Sexual maturation in male bowhead whales (*Balaena mysticetus*) of the Bering-Chukchi-Beaufort Seas stock

T.M. O'Hara*, J.C. George*, R.J. Tarpley+, K. Burek# and R.S. Suydam*

Contact e-mail: todd.ohara@north-slope.org

ABSTRACT

Since the mid-1970s, study has focused on reproductive biology of female bowhead whales, while little has been described for males. This study evaluates testicular morphology (mass and length) and histology in relation to body length to determine the onset of male sexual maturity. Mean testis mass and mean testis length were highly correlated. Body length and mean testis mass were significantly correlated and an inflection of increased testicular mass occurred at approximately 12.5-13.0m suggesting the onset of puberty, and also indicated by histologic findings. Biological variability and the fact that few male animals have been examined within this critical length cohort do not allow determination of the onset of maturity with higher precision. Too few mature males have been landed in spring to make statistical comparisons of testes mass with autumn-landed animals within specific size cohorts. Two large (15.7m and 17.7m) males landed in spring had relatively small inactive testes and were diagnosed as pseudohermaphrodites; body length and mean testis length and seminiferous tubule diameter (STD) were not correlated with the other 'normal' whales. The smallest male confirmed as mature based on the presence of spermatocytes was 12.7m. The largest testes measured (combined mass 203kg) were from a whale landed in autumn. Mean STD for individual whales ranged from 33.3-170.9µ and increased with mean testis weight and whale length. The STD is similar within a testis regardless of region evaluated, with minor variability. Some variation was noted for transverse sections within a cross section for some whales but no pattern was evident.

KEYWORDS: AGE AT SEXUAL MATURITY; ARCTIC; BOWHEAD WHALE; MALE; REPRODUCTION

INTRODUCTION

More effort has been focused on the reproductive biology of female rather than male bowhead whales, *Balaena mysticetus*, of the Bering-Chukchi-Beaufort (BCB) Seas stock (Nerini *et al.*, 1984; Koski *et al.*, 1993; Tarpley *et al.*, 1999a; b; c). Little has been published on male reproduction (Kenny *et al.*, 1981; Medway, 1981; Koski *et al.*, 1993; Tarpley *et al.*, 1995), primarily because an understanding of the reproduction of females is more central to the modelling of populations in the context of various management strategies. However information on male reproduction and breeding behaviour (e.g. seasonality) can improve the models used in management and can provide valuable additional information on the general health of populations (e.g. in the context of *Implementation Reviews* – see IWC, In press). The present study presents information on: testicular morphology; histological evidence of sexual maturation in relation to body length (as a proxy for age); and further description of testis appearance in two animals that were deemed pseudohermaphrodites as previously described by Tarpley *et al.* (1995).

Confirmation of male sexual maturation requires determining the presence of spermatozoa either through seminal smears from fresh epididymides or histological examination of testis and epididymis tissue. When these data are collected in concert with data on testis size (length, width, depth and/or mass) for a large number of animals, it may become possible to predict whether animals are mature or immature from the size of testes alone. Testes of intermediate size will still need to be examined histologically to determine whether an animal is pubertal, or mature with recrudescent testes outside the breeding season (if seasonality occurs). In a synthesis of the existing bowhead whale literature, Koski *et al.* (1993) reported 13.0-13.5m as a mean length at sexual maturity for females and 12.0-13.0m for males, based primarily on males having a smaller body length at physical maturity. This study presents additional information on morphometrics of bowhead whales (i.e. standard length) and of their testes (length and mass); and histological indicators of sexual maturity (presence of sperm and seminiferous tubule diameter between and within testis) to estimate the body length range at sexual maturation.

MATERIALS AND METHODS

Examination and tissue sampling of bowhead whales

A subsistence fishery for bowhead whales is undertaken by Alaskan Eskimos (Inuit) during the spring and autumn migrations. Whales landed at Barrow and occasionally in other villages along the northern coast of Alaska were examined by North Slope Borough (NSB) Department of Wildlife Management (DWM) and/or Alaska Eskimo Whaling Commission (AEWC) personnel. Measurements were taken of standard body length, sex, and up to 43 morphological measurements including testicular mass, greatest testicular circumference, and/or length (pole to pole) for one or both gonads per animal. Where possible, epididymal or testicular fluid was collected. All tissue sections were saved in neutral buffered 10% formalin.

