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ORIGINAL ARTICLE

Biology

Comparison of progesterone concentrations in blubber and plasma among female Antarctic minke whales of known reproductive status

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Abstract

The utility of progesterone concentration in blubber as a means of determining reproductive status in the Antarctic minke whale *Balaenoptera bonaerensis* was assessed through a comparative analysis of progesterone concentration in blubber and plasma among 230 female whales of known reproductive status (immature, resting, ovulating or pregnant). Whales were sampled during the austral summer in the Antarctic Ocean. The general pattern of progesterone concentration by reproductive category was well correlated between blubber and plasma samples, validating in principle the use of progesterone concentrations in blubber to determine the reproductive status of females. However, some differences were found for resting and ovulating females, which require further consideration. For blubber, overlap of progesterone concentrations was observed between reproductive categories with the exception of immature/ovulating and immature/pregnant. This result suggests that the method of using progesterone concentration in blubber cannot distinguish between pregnant and non-pregnant mature females. However, it can be used to distinguish between immature and mature females. Although a low overlap ratio in concentration was found between immature and resting females, the method is still useful for determining sexual maturity, because resting females of the Antarctic minke whale are seldom found in the Antarctic Ocean.

Keywords Antarctic minke whale · Progesterone · Reproduction · Blubber · Plasma

Introduction

The Antarctic minke whale *Balaenoptera bonaerensis* is one of the smallest baleen whales, with maximum body length rarely exceeding 10.0 m. This species is believed to migrate seasonally between summer feeding grounds in the Antarctic Ocean and winter breeding grounds in tropical and warm temperate waters (Kasamatsu et al. 1995).

Information on reproductive status is needed to understand the life history and population dynamics of the species. For example, reproductive data were incorporated into a statistical catch-at-age analysis (SCAA) to investigate age-specific natural mortality rate and historical trends among populations of Antarctic minke whales in the Indo-Pacific sector of the Antarctic (Punt et al. 2014). Traditionally, the reproductive status of Antarctic minke whales has been determined by examining internal organs including testes and ovaries (Kato 1982, 1987).

Progesterone is a sex hormone produced by corpora lutea in the ovary following ovulation, and is required for the establishment and maintenance of pregnancy in mammalian species (Stouffer and Hennebold 2015). Some studies suggest that elevated concentrations of progesterone in serum can be indicative of ovulation and pregnancy in captive bottlenose dolphins *Tursiops truncatus* (O'Brien and Robeck 2012) and killer whales *Orcinus orca* (Robeck et al. 2016).

Other studies have used progesterone concentration as an indicator of reproductive status in caught whales. Yoshioka and Fujise (1992) reported that the progesterone levels in serum of immature and resting females without a corpus luteum in the ovaries were clearly lower than those of ovulating and pregnant females in the Antarctic minke whale. Progesterone concentrations in serum of North Atlantic sei

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whales *B. borealis* clustered mainly into two groups. The first group, composed of immature and resting females, presented concentrations at or below the detection limit, while the second group, composed of pregnant females, presented values about two orders of magnitude higher (Kjeld et al. 2003). In North Atlantic fin whales *B. physalus*, the concentration of progesterone in serum was significantly higher in pregnant than in immature females (Kjeld et al. 2006).

Some studies took advantage of the lipophilic nature of progesterone (Hillbrand and Elsaesser 1983) to investigate the reproductive status of cetaceans based on the concentration of progesterone in blubber. Mansour et al. (2002) showed that the progesterone level in blubber of pregnant females was almost 60 times higher than that of immature common minke *B. acutorostrata* females, from the North Atlantic. Kellar et al. (2006) reported that the progesterone levels in blubber of pregnant females were clearly higher than those of non-pregnant mature and immature females, regardless of fetal length, in short-beaked common dolphins *Delphinus delphis*, northern right-whale dolphins *Lissodelphis borealis* and Pacific white-sided dolphins *Lagenorhynchus obliquidens* from fishery bycatches in California, USA. Mingramm et al. (2019) reported that the progesterone levels in blubber of pregnant females were clearly higher than in immature and non-pregnant mature in captive bottlenose dolphins *Tursiops* spp. These results suggest that progesterone levels in blubber can distinguish pregnancy status, although they could not estimate pregnancy stage. Blubber samples from whales can be obtained by biopsy sampling and therefore measuring the level of progesterone in blubber has the potential to investigate the reproductive status in free-ranging cetacean species. For example, Pallin et al. (2018) used blubber biopsy samples for assigning pregnancy in humpback whales *Megaptera novaeangliae*. It is expected that the application and development of such non-lethal methods will increase in the future.

