

Changes in blood testosterone and progesterone concentrations of the North Atlantic minke whale (*Balaenoptera acutorostrata*) during the feeding season

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Abstract: An opportunity to study seasonal changes of sex hormones in the North Atlantic minke whale (common minke whale, *Balaenoptera acutorostrata*) arose when we obtained access to fresh postmortem blood samples from 104 females and 83 males. The whales were caught in the North Atlantic during May–September 1992–1995. Serum progesterone (P) and testosterone (T) concentrations were measured and compared with anatomical data. The frequency distribution of female serum P values showed two clusters, one consisting mainly of immature animals and the second of pregnant ones, with mean serum values of about 0.49 ± 0.04 (SE) and 44.2 ± 2.84 nmol·L⁻¹, respectively. The frequency distribution of male serum T did not show any group-specific distribution during the hunting season. The mean serum T value for the males was 0.63 ± 0.13 nmol·L⁻¹. Contrary to earlier reports on the Antarctic minke whale (*Balaenoptera bonaerensis*), serum T values rose during the hunting season in mature males ($p < 0.0001$). Serum P values in immature females increased during the season ($p = 0.015$). This increase agrees with the predominantly annual reproduction cycle of minke whales. Blood sex hormone measurements seem to be useful for detecting cyclic changes and pregnancy of minke whales.

Résumé : L'accès à des échantillons de sang frais prélevés après la mort chez 104 femelles et 83 mâles du petit rorqual commun (*Balaenoptera acutorostrata*) nous a fourni l'occasion d'étudier les changements saisonniers des hormones sexuelles chez les petits rorquals de l'Atlantique-Nord. Les rorquals ont été capturés dans l'Atlantique-Nord de mai à septembre, en 1992–1995. Nous avons mesuré les concentrations de progestérone (P) et de testostérone (T) sériques et noté les caractéristiques anatomiques correspondantes. La distribution de fréquence des concentrations de P sérique chez les femelles indique deux regroupements, l'un correspondant surtout à des animaux immatures et le second à des femelles enceintes, avec des valeurs moyennes respectives d'environ $0,49 (\pm 0,04, \text{erreur standard (SE)})$ nmol·L⁻¹ et $44,2 (\pm 2,84)$ nmol·L⁻¹. La distribution des fréquences des concentrations de T sérique chez les mâles n'indique pas de répartition particulière pour un groupe ou un autre pendant la saison de la chasse : la valeur moyenne est de $0,63 \pm 0,13$ nmol·L⁻¹. Contrairement à ce qu'on a signalé antérieurement chez des petits rorquals de l'Antarctique (*Balaenoptera bonaerensis*), les concentrations de T sérique augmentent durant la saison de la chasse chez les mâles matures ($p < 0,0001$). Les concentrations de P sérique augmentent chez les femelles immatures ($p = 0,015$) durant la saison. Cet accroissement correspond au cycle de reproduction surtout annuel des petits rorquals. La détermination des hormones sexuelles du sang semble donc être utile pour détecter les changements cycliques et la grossesse chez les petits rorquals.

[Traduit par la Rédaction]

Received 17 December 2002. Accepted 28 November 2003. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 22 March 2004.
J17245

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Introduction

The North Atlantic minke whale (*Balaenoptera acutorostrata*) species (the International Whaling Commission recommends the name "common minke whale", which will be used hereafter in this article) is one of the smallest in size of the genus *Balaenoptera*, which belongs to the Balaenopteridae family. As reviewed recently (Lockyer 1984, 1999; Horwood 1990), a considerable body of knowledge has been gathered by pioneering studies mainly during the last 40–50 years on the reproduction of the common minke whale. Contrary to other baleen whales, which generally reproduce every second year or even less frequently, the evidence available at present indicates that the common minke whale has mostly a yearly reproductive cycle. Apparent pregnancy rates (proportion of sexually mature females with fetuses, females with calves not included) between 90% and 100% of caught common minke whales have persistently been reported (Christensen 1981; Sigurjónsson 1995). This is about 50% higher than in the northern fin whale (*Balaenoptera physalus*) (Martin 1982; Lockyer and Sigurjónsson 1991) and sei whale (*Balaenoptera borealis*) (Lockyer and Martin 1983). Likewise, the ovulation rates (number of corpora counted in ovaries per year by age) have generally been reported to be about 90% and higher, which is roughly two times greater than those for fin and sei whales (Horwood 1990; Lockyer 1999).