A triple beam balance was used to weigh testis < 3.0kg, a 45.3kg (+/- 0.45kg) spring scale for testis < 40kg, and a 136kg spring scale (+/-2.2kg) for larger testis. A transverse core sample (capsule to centre of cross section) from each pole (anterior and posterior) and mid-section (equatorial) plane (cross section) were taken and fixed in formalin for selected whales (Fig. 1). These three different planes or cross sections were further sub-divided from the capsular surface to the centre along the transverse core (Fig. 1). Transverse cores (or entire cross sections with core removed later) were taken from the posterior and anterior poles, and equatorial

* *Department of Wildlife Management, North Slope Borough, Box 69, Barrow, Alaska, USA.*
+ *Department of Veterinary Anatomy and Public Health, College of Veterinary Medicine, Texas A&M University, College Station, Texas, USA.*
# *Alaska Veterinary Pathology Services, PO Box 773072, Eagle River, Alaska, USA.*

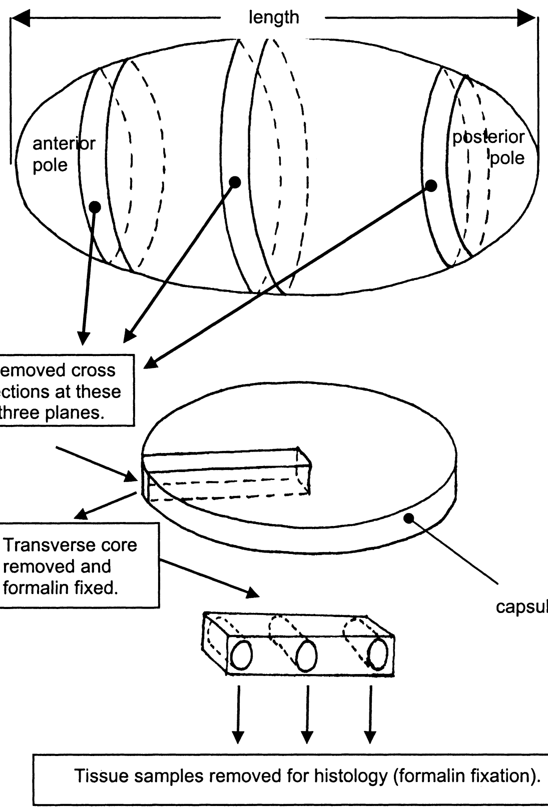

Fig. 1. Diagram of the measuring and sampling sites of a bowhead whale testis.

(mid-section) cross section early in the study (1980-1984) to determine if significant regional differences (between the three planes and within the cross-section or plane) existed. In later samples (1992-1998), only equatorial sections (mid-sections) were taken and sampled near the capsule, in the centre of the cross section, and equidistant between these two landmarks (three tissue samples per testis).

Histological examination

Assessment of maturity

Samples of testicular tissue were trimmed, embedded in paraffin blocks and thin sections were placed on a glass slide and stained with haematoxylin and eosin for microscopic examination following Tarpley *et al.* (1995). Histological examination was similar to that described by Clarke *et al.* (1994) and Tarpley *et al.* (1995) and included: (1) a morphological description; (2) measurement of ten seminiferous tubular cross section diameters (STD) per glass slide or site sampled; and (3) a count of the number of interstitial cells (i.e. Leydig cells) per high dry (40X) field (HDF). For each testis, Clarke (1956) used the mean of 10 tubule diameters; Clarke *et al.* (1994) found no statistical differences between measuring 10 and 20 tubules. For some whales, impression smears and/or wet smears were made from the epididymis and slides were examined under a light microscope (40x). A whale exhibiting 'copious' mature spermatocytes was considered to be sexually mature.

The STD was measured based on the opening in the stroma, as the epithelial cells were often slightly displaced from the supporting stroma and distorted due to processing. Two measurements were taken at right angles to one another across the tubule to determine whether the section was round and therefore a true cross section; only 'round' tubules were measured. Tubules that were closed, with an epithelium with no evidence of mitoses and an approximate tubular diameter of 60μ were considered immature. Tubules that were open with evidence of mitotic activity with a thickened epithelium and a diameter of approximately 130-140μ, were considered mature. Animals with intermediate (approximate diameter 85μ) sized tubules that were open but lacked mitotic activity with a flat epithelium were suspected to be pubertal.

Site of sampling comparison

Formalin-fixed sections of tissue for embedding into paraffin blocks were collected from the transverse core starting inside the capsule (outer connective tissue layer of the testis) and sequentially sampled from this point until reaching the centre of the testis (Fig. 1). These sections were labelled (A, B, C, etc.) sequentially until the centre was reached. For testes collected from 1980-1984, this procedure was conducted for the anterior and posterior poles, and the equatorial cross sections of the testis. For each site sampled (i.e. anterior pole section A) 10 different STDs were measured and the mean STD determined. This was done for 10 male whales landed in the spring, ranging in body length from 7.8-13.6m, and did not include the pseudohermaphrodites. Three different sites of the equatorial (mid-section) plane were examined for samples collected from 1992-1998; the central site, peripheral site and a site equidistant between these two sites (Fig. 1) and a mean STD for that testis is determined from 30 STD measurements (three sites with 10 STD measurements per site).