To further evaluate the utility of progesterone concentration in blubber for determining reproductive status in the Antarctic minke whale, a comparative analysis of progesterone concentrations in blubber and plasma among female Antarctic minke whales of known reproductive status was carried out. Reproductive status of the whales investigated for progesterone was determined by direct observation of reproductive organs. Previous studies showed that progesterone concentration in plasma is a reliable estimator of reproductive status, and thus concentrations in plasma can assist in the interpretation of the concentration of progesterone in blubber. The study made use of a substantial number of biological samples and data available from caught Antarctic minke whales in the Antarctic Ocean. Blubber samples from these whales were used as a proxy for biopsy samples.

Materials and methods

Whale sampling

Antarctic minke whales used in the present study were caught between December 2015 and February 2016 during surveys of the New Scientific Whale Research Program in the Antarctic Ocean (NEWREP-A) in the Pacific sector of the Antarctic Ocean, which corresponded to the International Whaling Commission's (IWC) management Area V (130°E–170°W), south of 60°S. Whales were sampled randomly from a predetermined zigzag track line designed to cover the entire research area (Fig. 1). A total of 333 Antarctic minke whales (103 males and 230 females) were randomly sampled during the survey. All sampled females ($n = 230$) were used in the present study. The NEWREP-A program was conducted under a permit issued by the Government of Japan.

Reproductive information

In the field, information was obtained on body length, occurrence and number of corpora lutea and corpora albicantia in ovaries and the presence of a fetus. Body length of the whales, in units of 0.01 m, was measured from a straight

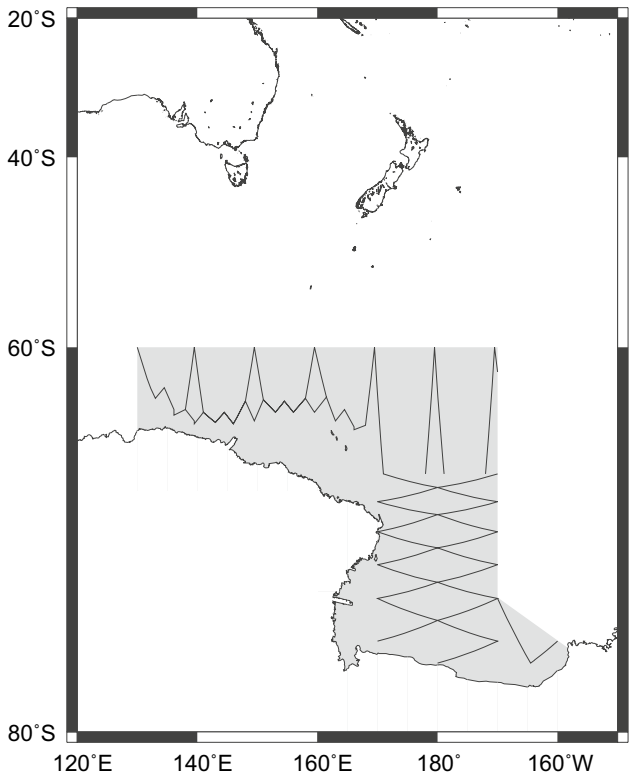

Fig. 1 Research area (gray shaded area) and survey track lines (thick lines) used for random sampling of the Antarctic minke whales used in this study

line from the tip of the upper jaw to the notch of the fluke by researchers on board the research base ship.

Reproductive status of the caught whales was determined by direct examination of reproductive organs (Lockyer 1984, 1987). The sexual maturity of females was determined by the presence of at least one corpus luteum or corpus albicans in either ovary. In the cases where no corpus luteum and no corpus albicans was observed, the female was categorized as immature. Reproductive status of mature female whales was classified into three categories (resting, ovulating and pregnant), based upon observation of the ovary and uterus. Classification of females according to their reproductive status was as follows:

Immature no corpus luteum and no corpus albicans in either ovary;

Resting no corpus luteum, one or more corpus albicans present;

Ovulating one or more corpus luteum present, corpus albicans may or may not be present, no fetus in uterus;

Pregnant corpus luteum present, corpus albicans may or may not be present, fetus present in uterus.