The common minke whale, like most of the other baleen whales, has an annual migration cycle of feeding, which should be in step with its breeding cycle. The animals breed at lower and warmer latitudes but go to colder areas in the north during the summer for feeding. Gestation period is 10 months, a month or two shorter than for the other baleen whales, and the suckling period is thought to be less than 6 months (Lockyer 1999). Many lactating female minke whales have been found to be ovulating as evidenced by corpora lutea in their ovaries (International Whaling Commission 1979), and it seems probable that they do conceive while being suckled. If conception occurred mainly before the middle of the suckling period, the minke cows could maintain an annual reproduction cycle that fitted into their yearly migration. The postpartum inhibition of ovulation during suckling is variable in different animals but seems to be mainly controlled by the suckling frequency of the offspring (McNeilly 1994), which causes suppression of the pulsatile secretion of gonadotropin-releasing hormone. Progesterone (P) and the endogenous opioid system are probably involved (Soaje et al. 2002), but the exact mechanism at the hypothalamic level is not yet clear.

The yearly reproductive cycle of common minke whales with increased ovulation and pregnancy rates, i.e., increased ovarian activity, should be reflected in different serum P concentrations when compared with other rorquals with a 2-year cycle. This comparison applies to the North Atlantic fin whale (Kjeld et al. 1992) and sei whale (Kjeld et al. 2003) in both of which serum P concentrations have been measured.

Antarctic minke whales caught off Durban, South Africa, during the winter months were reported to have higher mean testicular weights per length than those taken in the Antarctic during the summer months (Best 1982). However, no definite

seasonal variation in serum testosterone (T) or P concentrations has so far been found in either sex of the Antarctic minke whale during the months of December–March (Yoshioka and Fujise 1992; Iga et al. 1996; Mogoe et al. 2000). Using heterologous antisera, Suzuki et al. (2001) also studied the concentrations of gonadotropins in the pituitary of the Antarctic minke whale during the months of December–March and found no rise in luteinizing hormone values and a significant rise in follicle stimulating hormone values only from February to March. However, serum T and P concentrations were mostly undetectable in immature males as well as mature males and immature females, respectively. This is contrary to our own findings for two other species of the same genus, the northern fin whale (Kjeld and Arnason 1990; Kjeld et al. 1992) and the sei whale (Kjeld et al. 2003), both of which showed significant increases of serum T concentrations during the hunting season.

Here, using relatively sensitive radioimmunoassays, we report our serum T and P measurements on samples available from the common minke whale. The frequency distributions of the serum values are presented and the concentrations related to the time of the season, the length of the animals, and their anatomically assessed sexual status.

Materials and methods

Collection and storage of samples

The whales were caught off Lofoten and Vesterålen (15 females and 27 males) and off Finnmark (17 females and 20 males), both northern Norway, off the coast of the Kola Peninsula, Russia (eight females and seven males), and off the coast of Bear Island (23 females and 27 males) and Spitsbergen (41 females and two males), both Svalbard, Norway, during the period May–September 1992–1995. The whales were caught for scientific purposes and a few papers have already been published based on this material alone or related common minke whale material (Haug et al. 1995; Nordoy 1995; Tryland et al. 1999). Blood samples were collected by cutting into the jugular vein immediately after the animals had been taken aboard the vessel, generally less than 40 min postmortem. Blood was left to coagulate in the vacutainers for 40–50 min and then centrifuged and serum separated and kept at -20°C .

Radioimmunoassays

Serum T was measured by a modified radioimmunoassay method described by Kjeld et al. (2003) using a more sensitive and specific antiserum (rabbit anti-T-19; Cat. No. 20-TR05; Fitzgerald Industries International, Inc., Concord, Mass.). The antiserum had cross-reactivity of 1.0% for dihydrotestosterone, <1.0% for nortestosterone, <0.02% for P, and <0.01% for other steroids tested. The assay had an interassay imprecision (coefficient of variation) of 10% for a sample of $3.1\text{ nmol}\cdot\text{L}^{-1}$ and an intraassay imprecision of 8% for a sample of $1.4\text{ nmol}\cdot\text{L}^{-1}$. The detection limit of the assay was $0.05\text{ nmol}\cdot\text{L}^{-1}$.

Serum P was measured by a modified radioimmunoassay method described by Kjeld et al. (1980, 1992). By using a more sensitive and specific antiserum (rabbit anti-P-11; Cat. No. 20-PR20; Fitzgerald Industries International, Inc.), the

Table 1. Female common minke whales classified into reproductive groups (I, II, and III) by the specific serum progesterone (P) distribution.