Statistics

For testes from whales sampled from 1980-1984, each cross section plane (anterior pole, posterior pole or mid-section) had the transverse core sequentially sampled from the periphery (capsule) to the centre and the STD values were compared by ANOVA within each plane (significance determined at a $p < 0.05$). This within-plane comparison was conducted to determine if STD varied significantly by location of the sample (i.e. centre versus closer to capsule) such that sampling site would affect assessment of 'mature' versus 'immature'. The means of STD values within a plane were used to determine an overall mean and SD for each cross section or plane. ANOVA was used to determine if STD differed by plane (anterior pole vs posterior pole vs mid-section) within a testis. For testes for which STD was determined for three cross sections, an overall mean was also calculated. If two testes were assessed for an animal, the average of both testes was calculated to represent the overall animal STD (mean testis STD). Means, SD (standard deviation), ANOVA, Student's *t*-test (Table 1) and figures were derived using *Microsoft Excel 2000* for Windows. Regression analyses were performed on testis morphology using SPSS PC (7.5 for Windows). Models were fitted using the 'curve estimation' function.

RESULTS

Gross morphology

Testes weights were plotted versus whale length (1980-1998 whales) and a steep inflection of increased mean testes mass occurs at 12.5-13.0m body length (Fig. 2). Whale length was linearly related to the *ln* transformed mean testis mass (Table 2). Whale length versus mean testis length was compared using regression analyses with and without the two pseudohermaphrodites and in both cases the relationship was significant and positive. Removing the two male pseudohermaphrodites from the data achieved a better fit (R^2 increased from 0.68 and 0.79, to 0.91 and 0.91 for

Table 1

Mean, standard deviation (SD), and range for body length, mean testis mass and length, and mean seminiferous tubule diameter (STD) for mature and immature (with and without pseudohermaphrodites) whale classes, and mature whale active or inactive spermatogenesis.

Whale class	Whale length (cm)	Mean testis mass (kg)	Mean length of testis (cm)	Mean STD (μ)
All mature				
Mean	1407.6	53.1	92.3	125.8
SD	105.2	28.8	19.2	24.5
No. of whales	18	13	16	15
Range	1270-1660	11.3-101.6	59.0-134	88.0-170.9
All immature*				
Mean	1059.7	4.27	40.4	51.8
SD	245.5	3.32	12.8	9.74
No. of whales	23	9	13	23
Range	760-1770	0.44-9.8	20.4-58	33.3-69.1
All immature except pseudohermaphrodites				
Mean	1000.6	4.27	37.6	51.5
SD	152.7	3.32	11.6	10.1
No. of whales	21	9	11	21
Range	760-1260	0.44-9.8	20.4-58	33.3-69.1
Mature and active				
Mean	1442.5	62.0	101.6	132.5
SD	119.1	25.6	13. 6	25.6
No. of whales	8	7	6	5
Range	1270-1660	20.6-92.1	84-122	102.8-168.8
Mature and inactive				
Mean	1379.6	42.3	86.7	122.5
SD	889.0	30.7	20.4	24.6
No. of whales	10	6	10	10
Range	1290-1528	11.3-101.6	59-134	88.0-170.9
All mature *v.* all immature				
P value**	< 0.0005	< 0.0005	< 0.0005	< 0.0005
Mature-active *v.* mature-inactive				
P value**	0.130	0.124	0.092	0.336

*Includes two pseudohermaphrodites (Tarpley *et al.,* 1995).
** Student's *t*-test.
Note: for mature whales, 'early mature' was diagnosed for four whales. For immature whales, three were classified pubertal. These seven whales have intermediate STDs (mean 85.3μ) and likely represent pubertal whales.

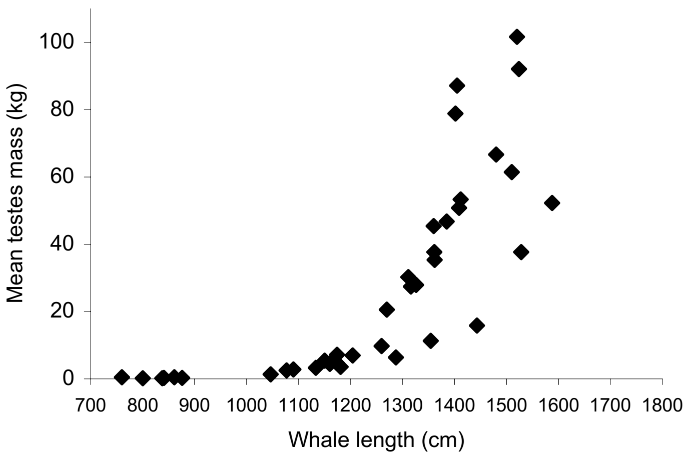

Fig. 2. Mean testis mass (kg) versus whale body length (cm) for select bowhead whales landed in northern Alaska 1980-1998.

non-transformed and *ln* transformed data, respectively) for whale length versus mean testis length (Table 2), and these data are presented in Fig. 3. A strong relationship was found between mean testis mass and mean testis length ($R^2 = 0.89$) and these data are presented in Fig. 4.