There were two individuals with milk in the mammary glands. These individuals were classified into the 'lactating' category according to Lockyer (1984, 1987). These two whales were also pregnant and therefore were included in the category 'pregnant' for the statistical analyses.

Tissue sampling

For the purpose of the progesterone analysis, blubber samples were obtained from each whale by researchers on board the research base ship. The blubber samples were collected from the lateral side of the whale and were immediately stored at −20 °C until analysis at the laboratory.

Progesterone is transported to different tissues, including blubber, through the blood. Most of the previous studies on progesterone in cetaceans have been based on serum samples, and as a consequence, there is more information on the behavior of progesterone in blood. In this study, plasma samples were also obtained and examined for progesterone to assist the interpretation of the progesterone concentration in blubber. This was important for validating the use of progesterone concentration in blubber as an index of reproductive status. To this end, blood samples were collected from the same individuals sampled for blubber. This was done from the flukes of the whales into tubes containing EDTA-2Na (Terumo, Japan). The plasma was obtained after centrifugation of the blood at 3000 rpm for 10 min. Plasma samples were stored at −80 °C until analysis in the laboratory. All samples were collected within five hours post-mortem.

Extraction and measurement of progesterone

The extraction of progesterone in blubber was performed following the procedures described by Kellar et al. (2013) with slight modification. Approximately 0.25 g of blubber was homogenized in 1 ml of ethanol; the homogenates were centrifuged, and the supernatants were then collected. The supernatants were extracted with 2 ml of ethanol: acetone (4:1) and 2 ml of diethyl ether, respectively. One milliliter of acetonitrile and 1 ml of hexane were mixed with the residues, and the resulting acetonitrile layers were collected. The extracts were washed with 1 ml of hexane in duplicate for de-lipidation, and the acetonitrile layers were then evaporated at 40 °C. The resulting residue containing the progesterone was stored at −20 °C until analysis.

Progesterone in plasma (0.2 ml) was extracted with 1 ml of diethyl ether twice, and the supernatant was then evaporated at 40 °C. The resulting residues containing the progesterone were stored at −20 °C until analysis.

Progesterone concentrations were determined by a commercially available enzyme-linked immunosorbent assay (ELISA) kit, Progesterone ELISA Kit No. 582601 (Cayman Chemical Company, USA) using the Crocodile Mini Workstation (Titertek Berthold, Germany). The manufacturer-reported intra-assay coefficient of variation (CV) ranged from 4.9 to 54.5%, and inter-assay CV ranged from 1.5 to 16.4%, with a standard curve ranging between 7.8 and 1000 pg/ml. When necessary, extracted samples were diluted with a buffer. All samples were processed and quantified in triplicate. Based on the kit specifications, the assay allowed for a lower limit of quantitation of 0.2 ng/g in blubber and 0.07 ng/ml in plasma. Half of these values were used for cases below the detection limit for statistical analysis.

Analytical procedures

Concentrations of progesterone in blubber and plasma were compared among the reproductive categories determined by direct examination of reproductive organs. Descriptive statistics included the median values. Since most of the data used in this study presented a non-normal distribution, non-parametric tests were performed. The concentrations of progesterone among reproductive categories were first analyzed by the Kruskal–Wallis test. Pairwise comparisons between reproductive categories were then performed by the Steel–Dwass post hoc test for multiple comparisons. Additionally, the correlation of concentrations of progesterone in blubber and plasma was investigated using Spearman's rank correlation coefficient. All differences with $p < 0.05$ were considered statistically significant.

Table 1 Reproductive categories of female Antarctic minke whales used in the present study

	Immature	Mature		
		Resting	Ovulating	Pregnant
Body length (m)				
Mean	7.03	8.70	8.94	8.78
Range	5.17–8.51	7.65–9.32	8.45–9.40	7.71–10.06
Ovary				
Total CL[a]				
Mean	0	0	1	1
Range	0	0	1–1	1–2
Total CA[b]				
Mean	0	18	16	13
Range	0	1–44	0–45	0–40
N[c]				
Blubber	56	11	6	157
Plasma	42	10	4	140

[a]Total number of corpora lutea in ovaries

[b]Total number of corpora albicantia in ovaries

[c]The total number of samples examined for blubber and plasma was 230 and 196, respectively

Results

Classification of whales by reproductive categories

Table 1 shows the results of the direct examination of reproductive organs to determine reproductive categories in the female samples. Among the total 230 samples, 76% were mature females, and 90% of the mature females were pregnant. Sampling of blood was not possible for a number of whales. This explains the difference in sample sizes between blubber and plasma samples.

