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Skull foramina asymmetry in East Greenland and Svalbard polar bears (*Ursus maritimus*) in relation to stressful environments

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Fluctuating asymmetry (FA) of foramina as a measure of environmental stress was studied in polar bear (*Ursus maritimus*) skulls from East Greenland ($n = 300$, collected 1892–2004) and Svalbard ($n = 388$, collected 1950–2004). Levels of FA for each of the 11 traits used in the study were compared between sex/age groups (subadults, adult females, adult males), localities (East Greenland, Svalbard), and periods (≤ 1960 [pre-pollution] and > 1960, [pollution]) using general linear models (GLMs). The GLMs revealed that adult males had higher FA in two traits than other sex/age groups. Also, the Svalbard bears had higher FA in number of intracondylar foramina than had those from East Greenland, a trend corresponding well with skull differences found previously between the two subpopulations. No correlation was found between the bears' year of birth ($n = 468$) and FA or between levels of contaminants and FA ($n = 65$).

Introduction

Fluctuating asymmetry (FA) refers to small, random deviations from the ideal morphological symmetry and is typically measured as the absolute difference between a trait on the left and the right side of a bilaterally symmetrical organism (Møller & Swaddle 1997, Palmer & Strobeck 2003). FA is often taken as a measure of developmental stability (DS), "the ability to attain equal development under the given circumstances" (Zakharov 1992), and its counterpart developmental instability (DI). In principle, DS reflects the organism's ability to buffer its development against disturbances (Møller & Swaddle 1997), such as temperature, noise, food access and quality, chemicals, parasites and diseases (e.g. Siegel & Mooney 1987, Borisov *et al*. 1997, Stige 2004, Jones *et al*. 2005, Møller 2006, Petavy *et al*. 2006). The more fit the genotype of an organism is, and the less stress from the surrounding environment it is exposed to, the higher

DS and thus lower FA the organism is expected to have (Stige 2004).

FA is therefore often taken as an indicator of phenotypic and genotypic quality (Møller & Swaddle 1997) and could, as such, be used as a helpful tool in population dynamics research (Clarke 1995, Baranov *et al*. 1997, Zakharov *et al*. 1997, Stige 2004). An organism's DS is often believed to be largely determined during the foetal stage (e.g. Siegel *et al*. 1977b, Møller & Swaddle 1997, Valetsky *et al*. 1997). However, aspects such as canalization (Nijhout & Davidowitz 2003) and plasticity (Nijhout & Davidowitz 2003, Palmer & Strobeck 2003) might buffer the organism's morphological expression.

Studies of FA have been conducted on metric and meristic traits of a multitude of organisms (plants: Pelabon *et al*. 2006; arthropods: Lajus & Alekseev 2004, Vilisics *et al*. 2005, Andersen *et al*. 2006, fish: Jagoe & Haines 1985, Green & Lochmann 2006; mammals; Zakharov & Yablokov 1990, Pertoldi *et al*. 2003). Exogenous factors such as social (Valetsky *et al*. 1997, Gibbs & Breuker 2006), inbreeding (Pertoldi *et al*. 2000), sexual selection (Voigt *et al*. 2005), nutritional (Pravosudov & Kitaysky 2006), heat (Siegel *et al*. 1977a, Petavy *et al*. 2006), and disease and parasites (Møller 2006) have been found to be positively correlated with levels of FA. Anthropogenic organic chemical pollution is another form of environmental stress that has been found to be positively correlated with FA (e.g. Zakharov & Yablokov 1990, Borisov *et al*. 1997, Zakharov *et al*. 1997, Maul & Farris 2005, Bechshøft *et al*. 2008). The Arctic acts as a sink for a range of persistent organic pollutants (POPs), comprised largely of organohalogens such as polychlorinated biphenyls (PCBs), chlordane (CHL), DDT, dieldrin, hexachlorocyclohexane (HCH), hexachlorobenzene (HCB), and polybrominated diphenyl ethers (PBDEs) (AMAP 2004). Many of these pollutants are highly lipophilic and bioaccumulate in marine food chains, particularly in the fatty tissue of marine mammals, including polar bears, and in particular bears from East Greenland and Svalbard (Borgå *et al*. 2001, AMAP 2004, Verreault *et al*. 2005, Muir *et al*. 2006, Gebbink *et al*. 2008) which have been found to carry some of the highest POP loads of any mammal species (Norstrom *et al*. 1998, Dietz *et al*. 2004, Verreault *et al*. 2005, Muir *et al*. 2006, Gebbink *et al*. 2008). Chronic exposure to these pollutants in the polar bears has been associated with afflictions such as endocrine disruption, reduced size of sexual organs and bone mineral density, and organ histopathology (e.g.Wiig *et al*. 1998, Derocher *et al*. 2003, Braathen *et al*. 2004, Lie *et al*. 2004, Sonne *et al*. 2004, Kirkegaard *et al*. 2005, Sonne *et al*. 2005b, 2006a, 2006b). The widespread use and output of for example PCBs, one of the major organohalogens, began in the 1950s and peaked in the 1960s (AMAP 2004, Dietz *et al*. 2004). Reports on the temporal trends of the persistent organic pollutants in the Arctic now show a possible decline in several of these toxic substances over the last decades (e.g. Derocher *et al*. 2003, Dietz *et al*. 2004, Verreault *et al*. 2005, Riget 2006), while many novel contaminants seem to increase (Corsolini *et al*. 2002, Bossi *et al*. 2005, Muir *et al*. 2006, Smithwick *et al*. 2006, Dietz *et al*. 2007). The potential adverse health effects of this organohalogen cocktail is unknown and makes for a complex pattern when attempting to link organohalogen pollutants with FA.

