First Case of a Monitored Pregnancy of a Harbour Porpoise (*Phocoena phocoena*) Under Human Care

Marie-Anne Blanchet,[1] Tiffany Nance,[1] Colleen Ast,[1]
Magnus Wahlberg,[1] and Mario Acquarone[2]

[1]*Fjord&Baelt, Margrethes Plads 1, DK-5300 Kerteminde, Denmark*
[2]*NAMMCO, Polar Environmental Centre, N-9296 Tromsø, Norway*

Current Addresses: Audubon Zoo, 6500 Magazine Street, New Orleans, LA 70118, USA (M-AB)
The Mirage, Dolphin Habitat, 3400 Las Vegas Boulevard South, Las Vegas NV 89109-8907, USA (TN)

Abstract

Most of the data collected on the reproduction of harbour porpoises *(Phocoena phocoena)* comes from by-caught or stranded animals and is therefore opportunistic in nature. Harbour porpoises kept in a human-controlled environment offer a unique opportunity to gather data on the same individual with a known history over a long period of time. At Fjord&Baelt in Kerteminde, Denmark, Freja, a 10-y-old female harbour porpoise, became pregnant in September 2005 and gave birth during the night between 24 and 25 July 2006. Routinely sampled parameters, such as food intake, weight, blubber-thickness, body-girth measurements, and respiration rates, did not follow the seasonal patterns observed the preceding years at the facility. These variables either increased or remained stable during the pregnancy.

As the first sign of the approaching parturition, a dramatic drop in food intake occurred 8 d prior to her giving birth followed by a decrease in body temperature of 1° C at about 62 h before giving birth. Freja's intermammary distance also increased as the date of the birth approached, although this parameter cannot be used for immediate diagnosis of impending parturition. The newborn calf was found dead a few hours after the birth and appeared to be the result of a full-term gestation. This study describes some observable changes in behavioural, physical, and physiological parameters occurring in a primiparous harbour porpoise during gestation, which could be used in animal husbandry for this species.

Key Words: pregnancy, husbandry, birth, parturition, harbour porpoise, *Phocoena phocoena*

Introduction

The harbour porpoise (*Phocoena phocoena*) is a relatively common cetacean living in coastal and continental shelf waters (Haug et al., 2003) and widely distributed in the northern hemisphere (Read et al., 1997). It is one of the smallest cetaceans found close to areas inhabited by humans and is very vulnerable to anthropogenic disturbances. Concerns have been expressed regarding the status of harbour porpoise populations in the Baltic and the North Seas and the effects of pollutants on their reproductive success (Desportes et al., 2003; Hasselmeier et al., 2004). The reproductive cycle of harbour porpoises is generally poorly understood (Read & Gaskin, 1990; Kastelein et al., 1997), and most data come from stranded or by-caught animals. The paucity of *in vivo* information on reproductive parameters is a major obstacle both in population modelling for this species and for the design of effective management procedures. Having animals under human care is thus a unique opportunity to collect data on the same individuals over long periods of time and throughout different physiological states (Desportes et al., 2003).

Pregnancy in harbour porpoises has never been formally described in nature nor in a human-controlled environment. The primary objective of this study is to describe the behavioural, physiological, and anatomical development of a captive harbour porpoise throughout pregnancy. This work includes observations of food intake and physical changes of the mother's body and compares these to the same data collected over previous years from the same animal.

Materials and Methods

The Animal
The study animal (Freja) was approximately 10 y old at the time of the study (Lockyer et al., 2003b) and was housed at the Fjord&Baelt Centre in Kerteminde, Denmark, together with two other harbour porpoises: an 11-y-old male (Eigil) and

a 3-y-old female (Sif). The age of the animals is estimated on the basis of extrapolating their growth curves back to a birth size of 70 cm in June (Lockyer et al., 2003). These three animals were taken under human care after having been rescued from pound nets set in the inner Danish waters. Eigil and Freja arrived together at the Centre on 7 April 1997 and Sif on 23 July 2004.

Harbour porpoises are known to become sexually mature between 3 and 4 y old for females and between 2 and 3 y old for males (Lockyer & Kinze, 2003). Mating behaviour between Eigil and Freja has been observed since 1997 (Desportes et al., 2003). However, Freja never conceived to our knowledge until 2003 when Freja suffered a miscarriage in October.

The Environment

The animals were housed in an outdoor, open-sea enclosure forming a pool in the Kerteminde Fjord. The environment is subject to the seasonal variations of light, temperature, and weather conditions. The winter months were defined as December through February and the summer months as June through August. The rectangular enclosure was approximately 15 m × 36 m and had an average depth of 3.5 m, with a natural sandy and rocky bottom. The habitat was subject to a strong daily tidal flow, causing a water level variation of 1 m on average.

Data

Various types of data were gathered from Freja's life at the Center both before and during her pregnancy: food intake, physical parameters (i.e., girth, weight, blubber thickness, intermammary distance), and physiological parameters (i.e., plasma progesterone, body temperature, and respiration rate).

All the samples requiring close contact with the animal were collected using voluntary husbandry behaviours (VHB), which were trained using operant conditioning (for a definition, see McFarland, 2006) and positive reinforcement (Pryor, 1984; Ramirez, 1999). This method allowed collecting a wide variety of biological samples without undue capture-related stress to the animal (Lacinak et al., 1996; Desportes et al., 2007).

Progesterone—The plasma progesterone levels were measured opportunistically during routine blood sampling. The blood was collected from the dorsal fluke vessels with a butterfly needle (Nipro scalp vein set 21G*$\frac{3}{4}$") and was transferred into a 5-ml Luer syringe. After a centrifugation (in NH4-heparin tubes, 10 min at 2,000 rpm), the separated plasma was frozen at -20º C until assayed. The laboratory (Veterinary Department, Rotterdam Zoo, P.O. Box 532, 3000 Rotterdam,

The Netherlands) used an Immulite 1000 system by Siemens Medical Solutions Diagnostics. The progesterone assay was a sequential competitive immuno-assay. The intra- and inter-assay tests were based on humans but also have been used on Asian elephants (*Elephas maximus*) (de Boer & Schaftenaar, 2004). They have a variation of 17.4% (inter-assay based on 52 different runs) and 15.7% (intra-assay based on one run analyzed 18 times). Similar data were currently not available for harbour porpoises.

