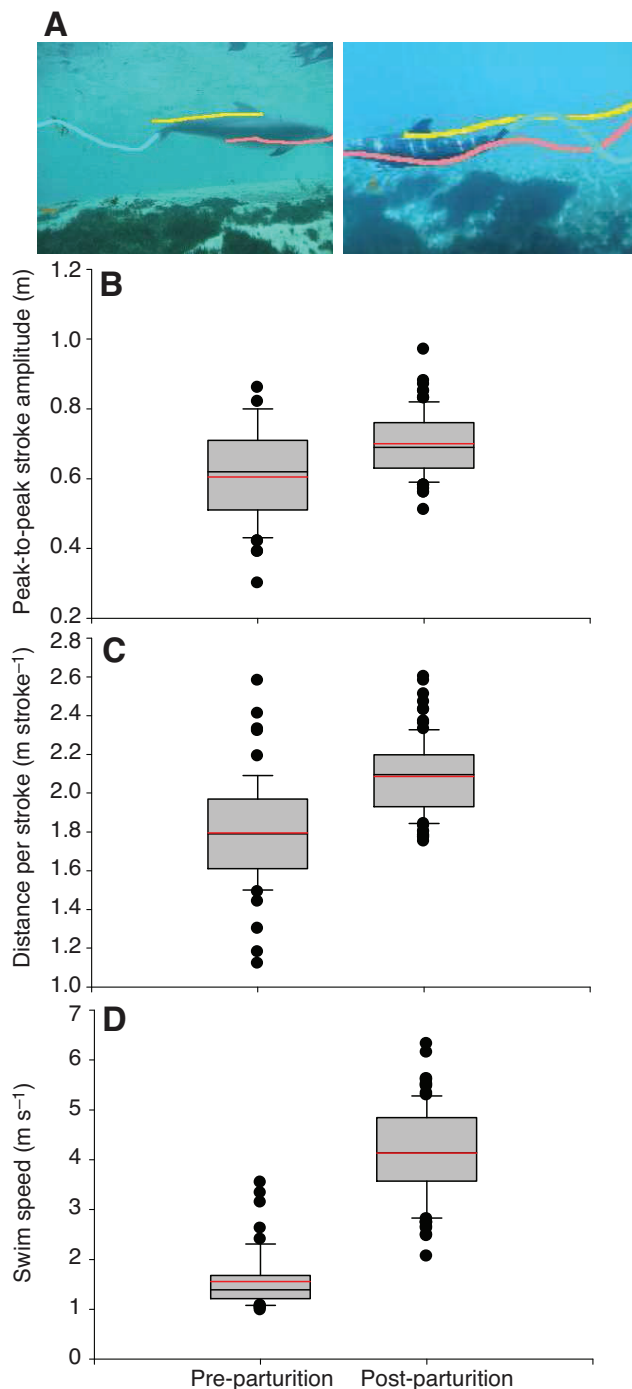
Fig. 4. Swimming kinematics were significantly different between pre-parturition and post-parturition periods of two bottlenose dolphins. (A) Digitized video clips for an individual dolphin in the pregnant and non-pregnant state show distinctive traces for the movements of each digitized anatomical point, pink for the rostrum, yellow for the cranial insertion of the dorsal fin, and blue for the fluke tip. Stroke amplitude was lower during the pregnant state compared with the non-pregnant state (B). As a result, females had a lower distance per stroke (C) and lower mean swim speed (D) during pre-parturition compared with post-parturition periods. These differences were significant at $P<0.05$ (see Results for statistics). In the box plots, the red lines represent the means, the black lines represent the median, the lower and upper boundaries represent the 25th and 75th percentiles, respectively, the lower and upper whiskers represent the 10th and 90th percentiles, respectively, and the dots represent outliers.

also constrained by the availability of oxygen to the locomotor muscle (Vock et al., 1996).

There was a pronounced change in the morphology of the female dolphins when they were pregnant (Fig. 1). There was a surprisingly large increase in frontal surface area (43 and 69%) for the two individual dolphins during pregnancy that effectively increased the gliding drag of these animals compared with 18 months post-parturition (Fig. 2). Indeed, the drag coefficient based on frontal surface area of the dolphins prior to parturition ($C_{d,F}=0.22\pm0.04$, $Re=3.29\pm0.31\times10^6$) was significantly greater than that at 18 months post-parturition ($C_{d,F}=0.09\pm0.01$, $Re=8.63\pm0.34\times10^6$). To put this result in perspective, the drag coefficients based on frontal surface area for pregnant dolphins were greater by an order of magnitude than those of all other marine mammals measured to date (0.038–0.080 at Re ranging from 1 to 5.52×10^6) (for a review, see Stelle et al., 2000) whereas the drag coefficients of the females 18 months post-parturition were in agreement with those measured for other marine mammals. Ultimately, the higher drag coefficients for the pregnant dolphins implies that pregnant dolphins would have greater energetic requirements during locomotion because, theoretically, greater drag forces require more power to overcome (Webb, 1975). In addition, as the speed of the dolphins increases, the power required to overcome drag theoretically increases with the cube of velocity (Fish, 1993). At the same time, the blubber of pregnant bottlenose dolphins contains 27% more lipid than that of other adult dolphins, which lowers the density of the blubber for the pregnant animals (Dunkin et al., 2010). As a result, the buoyant force of pregnant dolphins is four times that of non-pregnant adults, which ultimately increases the locomotor costs of the pregnant females (Dunkin et al., 2010) as they must generate a greater downward force to compensate, particularly while descending on a dive. As a greater proportion of power output is utilized to accommodate increased drag and increased buoyancy there is less energy available to propel the animal forward in the water.