Group P limits (nmol·L ⁻¹)	<i>n</i>	Serum P (nmol·L ⁻¹)		Length (m)	
		Mean (SE)	Range	Mean (SE)	Range
I: P ≤ 2.5	58	0.49 (0.04)	0.05–2.23	6.64 (0.10)	4.85–8.00
II: 2.5 < P < 6.0	6	4.30 (0.56)	2.83–5.69	6.82 (0.30)	5.55–7.45
III: P ≥ 6.0	40	44.23(2.84)	6.71–90.85	7.90 (0.07) ^a	6.70–9.00

Note: The number (*n*) in each group and mean (SE) and range of serum P values and body length are given. All P-value means in groups are significantly different ($p < 0.0001$) from each other.

^aSignificantly different ($p < 0.001$) from the mean value just above.

chromatography steps could be omitted. The antiserum used had a cross-reactivity of <1.0% for 17-hydroxyprogesterone, <1.0% for pregnenolone, <1.0% for cortisol, <1.0% for 11-deoxycorticosterone, and 0.0% for androstenedione. After addition of an internal tritiated P standard to each of the 0.5-mL serum samples, they were extracted in eight volumes of petroleum ether (boiling range 40–80 °C) (Merck). Mean intra- and inter-assay imprecision (coefficient of variation) was 7% ($n = 8$) and 10% ($n = 11$), respectively, for a serum control sample with a P concentration of 4.8 nmol·L⁻¹. The detection limit of the assay was 0.03 nmol·L⁻¹. Results were corrected by the recovery of the internal standard, which averaged 85%. Conversion factors for the hormones from SI units to conventional (older) units are as follows: T, nmol·L⁻¹ × 0.288 = ng·mL⁻¹; P, nmol·L⁻¹ × 0.315 = ng·mL⁻¹.

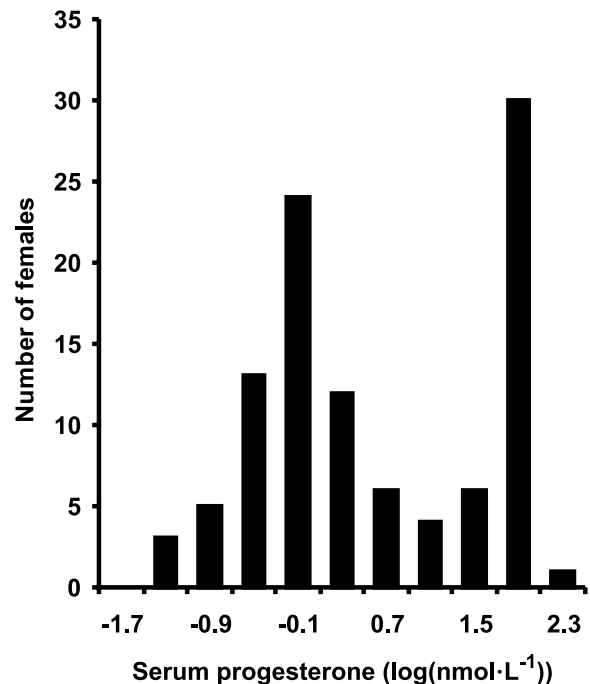
Gross anatomical studies

Before the hormonal measurements, the reproductive status of the females (immature, mature resting, pregnant, ovulating) was evaluated by studying the anatomy of the internal sex organs. In 96 of the 104 females, this was accomplished by looking for a fetus or either corpora lutea or corpora albicantia or both in the ovaries and by an examination of the uterine cornua width. Based on a previous study (Christensen 1981) of body length related to anatomic measures of the genital organs of both sexes of the whales, their reproductive status could also be estimated. This study showed that 50% of the females and males were sexually mature when they had reached a length of 7.15 and 6.75 m, respectively, and that approximately 70% of either sex became mature within a body length interval ranging 0.35 m above and below the respective means cited above (Christensen 1981). Here, this is used as an indicator of sexual maturity in the males, separating the mature from the immature bulls.

Statistics

A *t* test was used to compare groups by their means. An association between variables was assessed by the Pearson or Kendall correlation. Linear regression analysis was used to estimate the geometric mean serum hormone values as dependent on the time of hunting season. Means are presented with their standard error if used for comparison. For description of the data, the number of observations, ranges, means, and standard deviations are presented. The level of significance was set at 0.05. For the figures included herein, the log₁₀-transformed concentrations of serum P and T are given because the hormone levels had a near-normal distribution

Fig. 1. Frequency distribution of log₁₀-transformed serum progesterone (P) concentrations of 104 female common minke whales. Two clusters of values are clearly seen, one with a peak between log₁₀ P = -0.5 and -0.1 (0.32 and 0.79 nmol·L⁻¹) and the second between log₁₀ P = 1.5 and 1.9 (31.6 and 79.4 nmol·L⁻¹), i.e., about two orders of magnitude apart. The numbers on the horizontal axis refer to the right end of the respective intervals (bins), each 0.4 in width.



after being transformed to logarithmic values (Armitage and Berry 1987).