Previous studies have investigated metric FA in polar bears (Sonne *et al*. 2005a, Bechshøft *et al*. 2008), finding no substantial connection between pollution loads and FA. The present study, however, concerns FA of meristic traits in response to stress, an approach that has been successfully applied in other mammal species (McLellan & Finnegan 1990, Zakharov & Yablokov 1990, Hartl *et al*. 1995, Blagojević & Vujošević 2004). The prenatal period is critical for the development of skull foramina (Zakharov *et al*. 1991) but, according to Blagojević and Vujošević (2004), symmetry of foramina probably bears no importance to the fitness of an organism. Also, meristic traits are often thought to be more reliable, due to negligible error in counting (Blagojević & Vujošević 2004), and foramina are generally supposed to be independent of sex and age (Wiig & Andersen 1988, McLellan & Finnegan 1990, but *see* also e.g. Wiig & Lie 1984), and can thus be useful in determination of an organism's DS. In contrast to metric (continuous) growth, meristic characters are thought to have a physiological-developmental threshold (McLellan & Finnegan 1990), meaning that the potential stressors would have to reach a level above this threshold to elicit any response in the FA of e.g. foramina.

The aim of this paper was to study meristic FA in a combined sample of skulls of East Greenland and Svalbard polar bears in order to obtain information about spatial and temporal trends in the effects of environmental stress on DS.

Materials and methods

Samples

A sample of 300 polar bear skulls from East Greenland (held at the Zoological Museum, University of Copenhagen), and 388 polar bear skulls from Svalbard (held at the Natural History Museum, University of Oslo) were examined (Table 1). The skulls were collected during 1892–2004 (East Greenland, approx. 61°–82°N, 10°–42°W) and 1950–2004 (Svalbard, approx. 74°–81°N, 10°–35°E). Many of the skulls were more or less damaged, and thus the entire range of foramina registrations could not be done on those skulls. The age determination of the skulls had been carried out by counting the cementum Growth Layer Groups (GLGs) of the lower right incisor (I3) after decalcification, thin sectioning (14 μm) and staining (Toluidine Blue), using the method described by Hensel and Sorensen (1980) and Dietz *et al*. (1991). A total of 217 of the Svalbard polar bears were of determined age. For the East Greenland sample, the number was 265 individuals. The individuals were categorised as subadults, adult females, or adult males according to the following criteria: adult males ≥ 6 years, adult females ≥ 5 years, the remaining considered subadults (Rosing-Asvid *et al*. 2002). The individuals of unknown sex were determined according to the process described in Bechshøft *et al*. (2008). Measurements of individual levels of PCBs, HCB, HCHs, DDTs, dieldrin, CHLs, and PBDEs in subcutaneous adipose tissue were available from a subsample of 65 of the East Greenland polar bears. Further details on the levels of the organohalogen compounds in relation to sex, age, and season are given in Dietz *et al*. (2004, 2007), Sandala *et al*. (2004), and Muir *et al*. (2006). In order to study temporal variation related to change in pollution levels, the samples were divided into two periods according to the individuals' year of birth: ≤ 1960 and > 1960. The cutpoint was selected because the widespread use and outputs of for example PCBs, one of the major organohalogens, began in the 1950s and assumedly peaked in the 1960s (AMAP 2004, Dietz *et al*. 2004).