Food Intake—The three porpoises were fed whole fish with a diet combining mackerel (*Scomber scombus*), herring (*Clupea harengus*), sprat (*Sprattus sprattus*), capelin (*Mallotus villosus*), and sand eels (*Hyperoplus* sp. and *Ammodytes* sp.). The quantity in kilograms and kilocalories of fish eaten daily was routinely recorded. All batches of fish were analyzed for protein, fat content, and energy by the methods described by the Nordic Nutrition Recommendations (Nordic Council of Ministers, 2004) at the State Laboratory of the Ministry of Food, Agriculture and Fisheries or at the Steins Laboratory (Eurofins Steins Laboratorium, Hjaltesvej 8, DK-7500 Holstebro).

The assumption was made that the quantity of live fish caught by the animals in the enclosure outside of training sessions was negligible since the mesh size (10 cm × 10 cm) and the algae growth on the double-net barrier does not allow a significant passage of wild fish.

The porpoises were fed according to their motivation in training, their general appetite, and their physical status (i.e., weight).

Weight—Freja's weight was recorded weekly by her voluntarily beaching onto a scale (Kruuse model PS250), which was located behind a slide-out platform. However, from February 2006, this behaviour was stopped, assuming that the pressure of Freja's weight on her belly while hauled out would be hazardous to the fetus. Thereafter, her body weight was estimated using a formula initially developed by Lockyer (1995) and Lockyer et al. (2003b) for stranded British Isles data, and for by-caught pregnant and nonpregnant females from West Greenland (Lockyer et al., 2003a). This formula was derived from data on animals from a population geographically distant from Freja's wild Danish population. Still, when comparing with formulas from other populations as described in Lockyer (1995) and Lockyer et al. (2003b), it seems to be the best one to fit Freja's measurements collected previously to the pregnancy.

The formula was

$$W = 0.00028 * L^{1.713} * G^{0.782}$$

where, W = weight and G = mid-body girth G3.

Girth Measurements—The girths G2, G3, and G4 (Lockyer, 1995; Lockyer et al., 2003b) were measured every week with the animal in the water. A soft, inextensible nylon rope was placed around the body of the animal at the three positions successively and then measured. Lockyer et al. (2003b) found these measurements to be variable due to the movements of the animal like the expansion of the chest while breathing when taken on land. But, in the present case, the animal remained calmly in the water during the procedure, holding its breath.

Blubber Thickness—The full blubber thickness was measured weekly; it was measured dorsally, laterally, and ventrally in three positions along the body (Lockyer et al., 2003b) by means of a portable ultrasonic subdermal fat scanner (Lean Meter by Renco) designed for use in domestic pig husbandry and used with success in precedent studies (Desportes et al., 2003). The blubber thickness measurements were taken once a month until the diagnosis of the pregnancy and then once a week.

Intermammary Distance—The distance at the middle of the genital opening from the outer side of one slit to the other was measured twice a week from March until June and then every day until the parturition using a ruler placed against the body wall.

Body Temperature—The core body temperature was measured at least once a week until 31 May, then opportunistically until the delivery. The irregularity in the data collection was due to the unwillingness of Freja to cooperate during some of the training sessions as the delivery approached. The temperature was taken rectally using a soft probe (DM 852, Ellab Ltd. Copenhagen, Denmark) inserted up to the bowel wall to guarantee a consistency in the measurements (N. Van Elk, DVM, pers. comm.).

Breathing Rate—The breathing rate of all three animals was monitored once every day between 0830 h and 1600 h over a 10-min interval. The observer would stand at a position overlooking the whole pool and would record every surfacing of the animals during which both expiration and inspiration occurred.

Results

The pregnancy was detected by an ultrasonographic examination on 22 February 2006 using an ALOKA 500 machine and a 3.5 MHz convex probe.

The birth date (25 July 2006) is denoted as B, the number of days (x) prior to the parturition as B-x and number of days after the parturition as B+x.

Birth

Freja gave birth between 2200 h on 24 July and 0500 h on 25 July to a fully formed female calf that was recovered from the enclosure at 0600 h but was dead. The 7-h gap was a nighttime period when the staff was unable to observe the animals. Back-calculating by using the rectal temperature of the calf and the ambient water temperature, the birth was estimated to have occurred around 0200 h on 25 July (N. Van Elk, DVM, pers. comm.). A necropsy was performed the next day on the fresh neonate. The calf had reached full-term both morphologically and histologically. It weighed 8 kg and measured 76 cm in length. It is impossible to say whether the animal was born dead or alive, but the calf never took a breath since the lungs had not been inflated (N. Van Elk, DVM, preliminary pathology report PP060725, University of Rotterdam, The Netherlands).

Food Intake During Pregnancy

The proportion of each dietary fish in kilocalories is shown in Figure 1.

During the pregnancy, the food intake decreased at first until November and then increased until July (Figure 2). On average, the minimum food intake was 4,529 kcal/d in November 2005 and the maximum was 7,650 kcal/d in July 2006. Some peaks were observed in July at up to 9,086 kcal/d between 10 July and 15 July. The average of food intake during the pregnancy was 5,982 kcal/d (SD = 1,098 kcal).

Food Intake Around Parturition

The food intake from B-12 became irregular (Figure 3), swinging between 8,306 kcal/d (her steady diet in July 2006) and 5,666 kcal/d. It decreased to zero kcal/d at B-1. Freja resumed eating (3,536 kcal/d) on the very afternoon after giving birth and reached a regular diet on B+6 (3,600 kcal/d); however, she did not reach her pre-birth diet of 8,306 kcal/d. It is interesting to note that this post-birth diet was very similar to her diet in July 2005.