Results

The mean (SD) length of all of the animals ($n = 187$) was 7.26 (0.92) m (range 4.82–9.0 m) with no significant difference between sexes or between the five different hunting regions. Only 10 females and eight males were <6 m in body length. There was no significant difference between the log₁₀-transformed means of serum T or P values of comparable reproductive groups of whales from the different regions.

Females

Serum P concentrations were measured in 104 female minke whales. Two clusterings of values can be seen, one

Table 2. Female common minke whales classified into reproductive groups by anatomical indicators.

Reproductive group	<i>n</i>	Serum P (nmol·L ⁻¹)		Length (m)	
		Mean (SE)	Range	Mean (SE)	Range
Immature	51	1.62 (0.83)	0.05–43.9	6.56 (0.09)	4.85–7.65
Resting	2	0.32 (0.10)	0.22–0.41	7.34 (0.12)	7.22–7.46
Ovulating	9	18.6 (7.4) ^a	0.22–52.2	7.79 (0.07) ^b	7.48–8.10
Pregnant	34	44.0 (3.5) ^a	2.83–90.6	7.92 (0.08) ^b	6.70–9.00

Note: The number (*n*) in each group and mean (SE) and range of serum progesterone (P) values and body length are given.

^aSignificantly different ($p < 0.01$) from the mean value just above.

^bSignificantly different ($p < 0.001$) from the mean length of immature females.

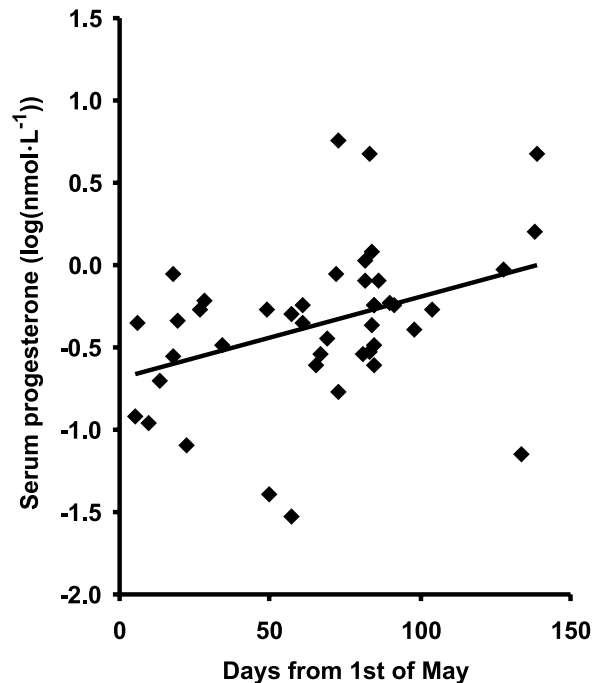
around a concentration of 0.50 nmol·L⁻¹ ($\log_{10} P = -0.3$) and the second around a concentration of 45 nmol·L⁻¹ ($\log_{10} P = 1.65$) (Fig. 1).

For separating the serum P concentrations into groups, the limiting P values (Table 1) were somewhat arbitrarily chosen after visual inspection of the serum P's frequency distribution with different bin ranges (P-value intervals in histograms). The 58 females with P below 2.5 nmol·L⁻¹ ($\log_{10} P = 0.4$) constitute a P-specific population, 84% of which consisted of immature and resting females when classified by anatomical data. The group with the highest serum P values (group III) was given the preliminary lower limit of 6.0 nmol·L⁻¹ ($\log_{10} P = 0.8$). This value was decided on after inspection of its P distribution and the fact that the three lowest fetus-confirmed pregnancies had P levels of 2.8, 6.7, and 9.9 nmol·L⁻¹ and the three highest values without confirmed pregnancy were 4.8, 4.8, and 5.7 nmol·L⁻¹. The P levels of group III had a mean (SD) of 44.2 (18.0) nmol·L⁻¹ (i.e., the 2.5% fractile is 4.1 nmol·L⁻¹, which may be compared with 6.0 nmol·L⁻¹ chosen above), which is almost two orders of magnitude higher than the mean (0.49) for the cluster (group I) with the lowest P values. All females with fetuses, except one, had serum values belonging to group III, which consisted of 40 females, 33 with fetus (83%), four ovulating, one immature, and two undetermined as judged by anatomical data. In between the two groups of high and low P values were six females, referred to as group II, with intermediate serum P concentrations.

The body length of group III had a near-normal frequency distribution (data not shown) with a mean (SE) of 7.90 (0.07) m, which was greater ($p < 0.001$) than that of the intermediary group (group II), which in turn was greater than that of group I (immature plus resting), but not significantly (Table 1).