Traits

Fourteen meristic traits were registered in this study (Table 2 and Fig. 1). All traits were foramina which were defined by minimum inner diameter size, depending on which area of the skull was studied (Table 2). Blunt metal pins with these dimensions were used to determine whether the size of the individual foramen fell within the predetermined accepted range. Observed foramina meeting the set criteria were counted on the right (*R*) and left (*L*) side of each skull. The foramina were only registered once

Table 1. Numbers of East Greenland and Svalbard polar bear (*Ursus maritimus*) skulls included in the present study. The total number of bears and the number of bears in relevant subgroups are given.

	East Greenland	Svalbard
Bears measured in total	300	391
Subadult	133 (68 ♀, 58 ♂)	132 (51 ♀, 65 ♂)
Adult female (≥ 5 years)	59	89
Adult male (≥ 6 years)	73	111
Bears of known age (and hence year of birth)		
Subadult	133	93
Adult female	59	61
Adult male	73	63
Bears born ≤ 1960		
Subadult	39	9
Adult female	24	43
Adult male	50	52
Bears born > 1960		
Subadult	87	99
Adult female	35	18
Adult male	23	15
Bears born ≥ 1950		
Subadult	94	93
Adult female	44	50
Adult male	36	55
Bears with available contaminant data and age		
Subadult	36	0
Adult female	18	0
Adult male	11	0

per skull, except for a randomly chosen subsample of 61 skulls which was registered twice, in order to determine the measurement (registration) error. All registrations were conducted by the same person, and the subsample registration was done on a separate day from the rest. Measurement error (%ME) of the 14 meristic traits was calculated according to Schandorff (1997). Trait 214 (%ME = 24.0), trait 223 (%ME = 20.0), and trait 225 (%ME = 50.0) were excluded from all further analyses because of high %ME. The remaining 11 traits had a %ME ranging between 0.03 and 14.01 (average = 5.29).

Statistical analyses

All statistical analyses were performed using SPSS (ver. 14.0) (SPSS Inc., Chicago, Illinois), except the GLMs which were generated using the free statistical software R (ver. 2.3.1). FA was applied in further calculations as $|R - L|$, and the significance level was set to $p = 0.05$ unless other is specified.

Examination of data

All traits in all subgroups (sex, age, and locality) were tested for directional asymmetry (DA) using one-sample Student's *t*-test conducted on $(R - L) = 0$ to see whether the distribution was centered around zero (Pertoldi *et al*. 1997). The magnitudes of skew and kurtosis of $(R - L)$ were calculated for each trait of each subgroup and tested with Student's *t*-test (Palmer 1994). Spearman's correlation coefficient (r_S) analyses between $|R - L|$ and condylobasal length were

Table 2. Definition and range of the 14 meristic traits (Fig. 1) registered on skulls of East Greenland and Svalbard polar bears (*Ursus maritimus*).