Food Intake Before and During Pregnancy

Comparing the daily food intake between September 2003 and July 2004 vs between September 2004 and July 2005, there was no statistically significant trend over time (ANOVA on the regression residuals of the difference in daily food intake per month as a function of time: $F = 0.16$, $df = 7$, $p = 0.7$). During these periods, Freja was not pregnant to our knowledge. In contrast, the difference in daily food intake between September 2004 and July 2005 (nonpregnant) and September 2005 and July 2006 (pregnant) showed a significant increase, with daily food intake increasing
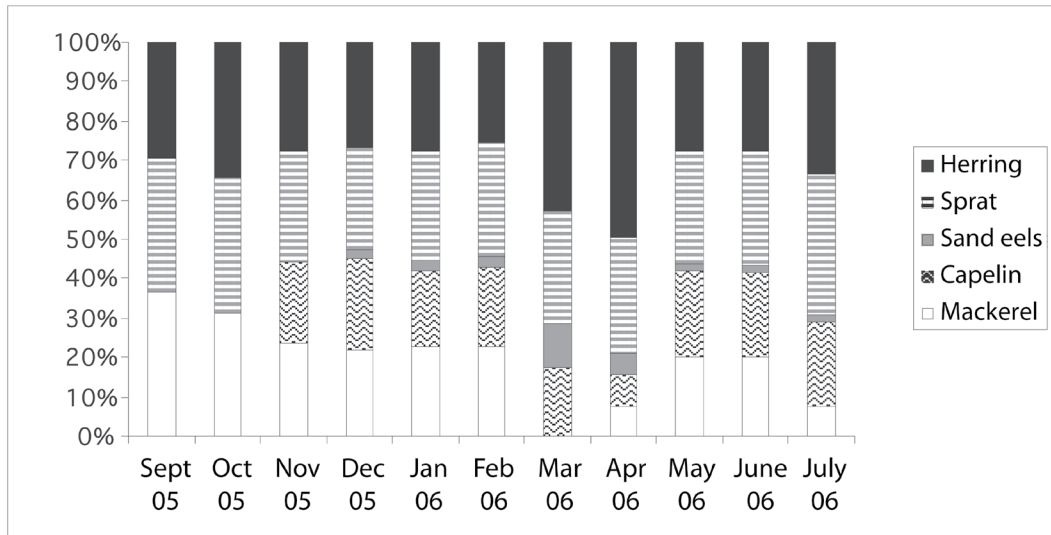
Figure 1. Diet composition for a pregnant female harbour porpoise in kilocalories; the absence of certain fish species for some months is due to a lack of fish supply.
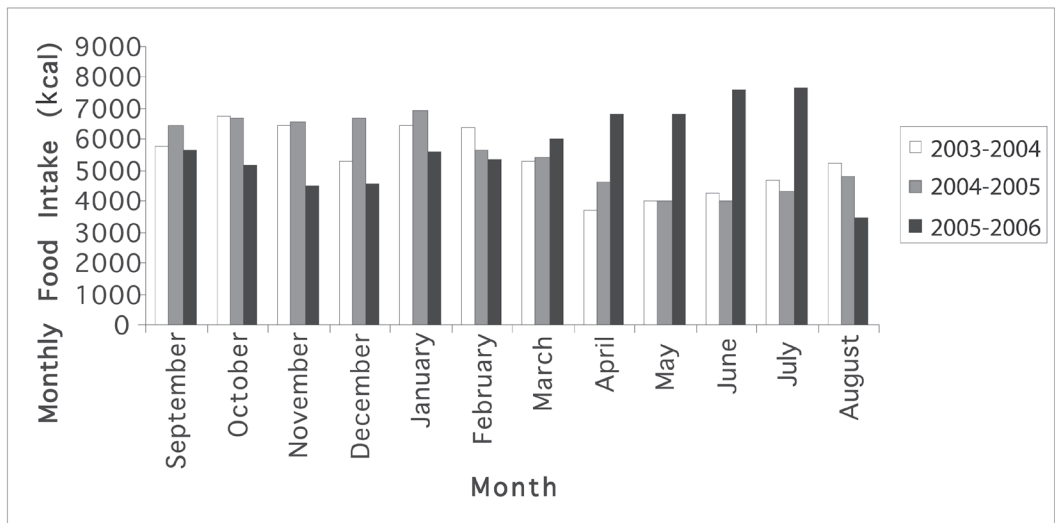

Figure 2. Monthly food intake for a female harbour porpoise for 2003-2004, 2004-2005, and 2005-2006; the average daily food intake in July was calculated until the 25th to compare similar periods before and during the pregnancy.

during the pregnancy (ANOVA: F = 91.52, df = 7, $p < 0.01$).

Weight
Between September 2003 and September 2005, Freja's weight varied seasonally between 47 and 64 kg (Figure 4) as described in Lockyer et al. (2003b). The lowest weight was observed in August-September (mean water temperature: 17.4° C, SD = 1.4° C; mean air temperature: 20.6° C, SD = 1.9° C), and the highest was observed

in February (mean water temperature: 3.6° C, SD = 2° C; mean air temperature: 5.3° C, SD = 3.1° C) during the coldest month. From September 2005, when the pregnancy was assumed to begin, the weight increased through July 2006 to reach a maximum of 68.9 kg on 9 July. Her average weight in July 2003, 2004, and 2005 was 53.8 kg. The weight gain at the end of the pregnancy was estimated to be 15 kg.
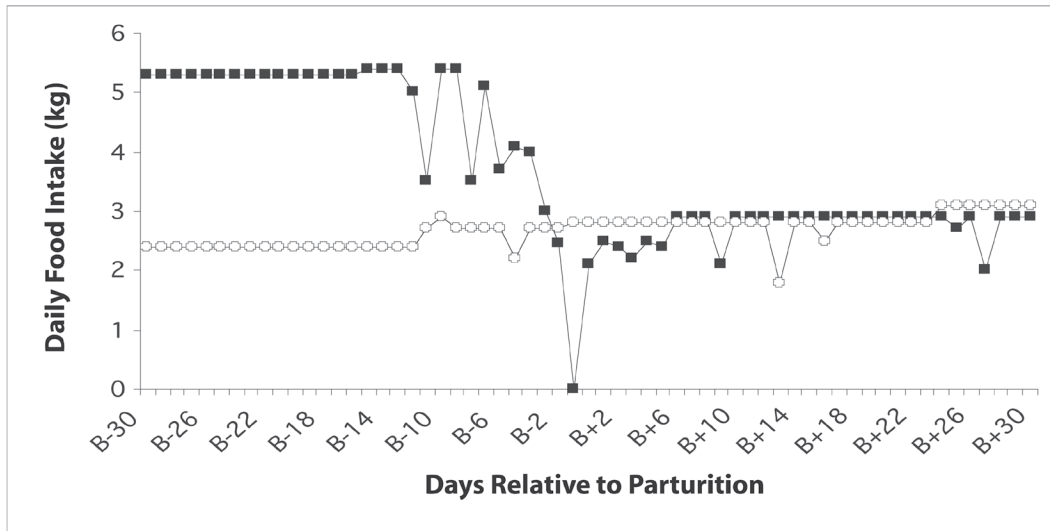
Figure 3. Daily food intake of a female harbour porpoise 30 days before and 30 days after parturition; the open circles represent the food intake at the same period the previous year. The food intake recorded in kilograms can be linked to the data presented in Figure 1 recorded in kilocalories.
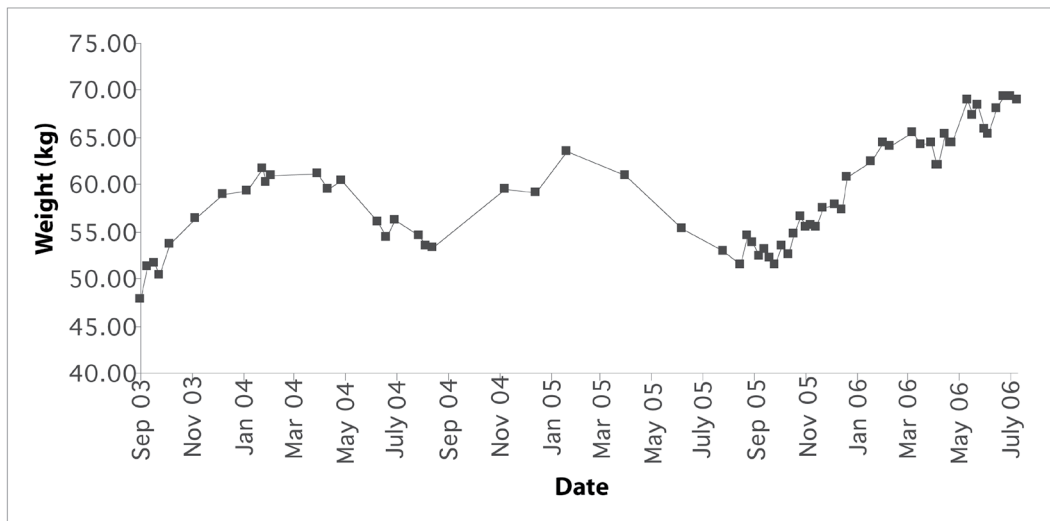