Although the dolphins faced greater forces countering locomotion during pregnancy, the animals seemed to modulate changes in swim speed in a manner similar to that of non-pregnant animals. Pregnant and non-pregnant dolphins modulated swim speed by changing tailbeat frequency but not stroke amplitude (Fig. 3), as has been demonstrated previously in non-reproductive adult odontocetes (Fish, 1993; Skrovan et al., 1999; Fish et al., 2003). Indeed, analyses of the product of tailbeat frequency and stroke amplitude in relation to speed revealed that the inclusion of stroke amplitude did not improve the predictive power for speed, but rather lowered the correlation value due to increased scatter. This is contrary to what had been found previously for fish (Webb, 1973). However, fish only modulated swim speed with tailbeat frequency and stroke amplitude at lower speeds (i.e. Bainbridge, 1958; Webb, 1975) because stroke amplitude reached its maximum (approximately 0.2 body lengths) at higher speeds (Bainbridge, 1958). In the present study, the majority of trials were from dolphins swimming $>1\,\mathrm{m\,s^{-1}}$ and size-specific stroke amplitudes clustered around 0.2 body lengths (pre-parturition: mean=0.25 ± 0.007 body lengths, $N=59$; post-parturition: mean=0.29 ± 0.004 body lengths, $N=92$), suggesting that the dolphins had attained their maximum size-specific stroke amplitudes.

Nonetheless, within these confines there was an obvious pregnancy-induced gait change. During pregnancy, the stroke amplitude of the dolphins was decreased by 13% compared with 1–24 months post-parturition (Fig. 4B). This gait change may be associated with decreased flexibility in the peduncle region and the

stretching of the locomotor muscles associated with the internal positioning of the fetus. Furthermore, if the fetus were to stretch the locomotor muscles beyond their optimal length, diminished actin–myosin filament overlap would decrease the available tension. It appears as though the pregnant dolphins compensated by increasing tailbeat frequency per a given speed; the normalized tailbeat frequency (ratio of tailbeat frequency to swim speed) (Rohr and Fish, 2004) for pregnant females was significantly greater than that during 1–24 months post-parturition. This in turn resulted in a significant decrease in distance covered per stroke during the pregnancy period compared with the non-pregnant state (Fig. 4C). In one stroke, pregnant females achieved only 86% of the distance covered by non-pregnant females.

Interestingly, although there was a gait change that accompanied near-term pregnancy, the optimal efficiency for these animals was not impacted. The principal wake parameter, termed the Strouhal number, is a non-dimensional number that is equivalent to the frequency of oscillation (or tailbeat frequency) divided by the maximum excursion of the propulsive foils trailing edge (or stroke amplitude). The Strouhal number is considered optimal in the range of 0.25–0.35 where efficiency is maximal (Triantafyllou et al., 1993). For dolphins in the present study, the Strouhal number was not significantly different between reproductive states. Furthermore, the mean values for the pregnant state (0.34 ± 0.01) and non-pregnant state (0.34 ± 0.01) were both within the range for optimal efficiency and were in agreement with those previously determined for dolphins (0.32 and 0.30) (Triantafyllou et al., 1993). This implies that even though the dolphins changed gait to accommodate changes in morphology, efficiency seems to have remained optimized.

Ultimately, increased drag concomitant with physiological changes associated with pregnancy (i.e. reduced lung volume and changes in blood flow away from working muscle) can act synergistically to lower swim performance. Indeed, mean and maximum swim speeds for the dolphins were lower during pregnancy than during 1–24 months post-parturition. The mean swim speed for pregnant females (mean=$1.55\pm0.07\,\mathrm{m\,s^{-1}}$) was only 38% of that achieved during the non-pregnant state (mean=$4.13\pm0.09\,\mathrm{m\,s^{-1}}$; Fig. 4D) and maximum swim speed for the near-term pregnant females ($3.54\,\mathrm{m\,s^{-1}}$) was only 56% of that attained during the non-pregnant state ($6.32\,\mathrm{m\,s^{-1}}$). As speed increases, drag and the power required to overcome drag increase disproportionately, making it difficult to sustain fast swim speeds for prolonged durations (Fish, 1993). This seems to be especially true for pregnant dolphins. The burden of pregnancy precluded the attainment of speeds greater than cruising speed, as the mean swim speeds of pregnant dolphins approached the minimum cost of transport speed for non-reproductive dolphins ($2.1\,\mathrm{m\,s^{-1}}$), where heart rate, respiratory rate and post-exercise blood lactate concentration is not significantly different than values at rest (Williams et al., 1993).