Comparison of progesterone concentrations among reproductive categories

Figure 2a shows the median of progesterone concentration in blubber by reproductive category. The median and range in immature, resting, ovulating and pregnant females were < 0.2 ng/g (range < 0.2–2.6 ng/g), 15 ng/g (range < 0.2–34 ng/g), 26 ng/g (range 24–150 ng/g) and 72 ng/g (range 13–740 ng/g), respectively. About 73% of the immature animals were below the detection limit of the assay (0.2 ng/g). The pregnant females had the highest median value and the immature females the lowest. Significant statistical differences were found between the immature category and each of the mature categories. No significant statistical differences were found between

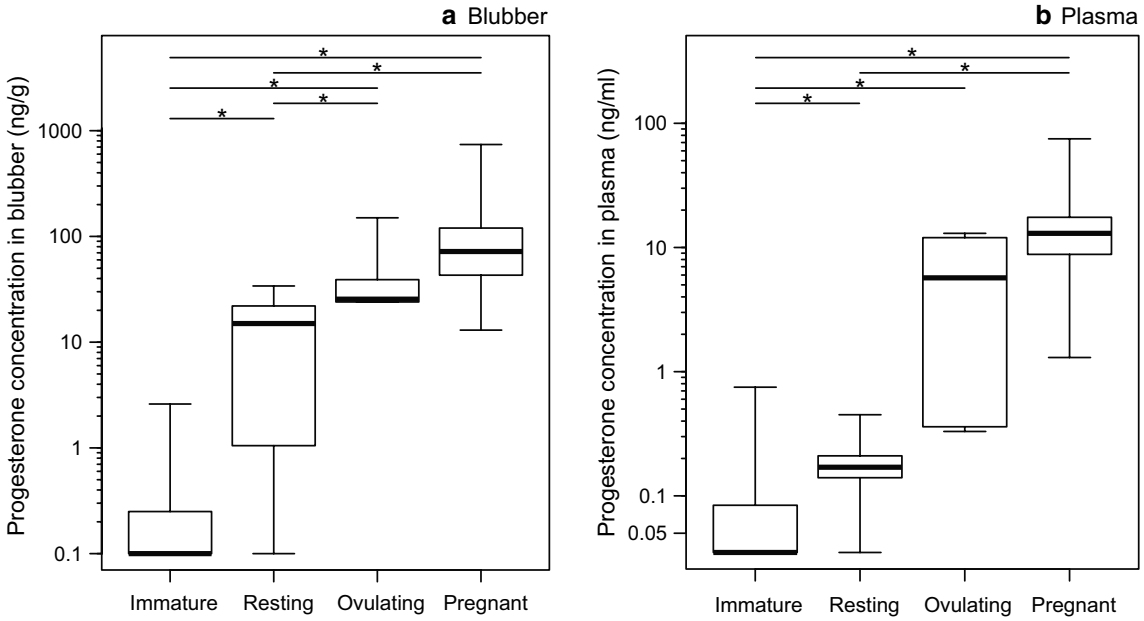

Fig. 2 Relationship between progesterone concentrations and reproductive categories in the Antarctic minke whales for both blubber and plasma samples. Boxes represent upper and lower quartiles, and the inside band represents the median. Whisker lines indicate minimum and maximum concentrations in each reproductive category. Horizontal bars at the top show the results of statistical tests of pairwise comparisons (*$p < 0.05$)

ovulating and pregnant categories. Overlap of progesterone concentrations was observed between categories, with the exception of immature/ovulating and immature/pregnant.