Trait	Description	Minimum inner diameter of foramina (mm)	*n*	Range		Range (FA)	
				Right	Left	Right	Left
Skull							
207	Number of premaxillary foramina	0.5	652	653	0–3	0–2	0–2
208	Number of maxillary foramina	1.0	653	650	0–4	0–4	0–3
209	Number of parietal foramina	1.0	529	538	0–3	0–4	0–3
210	Number of occipital foramina	1.5	565	561	0–2	0–2	0–2
211	Number of intracondylar foramina	All visible counted	531	541	0–3	0–3	0–2
214	Number of foramina on the jugal part of the zygomatic arch	0.5	619	618	0–14	0–14	0–7
215	Number of infraorbital foramina including possible accessory ones	All visible counted	665	662	0–2	1–2	0–1
216	Number of foramina found on the area between the main infraorbital foramen and the suture of the beginning of the jugal bone	0.5	640	648	0–5	0–4	0–3
217	Number of palatine foramina including possible accessory ones	0.8	632	634	1–4	1–4	0–3
218	Number of basioccipital foramina	0.5	466	467	0–3	0–4	0–3
Lower jaw							
222	Number of foramina on ramus	1.5	623	622	1–5	0–5	0–2
223	Number of foramina on the anterior outer part of the mandibular condyle	0.5	513	516	0–7	0–3	0–5
224	Number of anterior mandibular foramina including possible accessory ones	1.5 (only required for the accessory foramina; all visible anterior mandibular foramen were counted)	608	609	1–4	1–3	0–2
225	Number of foramina on the posterior part of the mandibular condyle	All visible counted	521	515	0–3	0–3	0–3

used to examine the relation between FA and size of the skull.

Temporal and spatial variation in FA

Single trait asymmetry as well as overall asymmetry was analyzed with regard to temporal and spatial variation. Overall asymmetry (FASUM) was obtained by adding all individual absolute FA scores for all registered traits (n = 318) (Leamy *et al*. 1998, Blagojević & Vujošević 2004).

A GLM was run for each trait (errors: Poisson errors, link: log, test: χ^2) and for FASUM (errors: quasi errors, link: log, test: F), in order to determine which factors and two-way interactions were of importance in determining the registered FA. The factors applied in the model were sex/age group (adult male/adult female/subadult), locality (East Greenland/Svalbard), and time period (≤ 1960 and > 1960). Trait 215 had, as the only trait, a binomial distribution (number of foramen registered in this trait were either 0 or 1, whereas the other traits ranged between 0 and 2 or 3). Therefore an additional GLM (errors: binomial, link: logit, test: χ^2) was performed for this trait.

Spearman's rank order correlation test was used to test FA of each individual trait versus the polar bears' year of birth for bears born 1950 or later. There were too few individuals born before 1950 for them to be included in the time trend analyses. The East Greenland and Svalbard samples were pooled in the analyses. The two samples were roughly equal in number of males and females, as well as number of adult males, adult females, and subadults. Trait 215 was not included in this analysis as it had a different distribution in the two geographical areas (*see* Results). Only bears with known scores in all 10 traits were included (n = 318). The temporal trend of FASUM for these same bears was also tested with Spearman's rank order correlation test.

FA and contaminant levels

The relationship between FA and contaminant levels (PCBs, HCB, HCHs, DDTs, dieldrin, CHLs, and PBDEs in the aforementioned subcutaneous adipose tissue samples) was explored using Spearman's rank order correlation test. FA was tested both on individual trait and overall level. Due to the large number of tests when examining the correlation on the individual trait