For comparison, the females were also classified on the basis of the anatomical indicators, dividing the cows into four reproductive groups: sexually immature, mature resting, mature ovulating, and mature pregnant (Table 2). The numbers in the different groups are similar in the two tables, but immature and mature resting animals are put into one group in Table 1 ($P \leq 2.5$ nmol·L⁻¹), as the P levels do not separate them. The anatomical classification shows 51 immature, two resting, nine ovulating, and 34 pregnant cows. Of the 51 immature cows, 47 (92%) had P values below 2.5 nmol·L⁻¹ and 33 (97%) of the 34 pregnant ones had serum P values above 6.0 nmol·L⁻¹. Nine cows, with an average body length of 7.79 m, had an ovarian corpus luteum without a fetus detected in the uterus, i.e., were classified as ovulating females

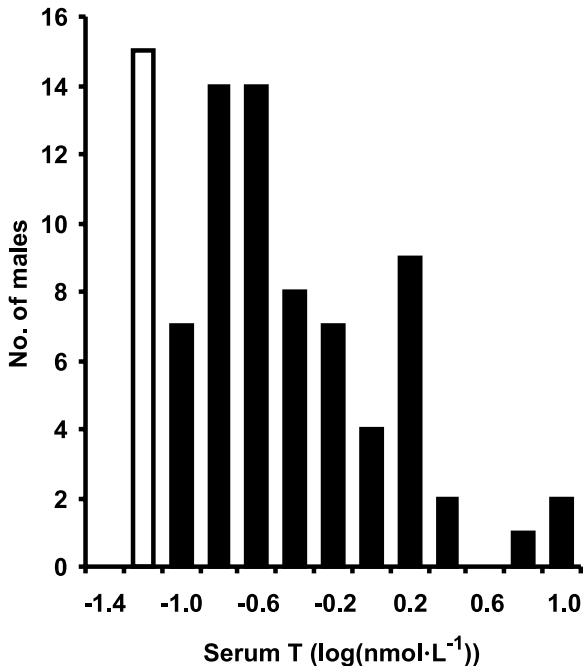
Fig. 2. The \log_{10} -transformed serum progesterone (P) concentrations of 43 female common minke whales, 90% immature by anatomical indicators, all shorter than 7.15 m, plotted against the days of catch of the summer season from 1 May. From the slope of the regression line $\log_{10} P = -0.69 + 0.005$ days ($R^2 = 14\%$, $p = 0.015$), the estimated relative change in the predicted geometric mean of the P values for every 10 days is $10^{0.05} = 1.12$, i.e., a 12% increase (95% confidence interval 2–23%).



by the anatomical data. Four of them had P values consistent with pregnancy levels, i.e., 23.4–52.2 nmol·L⁻¹, but the other five had P concentrations with a range of 0.19–2.19 nmol·L⁻¹. One cow, of 6.7 m with serum P levels of 43.9 nmol·L⁻¹, had been classified as immature by anatomical indicators. There was no anatomical classification for eight cows, which explains the difference of the total numbers of cows in Tables 1 and 2.

The apparent pregnancy rate was 85% when the anatomically mature cows were counted against the ones with serum P values above 6.0 nmol·L⁻¹. The length of fetuses (range 1–150 cm) correlated positively with time of catch during the hunting season ($n = 34$, $R^2 = 41\%$, $p < 0.0001$) but did not correlate with serum P levels.

Fig. 3. Frequency distribution of \log_{10} -transformed serum testosterone (T) concentrations of 83 male common minke whales. The open bar at the left includes the 13 whales at the assay's detection limits. Concentrations were widely scattered with about 80% under $\log_{10} P = 0$, i.e., $P = 1.0 \text{ nmol}\cdot\text{L}^{-1}$. Thirteen individuals had levels at or under the detection limits ($0.05 \text{ nmol}\cdot\text{L}^{-1}$) of the assay and three had levels higher than $5.0 \text{ nmol}\cdot\text{L}^{-1}$. The numbers on the horizontal axis refer to the right end of the respective intervals (bins), each 0.2 in width.