Figure 4. The body weight of a female harbour porpoise between September 2003 and July 2006; the weight from February 2006 is an extrapolation from the formula linking body weight and mid-body girth G3 (see text for details).

Girth Measurements

Data on girth measurements from previous years showed a seasonal trend, with the porpoise becoming thicker in winter than in summer. During the year of the pregnancy, there was a steady increase in Freja's girth throughout the gestation period (Figure 5). A linear regression applied to these data was highly significant (F = 97.31, df = 1, $p < 0.01$) and explained 84% of the variation in these data.

Blubber Thickness

Figure 6 shows the fluctuations in the fat layer thickness measured at the mid-dorsal position (D3) between September 2003 and July 2006. A seasonal variation was observed between summer and winter. The fat layer was usually the thickest during January and February (between 30 and 42 mm) and thinner during July and August (between 16 and 25 mm). These variations were similar to those described in Lockyer et al. (2003b) on data collected from April
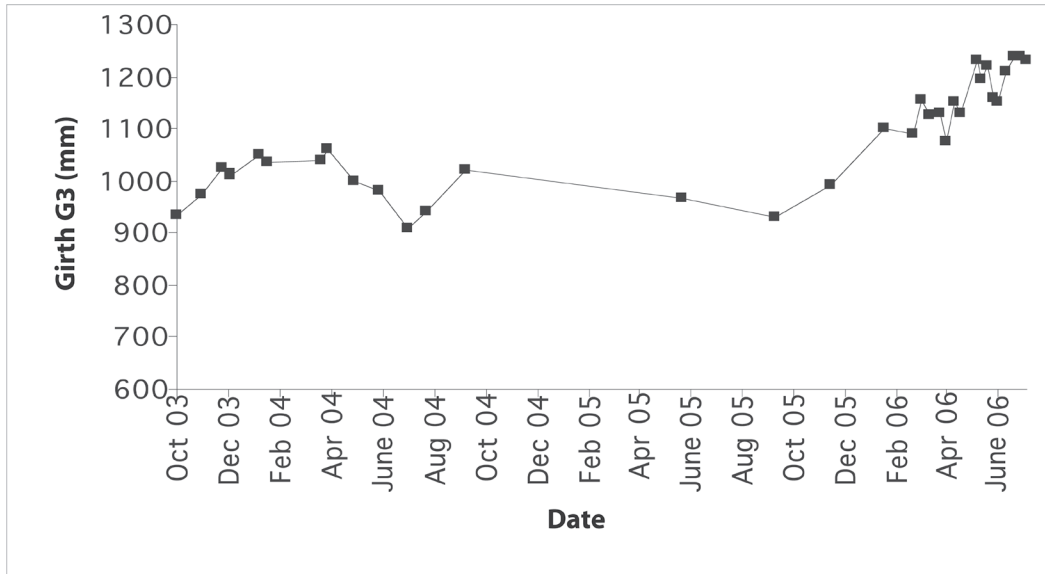
Figure 5. Change in a female harbour porpoise's mid-body girth G3 measurement between October 2003 and July 2006; the lack of measurements between October 2004 and June 2005 is due to a breakdown of the trained behavior for taking the measurement. More girth measurements were taken towards the end of the pregnancy because the trained behavior was more reliable.

A linear regression of the girth's data during the pregnancy data (September 2005 to July 2006) was y = 1.00033 × -37,804 with $R^2 = 0.8366$.
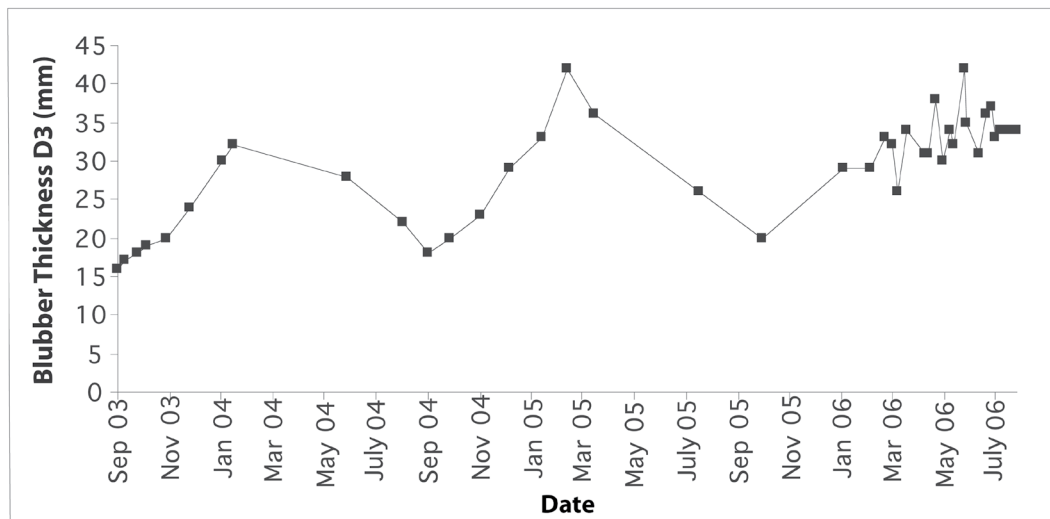

Figure 6. The dorsal mid-body blubber thickness of a female harbour porpoise between September 2003 and July 2006; the seasonal pattern observed in 2003-2004 and 2004-2005 disappears during the pregnancy.