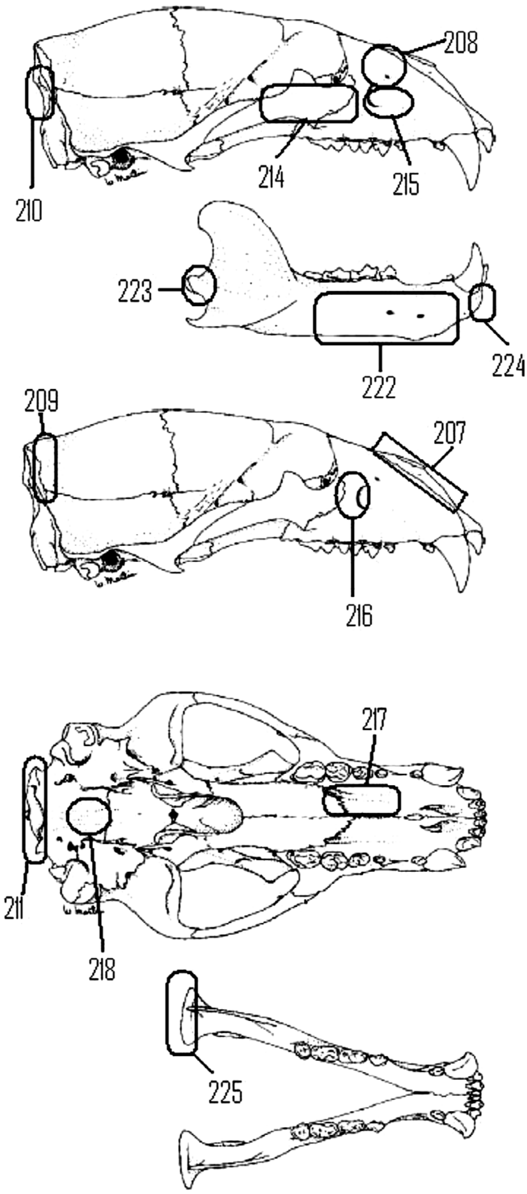

Fig. 1. Fourteen meristic foramina traits (Table 2) registered on skulls of East Greenland and Svalbard polar bears (*Ursus maritimus*). Figure from Amstrup and DeMaster (1988).

level (11 traits × 7 contaminant groups gives k = 77), a Bonferroni correction was applied to the p estimates, and the level of significance was thus set to $p = 0.05/77 = 0.0006$.

Overall contaminant level (CONTSUM) was obtained by adding all individual contaminant levels (mean sum = 8534.67 ng/g lipid weight). CONTSUM was tested against individual trait FA and against FASUM using Spearman's rank order correlation test.

Results

Examination of data

Of all combinations between sex, age, and locality, adult males were the only groups to show significant DA [East Greenland adult males, number of premaxillary foramina (trait 207), p = 0.010, Svalbard adult males, number of anterior mandibular foramina, including possible accessory ones (trait 224), p = 0.010)]. None of the traits were significantly skewed, but several of them were leptokurtic [East Greenland: adult males in number of parietal foramina (trait 209, p = 0.007) and number of anterior mandibular foramina, including possible accessory ones (trait 224, p = 0.005), adult females in number of intracondylar foramina (trait 211, $p < 0.0001$) and number of anterior mandibular foramina, including possible accessory ones (trait 224, $p < 0.0001$), subadults in number of anterior mandibular foramina, including possible accessory ones (trait 224, $p < 0.0001$), Svalbard: adult males in number of maxillary foramina (trait 208, $p < 0.0001$) and number of intracondylar foramina (trait 211, p = 0.0004), adult females in number of intracondylar foramina (trait 211, p = 0.002), subadults in number of anterior mandibular foramina, including possible accessory ones (trait 224, p = 0.017)]. FA was dependent on (increasing with) the general skull size in two instances: East Greenland adult males in number of foramina found in the area between the main infraorbital foramen and the suture of the beginning of the jugal bone (trait 216, East Greenland, r = 0.316, p = 0.022), and in East Greenland subadults in the number of parietal foramina (trait 209, r = 0.323, p = 0.001).

Temporal and spatial variation in FA

The GLM models testing for influence of sex/age group, locality, and period on the registered levels of FA showed three significant results, and three nearly significant results (Table 3). Adult males had higher FA than adult females and subadults in the number of foramina found in the area between the main infraorbital foramen and the suture of the beginning of the jugal bone (trait 216, $p < 0.0001$), number of foramina on ramus (trait 222, $p < 0.0001$), and FASUM ($p < 0.0001$). In the number of maxillary foramina (trait 208), adult males also had an almost significantly higher FA than the other two groups, but only during the second period (p = 0.07). In the number of intracondylar foramina (trait 211), the Svalbard bears were close to having a significantly higher FA than the East Greenland bears (p = 0.054). The test of the number of infraorbital foramina, including possible accessory ones (trait 215), as a binomial distribution showed the level of FA as almost significantly higher during the second period (p = 0.06).

Spearman's rank order correlation test was used to test FA of each individual trait *versus* the polar bears' year of birth for bears born 1950 or later. There were no significant differences ($-0.06 \leq r_S \geq 0.09$, $0.11 \leq p \geq 0.99$). The temporal trend of FASUM for these same bears was also tested with Spearman's rank order correlation test, but no significant correlations were found here either ($r_S = -0.004$, $p = 0.95$).