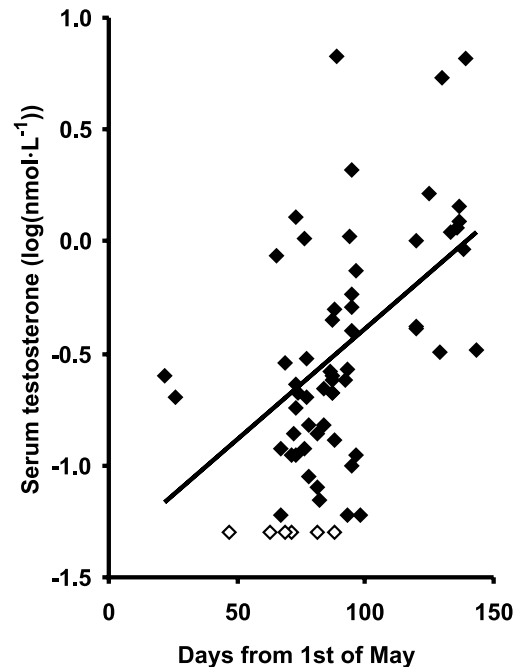


Whereas the serum P levels in group III ($>6.0 \text{ nmol}\cdot\text{L}^{-1}$) did not change significantly with days of catch during the feeding season, the P levels in group I ($<2.5 \text{ nmol}\cdot\text{L}^{-1}$) were found to increase significantly ($p = 0.026$) during the summer months. Females shorter than 7.15 m, 90% of which had been classified as immature by anatomical methods, were therefore studied further in this respect. There was a significant increase in the serum levels with time ($n = 43$, $R^2 = 14\%$, $p = 0.015$) (Fig. 2). The 6.7-m-long female mentioned above with serum P levels of $43.9 \text{ nmol}\cdot\text{L}^{-1}$ was considered pregnant and was not included in this regression analysis.

Males

Thirteen males had T concentrations at or below the detection limits ($0.05 \text{ nmol}\cdot\text{L}^{-1}$) of the assay. Seven of these animals were regarded as immature on the basis of their length ($<6.75 \text{ m}$). The mean (SD) of the serum T values for all of the males measured above the detection limits ($n = 70$) was $0.63 (1.21) \text{ nmol}\cdot\text{L}^{-1}$ (range $0.06\text{--}6.75 \text{ nmol}\cdot\text{L}^{-1}$). Three individuals, two of which were caught in September, had higher levels of serum T than the rest, i. e. 5.6 , 6.6 , and $6.9 \text{ nmol}\cdot\text{L}^{-1}$ (Fig. 3). Serum T values and body length for both immature ($<6.75 \text{ m}$) and mature ($\geq 6.75 \text{ m}$) males (maturity based on body length) did not correlate significantly. Mature males ($n = 58$), however, had higher mean T levels than the immature ones ($n = 12$), i.e., 0.73 and $0.28 \text{ nmol}\cdot\text{L}^{-1}$, respectively, but the means were not significantly different

Fig. 4. The \log_{10} -transformed serum testosterone (T) levels of 58 male common minke whales longer than 6.75 m (sexually mature) plotted against days of catch of the summer season from May 1. From the slope of the regression line $\log_{10} T = -1.39 + 0.010 \text{ days}$ ($R^2 = 26\%$, $p < 0.0001$), the estimated relative change in the predicted geometric mean of the serum T values for every 10 days is $10^{0.1} = 1.26$, i.e., a 26% increase (95% confidence interval 14–40%). Six values, indicated by open diamonds, at (or below) the detection limit of the assay are not included in the regression analysis.



($p = 0.24$) (animals at or below detection limits not included). No correlation between body length and time of the hunting period was found in either group.

For the mature males ($\geq 6.75 \text{ m}$), an increase of mean serum T values was found with days of catch ($p < 0.0001$) during the hunting season (Fig. 4). Six mature bulls, caught in the middle and earlier half of the season, had T values at or below the detection limit ($0.05 \text{ nmol}\cdot\text{L}^{-1}$) of the assay and were excluded from the regression analysis. These six males can be accounted for in this context, giving a total of 64 bulls, by using a nonparametric Kendall correlation to assess the relationship between serum T and the days of the season. By this method, a correlation coefficient of 0.41 ($p < 0.0001$) was obtained. For immature animals ($<6.75 \text{ m}$), no significant increase of T levels with time was found.

Discussion

The average length of the ("adult") Northeast Atlantic common minke whale has been reported to be 7.15 m (Jonsgard 1951), which is similar to the mean length of all of the whales in this study (7.26 m). The whales from the five different locations in our study did not differ in length. Furthermore, comparison of the mean sex hormone concentrations of animals from the different areas showed no significant difference between comparable reproductive groups. Our material is, however, biased, as the whalers tend to take

large animals, and they do not take either calves or cows with calves. The immature animals might, therefore, have a tendency to be near maturity.