1997 to January 2000 on the same animal. However, during the pregnancy (September 2005 to July 2006), these seasonal variations decreased in magnitude. The blubber thickness remained between 30 and 40 mm during the whole pregnancy.

Intermammary Distance
The intermammary distance remained constant (5 cm) up to B-46, and a fluctuation between 5 and 6 cm was observed until B-9. The distance increased from B-9 to reach 8 cm at B-2 (Figures 7, 8 & 9).
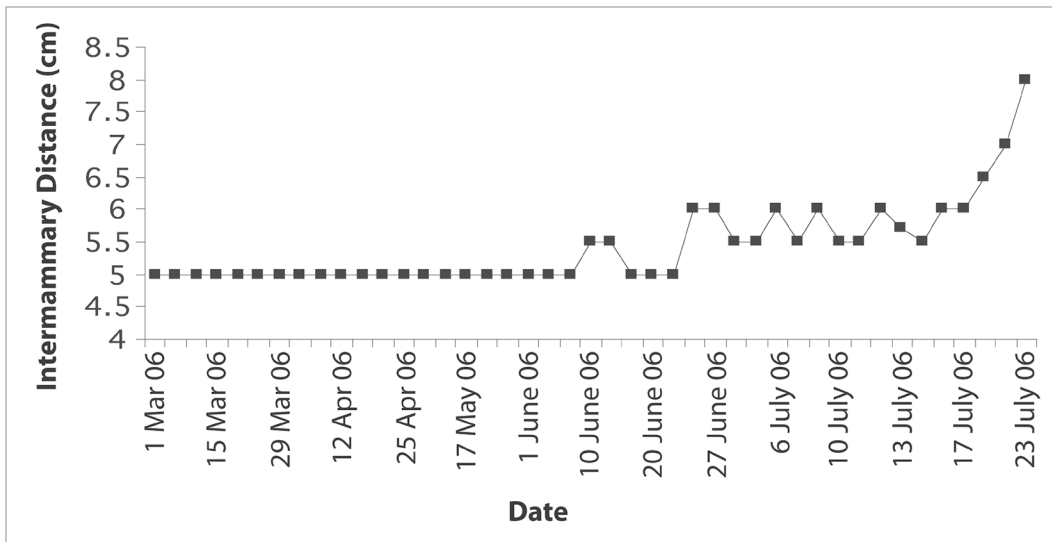
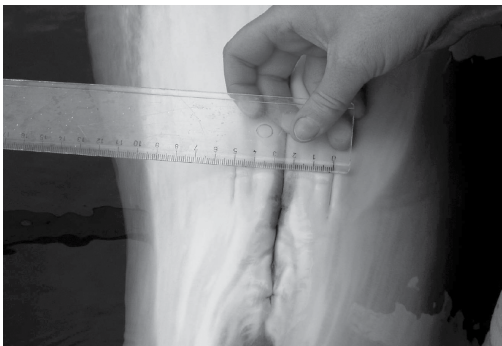**Figure 7.** Measurements of the intermammary distance during the pregnancy of a female harbour porpoise

Figure 8. Genital opening of a female harbour porpoise in a normal state; the intermammary distance is 5 cm.
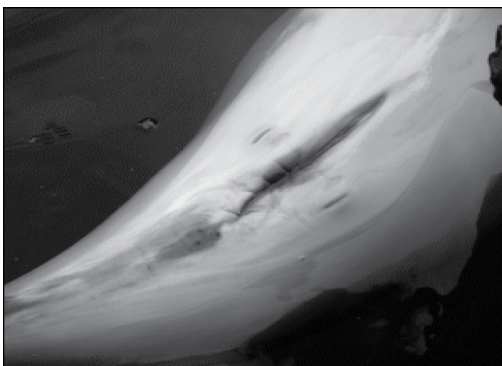

Figure 9. Genital opening of a female harbour porpoise two days prior to the delivery (23 July 2006); the intermammary distance is 8 cm.

During the last days of pregnancy (B-8 to B-2), there is an almost significant linear trend in the increase of the intermammary distance (F-test: F = 14.6, df = 3, p = 0.06), which explains 100% of the variation in these data.

Respiration Rate
Breathing rate from February 2003 until July 2006 showed seasonal variation (Figure 10), increasing during winters and decreasing during summers. However, during the pregnancy, this seasonal pattern disappeared and was substituted by a constant increase.

Core Body Temperature
The body temperature varied between 36º C and 37.7º C during the pregnancy (Figure 11). The average temperature was 36.7º C (SD = 0.4º C). At B-1, the temperature fell to 35.6º C. During the last 24 d before the birth, there was a significant linear trend in falling rectal temperature (F-test: F = 64.79, df = 10, $p < 0.01$), which explained 88% of the variation.