Figure 2b shows the median of progesterone concentration in plasma by reproductive category. The median and range in immature, resting, ovulating and pregnant females were < 0.07 ng/ml (range < 0.07–0.75 ng/ml), 0.17 ng/ml (range < 0.07–0.45 ng/ml), 5.7 ng/ml (range 0.33–13 ng/ml) and 13 ng/ml (range 1.3–75 ng/ml), respectively. Levels in about 69% of the immature animals were below the detection limit of the assay (0.07 ng/ml). As in the case of blubber, the pregnant females had the highest median value and immature females the lowest. Significant statistical differences were found between the immature category and each of the mature categories. No significant statistical differences were found between resting/ovulating and between ovulating/pregnant categories. Overlap of progesterone concentrations was observed between reproductive categories, with the exception of immature/pregnant and resting/pregnant.

Figure 3 shows the correlation of progesterone concentrations between individual blubber and plasma samples. The correlation was significant ($r = 0.69$). While the same pattern was found for the samples from immature and pregnant females, some differences between blubber and plasma were observed in the resting and ovulating female samples. All plasma samples from resting females had low progesterone concentrations; in some of these the concentrations were high in blubber. All blubber samples from ovulating females had high concentrations; in some of these the concentrations were low in plasma.

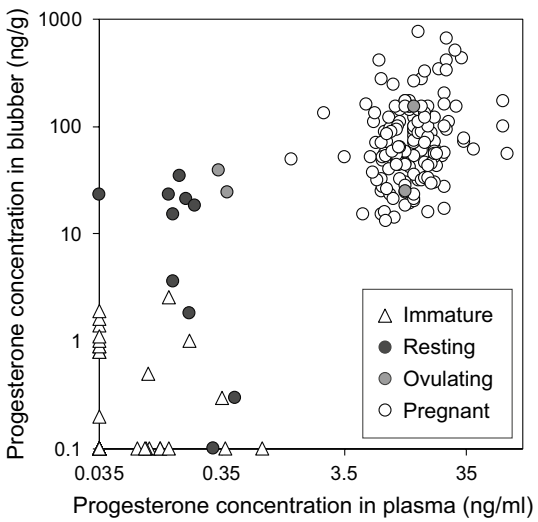

Fig. 3 Correlation of progesterone concentration between individual blubber and plasma samples of female Antarctic minke whales

Discussion

General aspects

Reproductive information on the whales examined for progesterone concentrations was based on direct observation of reproductive organs and was considered of high quality. This aspect assisted the interpretation of progesterone concentration values in blubber and plasma samples, in the context of reproductive status of Antarctic minke whale females. Another general aspect was that, unlike previous studies on whales based on blubber (Mansour et al. 2002; Kellar et al. 2006), the present study on Antarctic minke whales had the opportunity to examine resting and ovulating animals. This aspect enabled the investigation of the feasibility of using progesterone concentration in blubber to determine the reproductive status of non-pregnant mature whales. The average and range of progesterone levels in blubber of all reproductive categories of Antarctic minke whale were comparable to those of the North Atlantic common minke whale (Mansour et al. 2002). These values were somewhat lower than those in the short-beaked common dolphin, northern right-whale dolphin and Pacific white-sided dolphin (Kellar et al. 2006), but much higher than those in bottlenose dolphins (Mingramm et al. 2019). However, in the case of non-pregnant mature females, the Antarctic minke whales showed a wider range and higher concentrations than other species studied previously (Table 2).

Comparison of progesterone concentrations in blubber and plasma

The correlation of progesterone concentration between blubber and plasma was statistically significant. The median of progesterone concentration showed the same pattern in blubber and plasma samples, with the lowest concentrations in immature and the highest concentration in pregnant females. Concentrations in resting and ovulating females presented intermediate values. These concordant patterns between the two kinds of samples validated in principle the use of progesterone concentration in blubber for determining the reproductive status of Antarctic minke whale females. The results showing a positive correlation between plasma and blubber were in agreement with those of previous studies in the bowhead whale *Balaena mysticetus* (Kellar et al. 2013) and bottlenose dolphin (Mingramm et al. 2019).