Mean testes length increases with body length with a less dramatic inflection (Fig. 3) than seen with mean testis mass, showing more of a linear relationship (Table 2). Two confirmed pseudohermaphrodites fall outside the 'normal' male maturation curve for mean testis length versus body length (Fig. 3); and for mean STD (Fig. 5), as would be expected. Too few mature males have been landed in spring to make statistical comparisons of testicular mass with autumn-landed animals.

Histomorphology

An ANOVA was conducted to determine if a significant difference in STD occurred within each pole and equatorial (mid) cross section for each testis with respect to depth from the capsule along the transverse core sampled. Forty-three separate cross sections (anterior or posterior poles, and equatorial plane) were evaluated in this fashion and 25 cross sections (planes) showed a significant ($p < 0.05$) difference, while 18 did not ($p > 0.05$). However, no pattern was detected and the differences were small in magnitude (approximately 5μ). Ideally, this examination should be conducted on pubertal whale testes.

The average STD for each pole and equatorial cross section was calculated from the averages determined at each depth for testes collected from 1980-1984. An ANOVA compared the means of each pole and equatorial plane for each testis and no significant difference was observed among the two poles and the mid-section for most of the testes evaluated (data not shown). Only two (of 16 tested) testes indicated a regional difference by plane ($P < 0.05$) where the mean STD for one ranged from 36.6-40.1μ, and the other

Table 2

Regression analyses for morphologic measures of testicular mass (kg), length (cm), total whale length (cm), and seminiferous tubule diameters (STD, μ) for male bowhead whales.

Morphology measured	*n*	R^2	*P* value[1] for F statistic	Formula
Testis mass				
Mean testicular mass (x) *v.* mean testicular length	32	0.89	<0.0001	y=27.20+16.91*ln(x)
Whale length (x) *v.* ln mean testis mass [2]	36	0.93	<0.0001	y=-7.75+0.008(x)
Testis length				
Whale length *v.* mean testis length (x) [2]	44	0.68	<0.0001	y=-886.47+133.56*ln(x)
Whale length (x) *v.* ln mean testis length [2]	44	0.79	<0.0001	y=1.243+0.0022(x)
Whale length (x) *v.* mean testis length (w/out pseudos) [3]	42	0.91	<0.0001	$y=4.85*10^{-8}x^{2.93}$
Whale length (x) *v.* ln mean testis length (w/out pseudos) [2,3]	42	0.91	<0.0001	y=0.854+0.0025(x)
Seminiferous tubule diameter (STD)				
Whale length (x) *v.* mean STD	38	0.59	<0.0001	$y=0.00128x^{1.548}$
Mean testis weight (x) *v.* mean STD	17	0.79	<0.0001	y=44.50+21.80*ln(x)
Mean testis length (x) *v.* mean STD	21	0.71	<0.0001	y=-172.65+63.59*ln(x)

[1] *P* value for the ANOVA F-test that coefficient is different from 0.
[2] Data were ln transformed prior to regression analyses.
[3] Pseudohermaphrodites ('pseudos') were determined based on histology and morphology (Tarpley *et al.*, 1995).

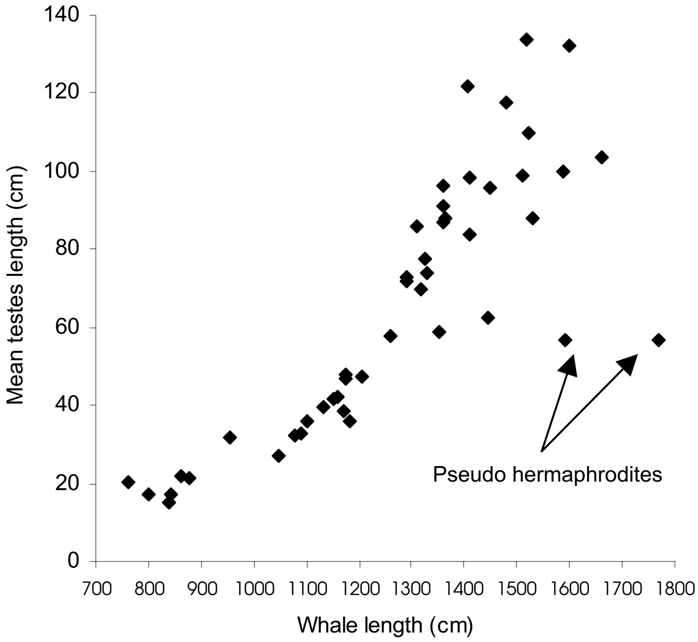

Fig. 3. Mean testis length (cm) versus whale body length (cm) for select bowhead whales landed in northern Alaska 1980-1998.