Progesterone Levels
A plasma progesterone level was measured on 30 August 2005 and was 1.34 nmol/l. The next level available was on 14 March 2006, and it was 40.89 nmol/l this time. The progesterone level remained high (between 47.22 nmol/l and 55.86 nmol/l) during the rest of the pregnancy and dropped dramatically after the birth to 4.17 nmol/l on 2 August 2006 (Figure 10).
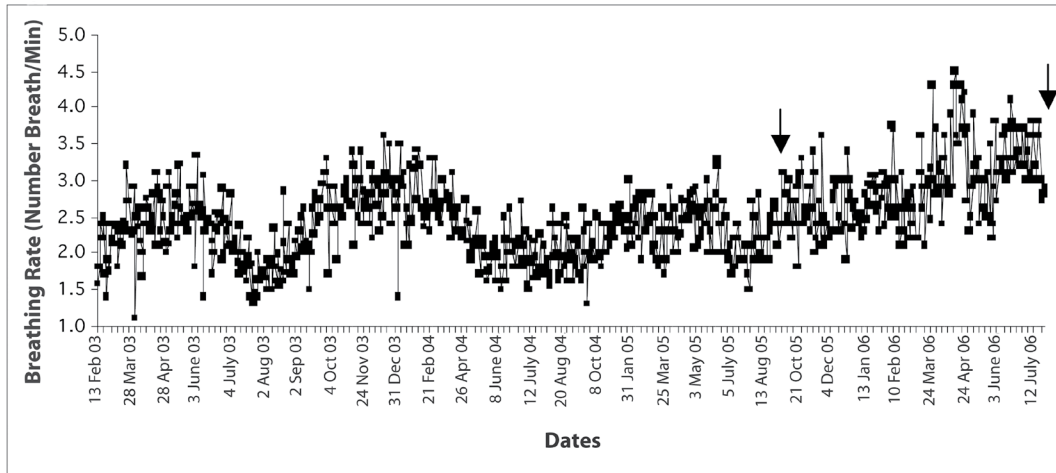
Figure 10. Daily respiration rate of a female harbour porpoise between February 2003 and July 2006; the arrows show the start and the end of the pregnancy.
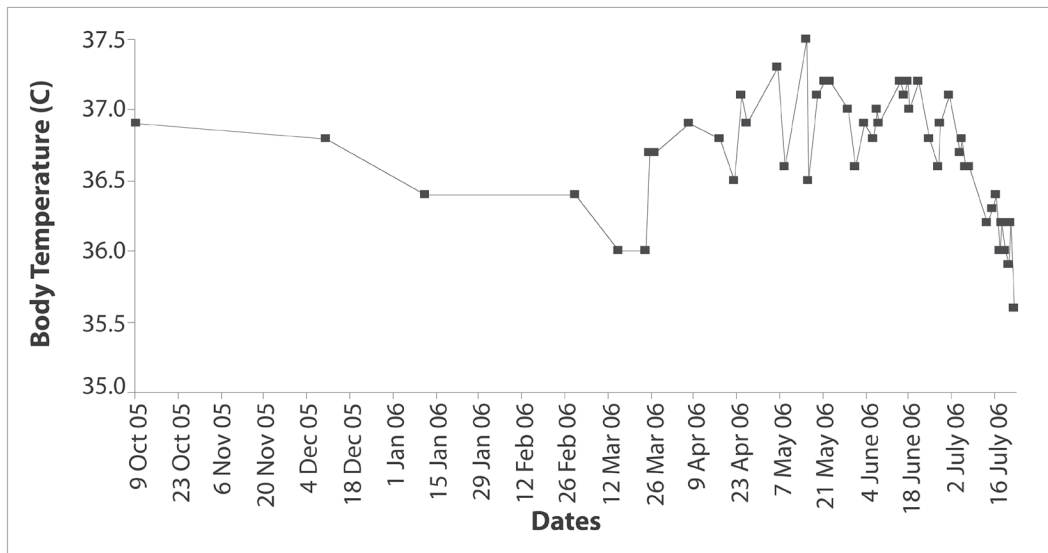

Figure 11. The core body temperature of a female harbour porpoise during pregnancy

Discussion

Duration of Gestation and Calving Period
Gestation in harbour porpoises lasts 10.5 to 10.6 mo (Read, 1990; Sørensen & Kinze, 1994), according to studies on Danish and Canadian populations. The body length of the newborn calf (76 cm) and the results of the necropsy indicated that Freja had been through a full-term gestation (e.g., Read, 1990; Sørensen & Kinze, 1994; Lockyer, 1995; Halldórsson & Víkingsson, 2003; Hasselmeier et al., 2004) and indicated that Freja carried the calf to term (25 July 2006). The back-calculation

of the time of conception indicated a date between 7 September and 10 September. Progesterone analysis indeed showed that Freja became pregnant after 31 August. Thus, it is very likely that conception did take place in early September.

Birth periods may vary considerably between populations (Read, 1990; Halldórsson & Víkingsson, 2003; Gol'din, 2004; Hasselmeier et al., 2004). In the Bay of Fundy in Canada, harbour porpoise births occur during mid-May (Read, 1990), while the parturition is calculated to occur between 6 June and 16 July for the North Sea population and one month later in the
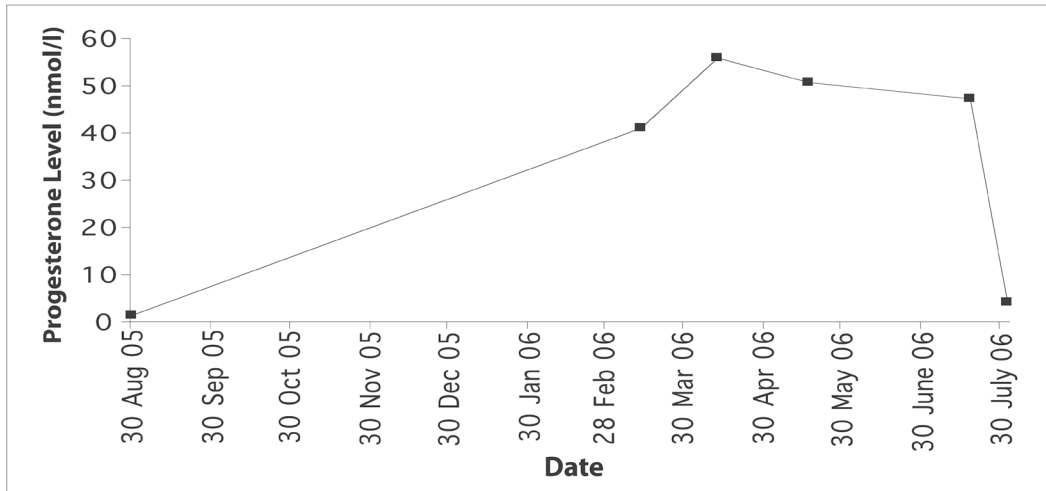
Figure 12. Serum progesterone levels of a female harbour porpoise between August 2005 and August 2006; the porpoise was pregnant between September 2005 and July 2006.

western Baltic Sea (Hasselmeier et al., 2004). Freja, coming from the area of southern Zealand in East Denmark, followed the pattern of the latter population.

Food Intake Changes During Pregnancy
Food intake varies in numerous species of marine mammals in relation to age, sex, season, and reproductive status (e.g., Kastelein et al., 1994; Blanchet et al., 2006). Seasonal variations are especially evident for harbour porpoises (Desportes et al., 2003; Lockyer, 2003; Lockyer & Kinze, 2003; Lockyer et al., 2003b). During the pregnancy monitored here, though, the seasonal drop in food intake normally observed from March to April did not occur. This could be related to the extra demand for energy from the fetus (Kastelein et al., 1994) but also to the energy storage in blubber for the milk production. Increased food intake during the late stages of the gestation has been observed in several species of cetaceans such as killer whales (*Orcinus orca*) reported by Clark & Odell (2000), beluga whales (*Delphinapterus leucas*) reported by Kastelein et al. (1994), and bottlenose dolphins (*Tursiops truncatus*) reported by Ridgway et al. (1994). However, Kastelein et al. (1993) showed the opposite tendency in Commerson's dolphins (*Cephalorhynchus commersonii*). It is interesting to note that 7 d after the birth, Freja regained a stable diet at the same level as the one from July 2004 and July 2005 when not pregnant.