FA and contaminant levels

There were no significant correlations at the p = 0.0006 level between FA and contaminants (all $r_S \leq 0.21$ and all $p \geq 0.02$), neither at the individual trait level nor at the overall level. No significant correlations were found in any of the tests incorporating CONTSUM and/or FASUM.

Discussion

Temporal and spatial variation in FA

The adult male polar bears had a higher level of FA than adult females and subadults in two single traits. This was also the case when looking at the traits overall, though this was probably caused by the previously mentioned single traits. Adult male polar bears were also shown to have higher FA levels than the other sex/age groups in some of the metric traits analyzed by Bechshøft *et al*. (2008). The reason for this lies in speculation only, but would in any case null the general view that meristic traits are independent of sex (Wiig & Andersen 1988, McLellan & Finnegan 1990), which has also been challenged by e.g. Wiig and Lie (1984) and Markowski (1995).

The Svalbard bears showed a non-significant trend (p = 0.054) of a higher level of FA in one trait than the East Greenland bears. This trend was also found in the metric FA data analyzed in Bechshøft *et al*. (2008), thus supporting the notion that the geographical difference is slight, but real. A difference in bear morphology between these areas was also found by Sonne *et al*. (2007) who found that Svalbard bears had a higher ratio of tooth wear than East Greenland bears. The authors speculated that this could be due to differences in bone consumption (food competition) related to population density and food availability. Perhaps the differences in FA could also be ascribed to a possible increased polar bear population density in Svalbard after the population was protected in 1973 (Derocher 2005). Polar bear population size and trend in East Greenland is unknown (Born & Sonne 2006). The occurrence of meristic characters has been shown to vary with population density (e.g. Andersen & Wiig 1982). Zakharov *et al*. (1991) found a positive correlation between population density and developmental homeostasis in the cyclic population of common shrew (*Sorex araneus*) in Siberia. It is assumed that population density is an important negative factor that affects pregnant females.

Only the number of infraorbital foramina, including possible accessory ones (trait 215) showed any sign of FA being positively correlated with pollution (or other stressors thought to affect the polar bear populations [e.g. global warming: ACIA (2005), Regehr *et al*. (2005), Wiig (2005), and excessive harvesting: Lønø

Table 3. Results from the generalized linear model testing for influence of sex/age group (subadult, adult females, adult males), locality (East Greenland, Svalbard), and period (≤ 1960, > 1960) on the measured levels of fluctuating asymmetry (FA) of foramina in skulls of East Greenland and Svalbard polar bears (*Ursus maritimus*). Traits 207–224 were applied as the absolute value of FA (|*L* – *R*|). FASUM was obtained by adding all individual absolute FA scores for all registered traits. Note: Since we chose to use several traits in analyzing the FA, it should be mentioned that increasing the number of tests also increases the likelihood that some tests were significant simply by chance.

Trait	*n*	Period		Sex/age group		Locality		Sex/age group × period		Period × locality		Sex/age group × locality	
		p	Resid. dev.	*p*	Resid. dev.	*p*	Resid. dev.	*p*	Resid. dev.	*p*	Resid. dev.	*p*	Resid. dev.
207	482	0.60	365.38	0.33	363.16	0.71	363.02	0.52	361.70	0.65	361.49	0.79	361.03
208	476	0.40	355.35	0.43	353.68	0.53	353.29	**0.07**	347.92	0.64	347.70	0.44	346.06
209	384	0.62	309.36	0.85	309.04	0.43	308.41	0.34	306.24	0.33	305.27	0.68	304.50
210	423	0.38	313.40	0.41	311.60	0.54	311.23	0.71	310.53	0.58	310.22	0.68	309.44
211	390	0.62	272.02	0.16	268.39	**0.06**	264.74	0.48	263.26	0.78	263.18	0.23	260.24
215	485	0.12	342.82	0.92	342.66	0.92	342.65	0.77	342.11	0.20	340.46	0.89	340.23
215_{binom}	485	**0.06**	570.23	0.90	570.01	0.91	570.00	0.70	569.27	0.13	567.01	0.84	566.66
216	472	0.84	374.01	**0.0007**	359.37	0.29	358.26	0.78	357.76	0.87	357.74	0.48	356.28
217	464	0.53	382.68	0.88	382.42	0.94	382.41	0.73	381.78	0.90	381.77	0.63	380.84
218	353	0.47	284.28	0.24	281.45	0.47	280.93	0.40	279.11	0.12	276.64	0.77	276.12
222	467	1.00	388.55	**0.02**	381.04	0.20	379.40	0.94	379.28	0.70	379.13	0.23	376.18
224	457	0.85	319.87	0.20	316.67	0.10	313.99	0.39	312.09	0.35	311.22	0.46	309.66
FASUM	271	0.53	62.89	**0.01**	61.09	0.42	60.97	0.93	60.94	0.57	60.87	0.42	60.54