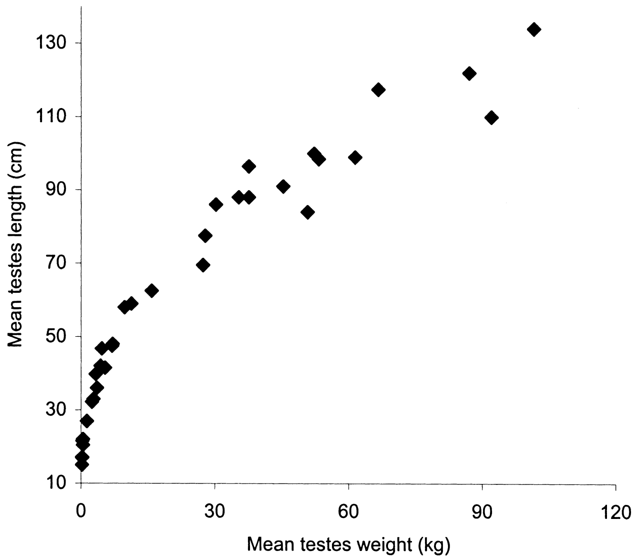

Fig. 4. Mean testis mass (kg) versus mean testis length (cm) for select bowhead whales landed in northern Alaska 1980-1998.

from 41.9-46.5μ. This indicates that mean STD by pole or mid-section does not vary significantly in most specimens; when it did it was only approximately 5μ.

Histological examination indicated that the tubules of immature whales were closed (did not have an obvious lumen), lined by an epithelium characterised by a single layer of prospermatogonia along the basement membrane, Sertoli cells closer to the centre of the tubule, and no evidence of mitoses (Fig. 6). Immature whales (mean whale length of sample 10.6m) had an average STD of 51.8μ (Table 1). Excluding the pseudohermaphroditic whales from the immature category results in a mean STD of 51.5μ (mean whale length of sample 10.0m).

The tubules in mature whales had an obvious lumen, the epithelium was thickened with evidence of mitotic activity, occasional spermatozoa within the lumen, average STD was 125.8μ (Fig. 7) and average whale length was 14.1m (Table 1). Whales with similar findings, but a flat epithelium and no evidence of spermatozoa were classified as suspected mature but inactive. Seven animals had intermediate sized tubules that were open but lacked mitotic activity with a flat

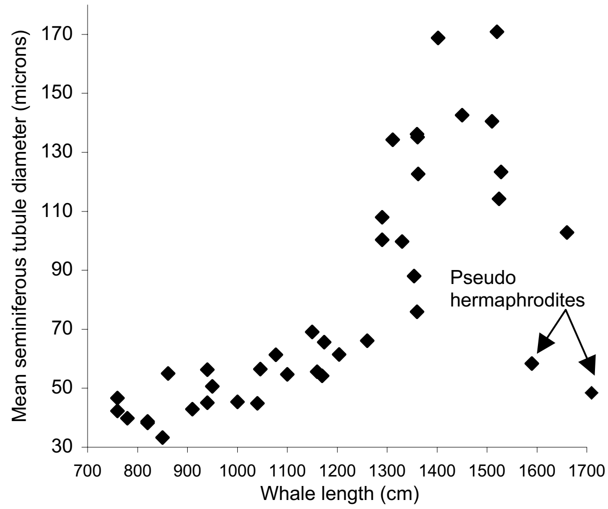

Fig. 5. Mean seminiferous tubule diameter (STD, μμ) versus the body length (cm) for select bowhead whales landed in northern Alaska 1980-1998.