Behavioural and appetite changes occur before parturition in various species of marine mammals such as harbour seals (*Phoca vitulina*) (Blanchet et al., 2006), beluga whales (Dalton et al., 1991), Commerson's dolphins (Kastelein et al., 1993),

and bottlenose dolphins (Cornell et al., 1987; Schroeder, 1990; Terasawa et al., 1999). Freja seemed to follow this tendency; she had a dramatic decrease in food intake the day prior to the parturition. Various hormonal mechanisms are involved in appetite changes. In some species, like mink (*Mustela vison*) (Tauson et al., 2004) and cattle (*Bos taurus*) (Ingvartsen et al., 1999), leptin is centrally involved. More studies are needed to investigate if the same mechanism occurs in harbour porpoises and other marine mammals.

Physical, Behavioural, and Physiological Changes During Pregnancy
Similar to food intake, morphological parameters evolved during the pregnancy. Blubber thickness at a mid-body position (D3) remained the same throughout the pregnancy instead of decreasing following the seasonal pattern observed the preceding years (Figures 5 & 6; Lockyer, 1995; Lockyer et al., 2003b). The blubber layer in harbour porpoises appears to have two distinctive functions: the thoracic and abdominal parts have energy storage and insulation functions whereas the posterior part plays a hydrodynamic role (Koopman, 1998). A decrease in the thickness of the blubber layer is linked to the increase in water temperature and less need for insulation in nonreproductive animals. During a pregnancy, though, the blubber layer can provide an extra energy source for use during lactation (Kastelein et al., 1993). The blubber layer can therefore remain thick throughout a pregnancy even though the need for insulation disappears.

Similarly, the mid-body girth (G3) did not follow the previously observed seasonal pattern

(see Figure 5; Lockyer, 1995; Lockyer et al., 2003b). The G3 increased throughout the pregnancy reflecting the volume occupied by the fetus and the thick blubber layer of Freja.

Concomitant to the increase in girth, an increase in weight was observed (Figure 4). At the end of the pregnancy, it represented a 15-kg difference in weight on the same date in the two preceding years. This reflects the growth of the fetus, the thickening of the blubber layer, and the development of the embryonic annexes. In wild animals, a female harbour porpoise reaches her asymptotic length at the age of 7 y old (Lockyer, 2003). Thus, the increase in weight was most likely caused by the pregnancy and not by any body growth.

A decrease in body temperature is characteristic of the prepartum events in several species of mammals (Terasawa et al., 1999) and often is associated with a decrease in the level of circulating progesterone (Katsumata et al., 1998). In bottlenose dolphins (Terasawa et al., 1999) and killer whales (Katsumata et al., 1998), a decrease in the core body temperature was observed before the delivery. A drop of 1° C is observed in bottlenose dolphins 12 to 24 h prior to parturition. In killer whales, the decrease in core body temperature can start as early as 5 d before the birth. In Freja's case, it is interesting to notice that the drop of 1° C occurred approximately 62 h prior to parturition (Figure 11); however, the time of birth was somewhat uncertain. The body temperature just before the parturition is unknown since Freja refused to participate in medical behaviours 2 d prior to the delivery.

An increase of the intermammary distance is a valuable indication for predicting the onset of parturition in many cetacean species such as killer whales, bottlenose dolphins, and beluga whales (Dalton et al., 1991). In cetaceans, one mammary slit is located on each side of the genital opening. During parturition, a maximal dilatation of the vagina and the cervix is necessary for the passage of the neonate. Thus, the increase in the distance between the two mammary slits can be considered a reliable indication of the magnitude of the cervix dilatation. For Freja, a slight but noticeable change in the intermammary distance first appeared 46 d before the parturition. An acceleration of the increase of the intermammary distance indicated the imminence of the delivery.

Respiration rate can be related to activity level and metabolic rate in harbour porpoises (Reed et al., 2000). Breathing rate varies among seasons, with higher rates in winter than in summer (Figure 12) and can be related to a higher heat production in winter than in summer and/or to responses to the environment (Lockyer et al., 2003b). During the pregnancy, these seasonal variations disappeared and the daily breathing rate even increased during the summer months prior to delivery. This could be due to an increase of the metabolic rate due to the needs of the fetus or to the physical constraint imposed by a growing fetus on the lungs. Without any further information regarding metabolic rates of porpoises, it is difficult to determine the cause.

There was an important at least forty-fold increase in serum progesterone levels of the pregnant vs the nonpregnant harbour porpoise. This is higher than the values measured in other cetacean species, in which progesterone elevates ten-fold during pregnancy (Sweeney, 2003). It is difficult, however, to compare progesterone levels obtained with different methods due to the risk of cross-reactions with various circulating progesterone metabolites.

Monitoring the pregnancy of a harbour porpoise allowed the gathering of valuable information on the morphological and physiological changes that occurred during this sensitive period of the life cycle. The seasonal fluctuations in body weight, blubber thickness, girth, breathing rate, and food intake are characteristic of nonparous females. Some information can help to pinpoint the imminence of parturition such as a dramatic loss of appetite, a drop in core body temperature, and a rapid increase of the intermammary distance.

More data are needed on Freja to determine whether all pregnancies in the same individual have comparable measures. Moreover, more data are needed on other animals within the species to verify if these observations can apply to all female harbour porpoises.

Literature Cited

Blanchet, M-A., Desportes, G., Nance, T., & Vanman, C. (2006). Description of the pregnancies, labour and pre- and post-partum events of two harbour seals *(Phoca vitulina)* in a zoological environment. *Aquatic Mammals, 32*(2), 145-151.

Clark, S. T., & Odell, D. K. (2000). Nursing parameters in captive killer whales *(Orcinus orca)*. *Zoo Biology, 18*, 373-384.

Cornell, L. H., Asper, E. D., Antrim, J. E., Searles, S. S., Young, W. G., & Goff, T. (1987). Progress report: Results of a long-range captive breeding program for the bottlenose dolphin, *Tursiops truncatus* and *Tursiops truncatus gilli. Zoo Biology, 6*, 41-53.

Dalton, L., Robeck, T., Calle, P., & Cook R. A. (1991). *Observation at parturition of eight beluga whales (*Delphinapterus leucas*).* Presented at the 24th Conference of the International Association for Aquatic Animals Medicine (IAAAM), Chicago, IL.

De Boer, A. M., & Schaftenaar, W. (2004). Monitoring of the estrous cycle of Asian elephant *(Elephas maximus)* as an important tool in reproduction and parturition management using a chemiluminescent immunoassay, Immulite®, to measure blood progesterone. *Proceedings of the 24th Annual Meeting of the Zoo Veterinary Technicians Association.*

Desportes, G., Buholzer, L., Anderson-Hansen, K., Blanchet, M-A., Acquarone, M., Shephard, G., et al. (2007). Decrease stress; Train your animals: The effect of handling methods on cortisol levels in harbour porpoises, *Phocoena phocoena*, under human care. *Aquatic Mammals*, *33*(3), 286-292.