The diminished locomotor performance of pregnant dolphins observed in this study is in accordance with those for other gravid and pregnant animals across aquatic, terrestrial and aerial environments (Shine, 1980; Winfield and Townsend, 1983; Berglund and Rosenquist, 1986; Seigel et al., 1987; Cooper et al., 1990; Lee et al., 1996; Shaffer and Formanowicz, 1996; Isaacs and Byrne, 1998; Seibel et al., 2005; Gu and Danthanarayana, 2000; McLean and Speakman, 2000; Veasey et al., 2001; Plaut, 2002; Guillemette and Ouellet, 2005; Svendsen et al., 2009) and has profound implications for animals that rely on speed for hunting and predator avoidance. Both speed and maneuverability (ability to turn in a confined space) (Norberg and Rayner, 1987) play key roles in predator–prey interactions (Howland, 1974; Maresh et al., 2004). For dolphins, maneuverability is constrained by body flexibility (Fish, 2002), and the positioning of the fetus may limit the flexion of the body. This, combined with diminished swim performance (Fig. 4D), could make pregnant dolphins less effective hunters and more susceptible to predation.

There are no reports regarding the effectiveness of pregnant dolphins as hunters; however, behavioral strategies during foraging may minimize the constraints of diminished maneuverability and swim performance. First, dolphins school and this behavior enhances the foraging efficiency of the animals within the group (Wells et al., 1980; Würsig, 1986). Second, the diets of pregnant porpoises (*Phocoena phocoena*) (Yasui and Gaskin, 1986) and dolphins (*Delphinus delphis*) (Young and Cockcroft, 1994) are different than those of non-reproductive females. Although this prey switching has been attributed to the greater energetic demands of reproduction (Yasui and Gaskin, 1986; Young and Cockcroft, 1994), the pregnant common dolphins preferentially foraged on low-calorie squid compared with the relatively high-calorie fish taken by the non-reproductive females (Young and Cockcroft, 1994). Thus, pregnant dolphins may be choosing alternate prey items in an effort to optimize foraging efficiency.

Although there are no studies on the changing vulnerability to predation related to reproductive status for dolphins, there are such studies for ungulates. Ungulates are close relatives of cetaceans and, like dolphins, live in open and relatively featureless habitats. To deter and evade predators in the absence of spatial refuges, ungulates react to threat by aggregating and running as a group (stampeding) away from the perceived source of danger (Lent, 1974; Leuthold, 1977). Similarly, an approaching shark elicits the flight response in bottlenose dolphins (Tayler and Saayman, 1972; Connor and Heithaus, 1996). For terrestrial mammals, it has been hypothesized that adult females may become more vulnerable to predation in the terminal stages of gestation because they are weighed down by the fetus. Indeed, the adult females of three African ungulates [African buffalo (*Syncerus caffer*), blue wildebeest (*Connochaetes taurinus*) and greater kudu (*Tragelaphus strepsiceros*)] showed a marked increase in predation rate by lions during late gestation (Owen-Smith, 2008).

With knowledge of the hunting speeds of the known predators of bottlenose dolphins, we can predict whether near-term pregnant dolphins have a higher risk of predation than non-pregnant dolphins. Sharks are the dominant predators of dolphins worldwide, but killer whales (*Orcinus orca*) also prey on dolphins in some regions (Shane et al., 1986). Species of shark that attack dolphins, such as tiger (*Galeocerdo cuvier*) and white (*Carcharodin carcharias*), use a stealth foraging tactic where they stalk and attack unwary prey (Heithaus et al., 2002). The burst speed for white sharks is 6–$7\,\mathrm{m\,s^{-1}}$ (Kimley et al., 2001), which is likely to be used in an attack. Thus, once a group of dolphins becomes aware of an eminent shark attack and attempts to flee, the near-term pregnant dolphins will be vulnerable to the predatory event because their maximum swim speed ($3.54\,\mathrm{m\,s^{-1}}$) is half that of the sharks' attack speed. Similarly, when we consider the 4.17–$8.33\,\mathrm{m\,s^{-1}}$ hunting speeds used by marine-mammal eating killer whales (Ford et al., 2005), which use the endurance–exhaustion method (Guinet et al., 2007), the maximum swim performance of near-term pregnant dolphins does not afford fast enough evasive speeds to outrun the killer whales. Meanwhile, the maximum swim speed of non-pregnant dolphins ($6.32\,\mathrm{m\,s^{-1}}$) could afford predator avoidance when the sharks and killer whales operate at the lower end of their range of hunting speeds.

In summary, this study quantified a dramatic change in body morphology associated with pregnancy that coincided with increased opposing forces to locomotion (drag), a gait change and decreased locomotor effectiveness in dolphins. These are undoubtedly some of the underlying mechanisms by which the physical load of pregnancy decreased locomotor performance. Diminished locomotor performance can in turn increase the susceptibility of pregnant females to predation. Ultimately, the results of this study support the notion that reproduction is a costly endeavour that may increase energetic expenditure, increase risk of predation and decrease longevity (Shine, 1988).

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