However, some differences between blubber and plasma samples were observed in the pattern of progesterone concentrations in ovulating and resting females (Fig. 2). In

Table 2 Concentrations of progesterone (ng/g) in blubber of females of several species of cetacean, by each reproductive status category

Reproductive status	Species	Antarctic minke whale	Common minke whale[a]	Short-beaked common dolphin[b]	Northern right-whale dolphin[b]	Pacific white-sided dolphin[b]	Bottlenose dolphin[c]
	(Sampling area)	(Antarctic)	(North Atlantic)	(California)	(California)	(California)	(Captive animal)
Immature	Mean ± SD	0.36 ± 0.54	1.95 ± 0.32	16.5 ± 2.7	14.2 ± 2.30	18.1 ± 9.1	0.83 ± 0.11
	Range	< 0.2–2.6	1.36–3.43	0.92–48.2	0.98–33.1	0.11–34.4	
	N	56	6	36	18	4	1 (twice)
Non-pregnant mature	Mean ± SD	25 ± 34		13.7 ± 1.8	15.0 ± 7.5	12.1 ± 8.4	1.20 ± 0.06
	Range	< 0.2–150		6.75–33.3	2.11–34.7	3.75–20.5	
	N	17[d]		19	6	2	3[e]
Pregnant	Mean ± SD	105 ± 110	132.96 ± 22.46	261 ± 29	312 ± 44	161	13.01 ± 0.72
	Range	13–740	22.84–453.49	132–415	196–402		
	N	157	22	18	5	1	2

[a]After Mansour et al. (2002); [b]after Kellar et al. (2006); [c]after Mingramm et al. (2019)

[d]Resting and ovulating females were combined in the present study

[e]Females during the estrous cycle

particular, the pattern of median values, the upper and lower quartiles and the range of concentrations of resting females were very different between blubber and plasma. For ovulating females, while the pattern of the median was similar, the pattern of the upper and lower quartiles and the range of concentrations differed between blubber and plasma. These differences are more clearly visualized in Fig. 3, which shows the correlation of progesterone concentration in blubber and plasma. Two ovulating females showed low concentrations in plasma but a high concentration in blubber. This is different from the case of the bottlenose dolphin, where the pattern of progesterone concentrations in ovulating females was similar for plasma and blubber samples, i.e. the concentrations in all ovulating females were clearly lower than those in pregnant females (Mingramm et al. 2019). The ovulation status was determined by direct observation of ovaries and uterus in the Antarctic minke whale while it was determined by indirect observations in the bottlenose dolphin. In the case of the Antarctic minke whale, if mature females fail to become pregnant, progesterone levels in blood will decrease even with the presence of corpora lutea. This could explain the result of low progesterone concentration in the plasma of two ovulating females.

On the other hand, all resting females showed low concentrations in plasma, while some of them presented high concentrations in blubber. Resting females have no secretion of progesterone from a corpus luteum. However, in the present study, a few resting females had high progesterone concentrations in blubber. It is considered that the changes in progesterone concentration in tissues where it is distributed through blood (including blubber) could occur at a slower rate than changes in progesterone concentration in blood. This is because the concentration of progesterone in blood decreases rapidly in the absence of pregnancy in terrestrial mammals (Zeleznik and Plant 2015). Additional studies are needed to further elucidate the reasons for the different patterns of progesterone concentration in some individuals between plasma and blubber samples.

Potential utility of progesterone concentration in blubber as a non-lethal method

Progesterone analysis in blubber samples is of particular importance, as blubber can be obtained by non-lethal methods (biopsy sampling), representing a potential non-lethal approach for determining the reproductive status of female Antarctic minke whales. For the blubber analysis, overlap of progesterone concentrations was observed between reproductive categories, with the exception of immature/ovulating and immature/pregnant. This result suggests that the method using progesterone concentration in blubber cannot distinguish between pregnant and non-pregnant mature females; however, it can be used to distinguish between immature and mature females, excepting for resting, due to a low overlap ratio in concentrations between immature and resting females (Fig. 2a). This overlap was seen for just a few resting animals with progesterone concentrations in blubber within the range of that for immature females, corresponding to only approximately 2% of all animals used in this study.

In summary, the potential usefulness of progesterone concentration in blubber for determining the reproductive status of female Antarctic minke whales was ascertained by a positive correlation between progesterone concentration in blubber and plasma. Progesterone concentration in blubber could not distinguish between pregnant and non-pregnant mature

females, including resting and ovulating, because of overlap in concentration values among mature categories. However, it can be used to distinguish between immature and mature females. Although a low overlap ratio in concentration was found between immature and resting females, the method is still useful for determining sexual maturity, because resting females of the Antarctic minke whale are seldom found in the Antarctic Ocean. As blubber can be obtained by biopsy sampling, the progesterone analyses of blubber is a promising non-lethal candidate procedure for determining sexual maturity in free-ranging Antarctic minke whales.

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