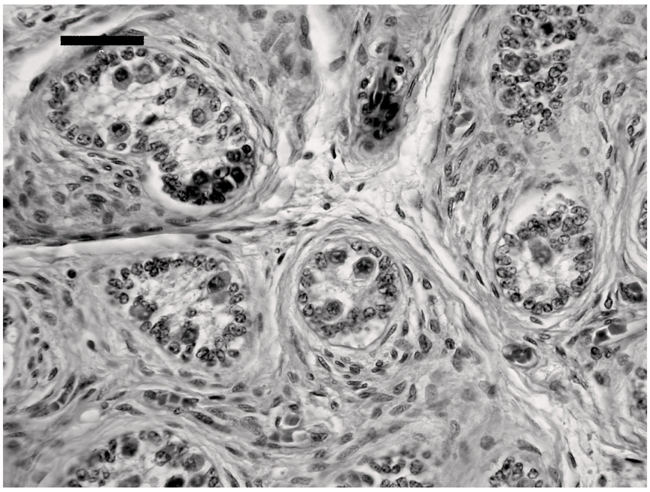

Fig. 6. The seminiferous tubules of immature whales were closed, lined by an epithelium characterised by a single layer of prospermatogonia along the basement membrane, Sertoli cells closer to the centre of the tubule, and no evidence of mitoses. The bar = 40μ.

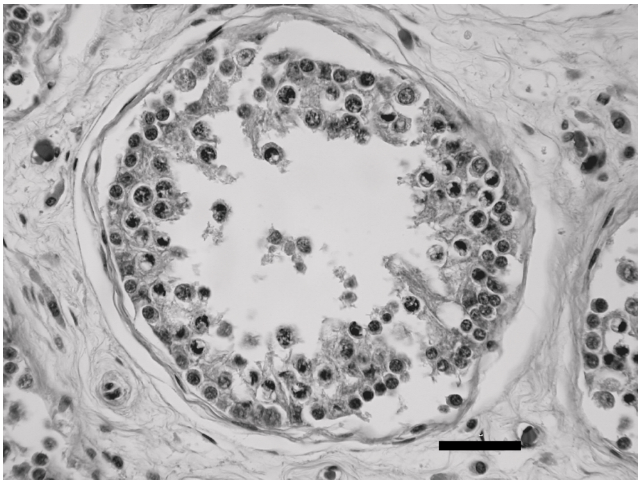

Fig. 7. The seminiferous tubules in mature whales had an obvious lumen and the average STD was 125.8μ. In mature whales with evidence of active spermatogenesis, the epithelium was thickened with evidence of mitotic activity and there were occasional spermatozoa within the lumen. Bar = 40μ.

epithelium and were classified as pubertal or early mature. Pubertal or early mature whales had a mean STD of 85.3μ and mean whale length was 12.6m (range 11.5-13.5m). The smallest whale for which maturity was confirmed was 12.7m in length and harvested in the autumn (Medway, 1981); maturity was determined by the presence of sperm in urine. Whale length, mean testis mass and length, and STD were significantly different for mature versus immature whales (Table 1). None of the endpoints measured comparing histologically determined mature-active to mature-inactive whales proved significantly different (Table 1).

Assessing the number of Leydig cells per HDF was not rewarding and the interstitium varied considerably thus affecting the count. The interstitial cells were very difficult to differentiate. These data are not reported here.

DISCUSSION

Using morphological data (testicular mass and dimensions, whale length) and histological evaluation (STD, presence of spermatozoa and changes in the germinative epithelium), this paper describes the sexual maturation of males of the BCB stock of bowhead whales. One method for estimating the onset of maturity is to determine at what point the testes mass to body length curve inflects sharply. Mean testes mass increases sharply once body length reaches approximately 12.7m, suggesting the onset of puberty can be less than 13.0m. In their review, Koski *et al.* (1993) noted that few data were available on male length at attainment of sexual maturity but predicted that it would occur at 12.0-13.0m. The results here concur with this; 'pubertal' or 'early mature' whales ranged in length from 11.5-13.5m. Durham (1972 *in* Marquette, 1977) reported that sexual maturity in the bowhead whale was estimated to occur at 11.58m but Marquette did not detail how this estimate was obtained. For females, Koski *et al.* (1993) reported values of 14.2m (landed whale data) and 13.0-13.5m (photogrammetric data). However, caution is needed when comparing data from landed whales to photogrammetric studies, as in our experience, stretching of the landed whale will probably increase length measurements. The shorter length at sexual maturation for males is not surprising since females of most baleen whales tend to be larger (Whitehead and Payne, 1981; Koski *et al.*, 1993; George *et al.*, 1999). The estimated age at sexual maturity as determined by stable carbon isotope analysis of the baleen is 17-20yr (Schell *et al.*, 1989; Schell and Saupe, 1993). The estimate mean age for 13m whales using aspartic acid racemisation was about 25 years (George *et al.*, 1999).

The mean STD increased at a body length of approximately 13.0m paralleling an increase in testicular size at a slightly lower body length of about 12.7m. Maturation has been studied in many other whale species (see Boness *et al.*, 2002). Comparisons to these studies of other species indicate male bowhead whales may have the oldest age at sexual maturation (George *et al.*, 1999).