One of the interesting results of this study on the common minke whale is the clear rise of serum T levels during the feeding season in the sexually mature males and the weaker, but still significant, rise of serum P levels in the immature females. The female immature group, selected by length (<7.15 m), contained no mature cows as judged by anatomical indicators, but the rising tendency is still there even if the cutoff point is lowered to <6.8 m. These hormonal changes have not been found in the Antarctic minke whale, the species most extensively studied in this respect so far (Yoshioka et al. 1990; Yoshioka and Fujise 1992; Iga et al. 1996). No similar studies have been done before on the common minke whale, but a rise of T levels during the feeding season has been described in the northern fin whale (Kjeld et al. 1992) and sei whale (Kjeld et al. 2003). Three reasons for the above discrepancy seem most likely. Firstly, our serum assays have lower detection limits than those used by the above cited Japanese scientists, three times lower limits for the T assay and five times lower for the P assay. Secondly, the Antarctic minke whale may have lower hormonal levels in its peripheral blood than the common minke whale, thus adding one more characteristic to several already known to differ between the two whale species. The Antarctic whale is, for instance, larger (Lockyer 1999), has a white band on its flippers, and has different genetic constitution (Árnason and Gullberg 1994). Thirdly, and probably most likely, the reason may be a combination of the two factors just mentioned.

Another result of interest is the relatively high serum P levels in the immature and resting females ($0.49 \pm 0.04 \text{ nmol}\cdot\text{L}^{-1}$), which are at least five times higher than those ($\leq 0.1 \text{ nmol}\cdot\text{L}^{-1}$) reported for the fin whale (Kjeld et al. 1992) and sei whale (Kjeld et al. 2003) during the same time of the year and probably higher than the undetectable levels of the Antarctic minke whale (Iga et al. 1996; Suzuki et al. 2001). Higher P levels have, however, been found ($0.96 \text{ nmol}\cdot\text{L}^{-1}$) in the immature group of the Antarctic minke whale (Yoshioka et al. 1990; Yoshioka and Fujise 1992), but, as mentioned above, no changes in levels with time were reported. The P levels in the immature and a few resting common minke whales suggest greater ovarian activity than in the fin and sei whales, which have a 2-year reproductive cycle. Increased P levels with time may indicate a first-time ovulation of prepubertal females with only a small elevation in serum P levels (about $1.6 \text{ nmol}\cdot\text{L}^{-1}$) as seen in suckled beef cows in their first ovulation after giving birth (Perry et al. 1991). More recently, it has become apparent by transrectal ultrasonography that ovarian follicular development in ruminants occurs in wave-like patterns where P levels have a definite modulating role (Adams 1999; Menchaca and Rubianes 2002). Anovulatory follicular waves are found in the prepubertal period as well as in pregnancy and the seasonal anestrus. Furthermore, P itself may have a role in initiating ovulation (Zalányi 2001), as a rise in peripheral P levels precedes the luteinizing hormone surge of ovulation. The small number of resting cows among the female minke whales in this study is in agreement with earlier results (Iga et al. 1996; Suzuki et al. 2001) on the Antarctic minke

whale, further supporting the assumption of mostly yearly reproductive cycles.

Elevated P values were always found when a fetus was present in a female except in one case where the level was $2.9 \text{ nmol}\cdot\text{L}^{-1}$, a level that belongs to the range of the ovulating or intermediary group (group II). The mean P levels for pregnant females found in our study are similar to those reported for the pregnant Antarctic minke whale ($54\text{--}58.2 \text{ nmol}\cdot\text{L}^{-1}$) (Yoshioka et al. 1990; Yoshioka and Fujise 1992) and to those found in pregnant fin whales off Iceland ($50.2 \text{ nmol}\cdot\text{L}^{-1}$) (Kjeld and Árnason 1990; Kjeld et al. 1992). They are, however, about two times higher than those reported for the Antarctic minke whale in more recent papers ($13.7\text{--}21.3 \text{ nmol}\cdot\text{L}^{-1}$) (Iga et al. 1996; Suzuki et al. 2001).