Desportes, G., Kristensen, J., Benham, D., Wilson, S., Jepsen T., Korsgaard, B., et al. (2003). Multiple insights into the reproductive function of harbour porpoises *(Phocoena phocoena)*: An ongoing study. *NAMMCO Scientific Publications*, *5*, 91-106.

Gol'din, P. E. (2004). Growth and body size of the harbour porpoise *Phocoena phocoena* (Cetacea, Phocoenidae), in the Sea of Azov and the Black Sea. *Vestnik zoologii, 38*(4), 59-73.

Halldórsson, S. D., & Víkingsson, G. A. (2003). Analysis of seasonal changes in reproductive organs from Icelandic harbour porpoises *(Phocoena phocoena)*. *NAMMCO Scientific Publications*, *5*, 121-141.

Hasselmeier, I., Abt, K. F., & Siebert, U. (2004). Stranding patterns of harbour porpoises (*Phocoena phocoena*) in the German North and Baltic Seas: When does the birth period occur? *Journal of Cetacean Research and Management*, *6*(3), 259-263.

Haug, T., Desportes, G., Víkingsson, G., & Witting, L. (Eds.). (2003). Harbour porpoises in the north Atlantic. *NAMMCO Scientific Publications*, *5*. 315 pp.

Ingvartsen, K. L., Friggens, N. C., & Faverdin, P. (1999). Food intake regulation in late pregnancy and early lactation. *British Society of Animal Balance Occasional Publication*, *24e*, 37-54.

Kastelein, R. A., Ford, J., Berghout, E., Wiepkema, P. R., & Van Boxsel, M. (1994). Food consumption, growth and reproduction of belugas *(Delphinapterus leucas)* in human care. *Aquatic Mammals*, *20*(2), 81-97.

Kastelein, R. A., McBain, J., Neurohr, B., Mohri, M., Saijo, S., Wakabayashi, I., et al. (1993). The food consumption of Commerson's dolphins *(Cephalorhynchus commersonii). Aquatic Mammals*, *19*(2), 99-121.

Katsumata, E., Katsumata, H., Tobayama, T., & Usuki, S. (1998). *Body temperature in reared killer whale (*Orcinus orca*): Useful predictive method of confinement in females?* Third International Symposium of the Asia and Oceania Society for Comparative Endocrinology.

Koopman, H. N. (1998). Topographical distribution of the blubber of harbour porpoises (*Phocoena phocoena*). *Journal of Mammalogy*, *79*(2), 260-270.

Lacinak, T. C., Scarpuzzi, M., Force D. L., & McHugh, M. B. (1996). Sea World's husbandry training program: Update. *The Association for Behaviour Analysis' Special Interest Group on Animal Training Newsletter.*

Lockyer, C. (1995). Aspects of the morphology, body fat condition and biology of the harbour porpoise, *Phocoena phocoena. Report of the International Whaling Commission, 16*(Special issue), 190-197.

Lockyer, C. (2003). Harbour porpoises *(Phocoena phocoena)* in the North Atlantic: Biological parameters. *NAMMCO Scientific Publications*, *5*, 71-89.

Lockyer, C., & Kinze, K. (2003). Status, ecology and life history of harbour porpoise *(Phocoena phocoena)* in Danish waters. *NAMMCO Scientific Publications*, *5*, 143-175.

Lockyer, C., Heide-Jørgensen, M. P., Jensen, J., & Walton M. J. (2003a). Life history and ecology of harbour porpoises *(Phocoena phocoena,* L.) from West Greenland. *NAMMCO Scientific Publications, 5*, 177-194.

Lockyer, C., Desportes, G., Hansen, K., Labberte, S., & Siebert, U. (2003b). Monitoring growth and energy utilization of the harbour porpoise *(Phocoena phocoena)* in human care. *NAMMCO Scientific Publication*s, *5*, 107-120.

McFarland, D. (2006). *Oxford dictionary of animal behaviour.* New York: Oxford University Press. 221 pp.

Nordic Council of Ministers. (2004). *Nordic nutrition recommendations 2004: Integrating nutrition and physical activity* (4th ed.). Copenhagen, Denmark: Author.

Pryor, K. (1984). *Don't shoot the dog: The new art of teaching and training*. New York: Bantam Books. 187 pp.

Ramirez, K. (1999). *Animal training: Successful animal management through positive reinforcement.* Chicago: Shedd Aquarium. 578 pp.

Read, A. J. (1990). Reproductive seasonality in harbour porpoises, *Phocoena phocoena* from the Bay of Fundy. *Canadian Journal of Zoology, 68*, 285-288.

Read, A. J., & Gaskin, D. E. (1990). Changes in growth and reproduction of harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences*, *47*, 2158-2163.

Read, A. J., Wiepkema, P. R., & Nachtigall, P. E. (Eds.). (1997). *The biology of the harbour porpoise*. Woerden, The Netherlands: De Spil Publishers. ISBN 90-72743-07-5.

Reed, J. Z., Chambers, C., Hunter, C. J., Lockyer, C., Kastelein, R., Fedak, M. A., et al. (2000). Gas exchange and heart rate in the harbour porpoise *(Phocoena phocoena). Journal of Comparative Physiology B, 170*, 1-10.

Ridgway, S. H., Reddy, M., Kamolnick, T., Skaar, D., & Curry, C. (1991). *Calorie consumption of growing, adult, pregnant and lactating* Tursiops. Presented at the International Marine Animal Trainers Association (IMATA) Conference, Vallejo, CA.

Schroeder, J. P. (1990). Reproductive aspects of marine mammals. In L. A. Dierauf (Ed.), *CRC handbook of marine mammal medicine: Health, disease, and rehabilitation* (pp. 353-369). Boca Raton, FL: CRC Press.

Sørensen, T. B., & Kinze, C. (1994). Reproduction and reproductive seasonality in Danish harbour porpoises *(Phocoena phocoena). Ophelia*, *39*(3), 159-176.

Sweeney, J. (2003). Reproduction. In E. M. Fowler & R. E. Miller (Eds.), *Zoo and wild animal medicine* (5th ed.) (pp. 789-790). St. Louis, MO: Saunders.

Tauson, A. H., Forsberg, M., & Chwalibog, A. (2004). High leptin in pregnant mink *(Mustela vison)* may exert anorexigenic effects: A permissive factor for rapid increase in food intake during lactation. *British Journal of Nutrition*, *91*, 411-421.

Terasawa, F., Yokoyama, Y., & Kitamura, M. (1999). Rectal temperatures before and after parturition in bottlenose dolphins. *Zoo Biology*, *18*, 153-156.