In some testes, a significant difference in STD was detected based on depth from the capsule or plane (anterior pole, posterior pole or equatorial) of sampling, but no clear pattern was evident and the difference was small (approximately 5μ). Thus, we conclude that intratesticular variation in STD does not affect the interpretation of testis maturity or activity if multiple sites are sampled. Whales have been defined as pubertal if immature and mature seminiferous tubules occur in the same testis section (Clarke *et al.*, 1994). In some animals, detection was made of what would appear to be a mean STD that is lower than the large obviously mature males, but higher than clearly immature whales with small STD. These intermediate mean STDs (approximately 85μ) could represent a pubertal or testicular development phase.

Best (1969) showed that sperm whale testes mature from the centre to the periphery and thus location of samples should be considered in any maturation assessment. In our sample, this pattern was only seen in two of 16 whales by comparing cross sections but significant STD differences were found based on depth from the capsule in some sections of 25 of 43 whales. Given this, we recommend sampling from the centre to the periphery of the testis, especially for suspect pubertal animals. With an increased sample of pubertal whales, the centre to periphery maturation theory could be tested in the future. It was reported that on occasion (3-12%), only one testis had detectable sperm in the sperm whale (Clarke *et al.*, 1994) and attempts to evaluate both gonads per bowhead whale should be encouraged.

The largest bowhead whale testes measured in this study had a combined weight of 203.2kg in a 15.2m whale landed in the autumn. Testes of mature northern right whales are often larger, up to 2m long with a combined weight of

1,000kg or more. The relatively large testicular mass for right whales and to a lesser degree bowhead whales may involve a sperm competition reproductive strategy (Brownell and Ralls, 1986). In humpback whales, the paired testes weigh approximately 4.0kg at puberty and are heavier on breeding areas than in feeding areas (Nishiwaki, 1959; Chittleborough, 1965). The combined maximum weight of both testes in the gray whale at the height of the breeding season was approximately 68kg (Rice and Wolman, 1971). The much heavier testes and larger seminiferous tubules of gray whales during the southward migration compared to the northward migration and in the summer feeding areas indicate a marked seasonal sexual cycle with a peak in spermatogenic activity in late autumn and early winter (Rice and Wolman, 1971; Wolman, 1985). Sample size precluded comparisons of spring versus autumn-landed mature males here; bowhead whales are thought to breed in March (Koski *et al.*, 1993).

In conclusion, based on testicular size (mass) and STD, male bowhead whales initiate significant testicular development at approximately 12.5-13.0m in length. In this study, seasonality could not be determined and Leydig cell (interstitial) assessment was found to be of very limited value given their cryptic nature. Future studies utilising special techniques to highlight interstitial cells (i.e. Leydig) and androgen measures in serum and other matrices may help to describe seasonally based changes in testicular activity and better define sexual maturity.

ACKNOWLEDGEMENTS

We greatly appreciate the cooperation of the many whaling captains and crews (Barrow Whaling Captains Association), and the Alaska Eskimo Whaling Commission (AEWC) for allowing us to sample landed whales for this study. We thank L.M. Philo, P. Nader, D. Ramey, V. Woshner, and many others for assistance with sample and data collection. We thank T. Albert, Charles D.N. Brower, and B. Nageak for supporting this study. We thank two anonymous reviewers for their constructive comments. C. Willetto prepared Fig. 1.

REFERENCES

Best, P.B. 1969. The sperm whale (*Physeter catodon*) off the West Coast of South Africa. 3. Reproduction in the male. *Investl Rep. Div. Sea Fish. S. Afr.* 72(3):1-20.

Boness, D.J., Clapham, P.J. and Mesnick, S.L. 2002. Life history and reproductive strategies. pp. 1-432. *In:* A.R. Hoelzel (ed.) *Marine Mammal Biology, An Evolutionary Approach*. Blackwell Publishing, Malden, USA.

Brownell, R.L. and Ralls, K. 1986. Potential for sperm competition in baleen whales. *Rep. int. Whal. Commn* (special issue) 8:97-112.

Chittleborough, R.G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Aust. J. Mar. Freshwater Res.* 16:33-128.

Clarke, R. 1956. Sperm whales of the Azores. *Discovery Rep.* 28:237-98.

Clarke, R., Paliza, O. and Aguayo, A.L. 1994. Sperm whales of the southeast Pacific. Part VI. Growth and breeding in the male. *Invest. Cetacea* XXV:93-224.

George, J.C., Bada, J., Zeh, J., Scott, L., Brown, S.E., O'Hara, T. and Suydam, R. 1999. Age and growth estimates of bowhead whales (*Balaena mysticetus*) via aspartic racemization. *Can. J. Zool.* 77:571-80.

International Whaling Commission. In press. Report of the Scientific Committee. *J. Cetacean Res. Manage. (Suppl.)* 5.