The discrepancies between the high P levels in the pregnancy range and the biological evidence for ovulation without conception in four cases might have been caused by small fetuses that were not detected or that were lost during the handling process. Conversely, the five females with evidence of a corpus luteum but low P levels ($0.22\text{--}2.23 \text{ nmol}\cdot\text{L}^{-1}$) may have ovulated or even aborted at some earlier time, as we do not have any data on the age of the corpora lutea. The question arises whether some non-pregnant ovulating females might have high enough P levels to be included in group III and therefore counted as pregnant. This is unlikely for several reasons. In many terrestrial mammal species (Niswender and Nett 1994), as well as in the captive killer whale (*Orcinus orca*) (Robeck et al. 1993) and bottlenose dolphin (*Tursiops truncatus*) (Kirby 1990), P concentrations are considerably higher in pregnancy than after ovulation. The P distribution curve for group III should, therefore, have shown negative skewness or trailing to the left had there been any number of ovulators with lower levels included. Ovulation of the mating season has not started, as the T levels of the mature males are still rising at the end of the season, but they generally reach a plateau before the mating season starts (Bronson and Heideman 1994). For the closely related fin whale, it has been shown that for the months of June and July, almost all of the corpora lutea found indicated pregnancy (Lockyer and Sigurjónsson 1991). Finally, Mansour et al. (2002) have recently studied postmortem P levels in common minke whales' blubber and found a very decisive difference in levels between pregnant (range $72.5\text{--}1441 \text{ nmol}\cdot\text{g blubber}^{-1}$) and nonpregnant females ($4.5\text{--}10.8 \text{ nmol}\cdot\text{g blubber}^{-1}$). This study does in fact suggest the possibility of correlating sex hormone levels in serum and blubber and then measuring the hormone levels in blubber biopsies of free-ranging whales to predict their reproductive status.

Female whales with P values $>6.0 \text{ nmol}\cdot\text{L}^{-1}$ do clearly belong to a population with high P values, the logarithm of which has a near-normal distribution, almost certainly a group of pregnant animals. When using the anatomical indicators, all females of 7.7 m body length or longer were sexually mature. About 42% of those between 7.3 and 7.7 m were mature. The length at which 50% of female common minke whales are sexually mature was estimated to be 7.50 m for minke whales off West Greenland during 1979–1981 (Larsen 1984) and 7.15 m for minke whales in the Barents Sea during 1972–1977 (Christensen 1981). These

estimates could vary with time and location, but our results seem to fall between the two cited above. A pregnancy rate of 85% was found when anatomical data were used to discriminate between sexually mature and immature animals and the P assay to decide on pregnancy. If only anatomical data were used, the rate would be 79%. Our results are similar to those of Larsen (1984) of 89%, but Christensen (1981) reported a 99% pregnancy rate, which would agree more with the longest animals in the present study. For the Antarctic minke whale, Yoshioka et al. (1990) found a rate of 95% and Kato (1982) reported an average rate of 89%. The pregnancy rates of mature female minke whales, therefore, seem higher than those of the fin whales, in which a larger percentage of nonpregnant mature females are found (Kjeld et al. 1992). This again is presumably related to the shorter 1-year reproductive cycle of the minke whale (Kato 1982; Horwood 1990) compared with the 2-year cycle of the fin whale (Lockyer 1984).

The serum T concentrations of the males were widely scattered. The mean overall T level ($0.63 \text{ nmol}\cdot\text{L}^{-1}$) was lower than that of the fin whale (Kjeld et al. 1992) and sei whale (Kjeld et al. 2003) off Iceland but evidently higher than the levels of the Antarctic minke whale (Yoshioka and Fujise 1992; Fukui et al. 1996; Suzuki et al. 2001) in which 40–100% of the T levels were reported undetectable during the months of December–March. Mogoe et al. (2000) even found a decrease in the weight of the testes in the Antarctic minke whale during the December–February period.

Mean serum T values in the mature males doubled each month and should be about $11 \text{ nmol}\cdot\text{L}^{-1}$ at the end of December. At that time, serum T levels should be much more clearly separated in mature versus immature males than has been found in this study. Days of peak conception for whales have been found by regression of the lengths of fetuses with time and its extrapolation backwards. For the common minke whale, February has been predicted to be the month of peak conception (Lockyer 1984). Present T values would seem to agree with that mating time. Thus, in captive bottlenose dolphins (Schroeder and Keller 1989) and seasonally breeding terrestrial herbivores (Bronson and Heideman 1994), serum T concentrations generally reach a peak or an elevated plateau before the rutting period starts and then the levels begin to fall during the rut. For fin and sei whales, the peak of conception has been estimated to occur a month or two earlier than for the common minke whale (Lockyer 1999).

It is concluded that sex hormone measurements are a valuable tool for studying reproductive aspects of baleen whales, and, contrary to earlier reports on the Antarctic minke whale, serum T and P levels in common minke whales do have changes during the feeding season in males and females, respectively. These changes and the increased ovarian activity indicated by comparatively high serum P levels in immature and a few nonpregnant mature cows would support the notion that the common minke whale has a predominantly annual reproductive cycle.

Acknowledgements

We wish to thank K. Loftsson for his encouragement and enthusiasm. The technical help of A. Theódórsdóttir is much

appreciated. A grant from the Icelandic Research Council is acknowledged. The minke whale samples were collected during the Norwegian Marine Mammal Research Program (1988–1994) and its contributors and participants are acknowledged for making the serum samples available to us.

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