(1970), Larsen (1986), Wiig (2005)]), by showing a higher level of FA during the second time period. The result was not significant however, and had the meristic FA been tightly connected with the factors mentioned above, one would perhaps have expected a similar trend in more than just this one trait. The temporal trend analysis showed no increase (or decrease) in FA on a continuous time scale from 1950 untill present, which is also contrary to the idea that pollution (or other stressors) has increased FA in skull foramina. In Bechshøft *et al.* (2008), a decline in levels of metric FA was found during 1950–2000, and partly explained with the anticipated declining trend in many of the major organohalogens during this period (Derocher *et al.* 2003, Dietz *et al.* 2004). The differences in results between metric and meristic traits may be because they have different thresholds and that their anatomical appearance and function differ (McLellan & Finnegan 1990).

FA and contaminant levels

No correlations were found between contaminants and levels of FA. Increasing levels of FA in meristic skull traits in connection with pollution have been found earlier by Zakharov and Yablokov (1990) and Schandorff (1997) in Baltic and Kattegat seals. However, in these studies, PCB and DDT concentrations were up to a hundred times higher than those found in the present study (*see* e.g. Olsson & Reutergårdh 1986, Blomkvist *et al.* 1992). The tissue samples used in measuring organohalogen levels in this study were collected during 1999–2002 (Dietz *et al.* 2004), a period in which concentration many of the "older" organohalogens were found to be decreasing (Derocher *et al.* 2003, Dietz *et al.* 2004). Furthermore, in polar bears, individual contaminant levels are often dependent on factors such as the bear's nutritional status and time of year, which could help explain the difficulty in correlating the organohalogen levels with FA at the individual level (Bernhoft *et al.* 1997, Polischuk *et al.* 2002, Dietz *et al.* 2004, 2007). Also, an organism's DS is often believed to be largely determined during the foetal stage (e.g. Siegel *et al.* 1977b, Zakharov *et al.* 1991, Møller & Swaddle 1997, Valetsky *et al.* 1997), which supposedly renders pollution levels measured in later life more or less useless in connection with FA. This at least seems to be the case in the present study.

As discussed in the introduction, meristic traits are often considered more reliable measurements of FA than metric traits. Even so, the results in this paper are not significantly clearer than those found in the metric FA study by Bechshøft *et al.* (2008). It seems that perhaps pollution loads must reach higher levels than now before an obvious effect is observed with regard to animals' FA. Seeing as the East Greenland and Svalbard polar bears have been found to carry some of the highest organohalogen loads of any Arctic mammal species (Norstrom *et al.* 1998, Borgå *et al.* 2001, Dietz *et al.* 2004, Verreault *et al.* 2005, Muir *et al.* 2006, Gebbink *et al.* 2008), it is highly probable that FA studies (at least those connected to pollution) of other polar bear subpopulations would show even less significant results. The FA studies of the East Greenland and Svalbard subpopulations did however reveal recurring trends, which could be of even more interest if further subpopulations were included in a similar study.

Conclusions

- Adult male polar bears had higher levels of meristic FA in several traits than the other sex/age groups.
- Svalbard polar bears showed a tendency towards a higher level of meristic FA than those of East Greenland, a trend that corresponds well with other differences found between the two subpopulations.
- No correlation was found between the bears' year of birth and FA, or between levels of contaminants and FA.

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