Kenny, R.M., Garcia, M.C. and Everitt, J.I. 1981. The biology of the reproductive and endocrine systems of the bowhead whale, *Balaena mysticetus*, as determined by evaluation of the tissues and fluids from subsistence harvested whales. pp. 89-157. *In:* T.F. Albert (ed.) *Tissue Structural Studies and Other Investigations on the Biology of Endangered Whales in the Beaufort Sea*. Report to the Bureau of Land Management from the Department of Veterinary Sciences, University of Maryland, College Park, MD 20742. 953pp. NTIS No. PB86-153566 [Available from: http://www.ntis.gov].

Koski, W.R., Davis, R.A., Miller, G.W. and Withrow, D.E. 1993. Reproduction. pp. 239-74. *In:* J.J. Burns, J.J. Montague and C.J. Cowles (eds.) *The Bowhead Whale*. 1st. Edn. Society for Marine Mammalogy, Lawrence, Kansas. Special Publication. No.2. 787pp.

Marquette, W.M. 1977. *The 1976 Catch of Bowhead Whales* (Balaena mysticetus) *by Alaskan Eskimos with a Review of the Fishery, 1973 −1976, and a Biological Summary of the Species*. Northwest and Alaska Fisheries Center, Seattle. 93pp.

Medway, W. 1981. The cytological and clinical evaluation of blood and urine of the bowhead whale, *Balaena mysticetus*. pp. 201-12. *In:* T.F. Albert (ed.) *Tissue Structural Studies and Other Investigations of the Biology of Endangered Whales in the Beaufort Sea*. Report to the Bureau of Land Management from the Department of Veterinary Science, University of Maryland, College Park, MD 20742. 953pp. NTIS No. PB86-153566 [Available from: http://www.ntis.gov].

Nerini, M.K., Braham, H.W., Marquette, W.M. and Rugh, D.J. 1984. Life history of the bowhead whale (Mammalia, Cetacea). *J. Zool., London.* 204:443-68.

Nishiwaki, M. 1959. Humpback whales in Ryukyuan waters. *Sci. Rep. Whales Res. Inst., Tokyo* 14:49-87.

Rice, D.W. and Wolman, A.A. 1971. *The Life History and Ecology of the Gray Whale* (Eschrichtius robustus). American Society of Mammalogists, Special Publication No. 3, Stillwater, Oklahoma. viii+142pp.

Schell, D.M. and Saupe, S.M. 1993. Feeding and growth as indicated by stable isotopes. pp. 491-509. *In:* J.J. Burns, J.J. Montague and C.J. Cowles (eds.) *Special Publication*. No. 2. *The Bowhead Whale*. 1st. Edn. Society of Marine Mammalogy, Lawrence, KS.

Schell, D.M., Saupe, S.M. and Haubenstock, N. 1989. Bowhead (*Balaena mysticetus*) growth and feeding as estimated by d13C techniques. *Mar. Biol.* 103(4):433-43.

Tarpley, R.J., Jarrell, G.H., George, J.C., Cubbage, J. and Stott, G.G. 1995. Male pseudohermaphroditism in the bowhead whale, *Balaena mysticetus*. *J. Mammal.* 76(4):1267-75.

Tarpley, R.J., Hillmann, D.J. and George, J.C. 1999a. Accumulation and persistence of *corpora albicantia* in the bowhead whale ovary. Paper SC/51/AS6 presented to the IWC Scientific Committee, May 1999, Grenada, WI (unpublished). 15pp. [Paper available from the Office of this Journal].

Tarpley, R.J., Hillmann, D.J. and George, J.C. 1999b. Observation on reproductive tract morphology in an immature female bowhead whale. Paper SC/51/AS8 presented to the IWC Scientific Committee, May 1999, Grenada, WI (unpublished). 23pp. [Paper available from the Office of this Journal].

Tarpley, R.J., Hillmann, D.J. and George, J.C. 1999c. Observations on ovarian morphometrics and morphology in the bowhead whale. Paper SC/51/AS7 presented to the IWC Scientific Committee, May 1999, Grenada, WI (unpublished). 45pp. [Paper available from the Office of this Journal].

Whitehead, H. and Payne, R. 1981. New techniques for measuring whales from the air. NTIS No. PB81-161143. US Marine Mammal Commission Report No. MMC-76/22, Washington DC. 36pp. [Available from: http://www.ntis.gov].

Wolman, A.A. 1985. Gray whale, *Eschrichtius robustus* (Lilljeborg, 1861). pp. 67-90. *In:* S.H. Ridgway and R. Harrison (eds.) *Handbook of Marine Mammals*. Vol. 3. *The Sirenians and Baleen Whales*. Academic Press, London and Orlando. xvii+362pp.