RESEARCH ARTICLE

Tusk anomalies in narwhals (*Monodon monoceros*) from Greenland

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Abstract

The elongated, spiraled tusk of male narwhals (*Monodon monoceros*) grows continuously throughout the life of the whale and is most likely a secondary sexual trait used in male–male hierarchical competition and possibly in female mate choice. Sex determination in narwhals is typically based on the presence (male) or absence (female) of an erupted tusk, but anomalies such as females with tusks, tuskless males or double-tusked whales occur, although infrequently. In this study, we collected reproductive data and recorded the presence or absence of a tusk in narwhals from the Inuit hunt in Greenland (1993 and 2010–19) with the purpose of estimating the frequency of tusk anomalies. We found that of the 173 whales, 2.9% displayed tusk anomalies. Tusked females constituted 1.5% of sampled females, tuskless males 2.8% of sampled males and double-tusked males 0.9% of sampled males. Biological information on a tusked female, a tuskless male and a double-tusked male was collected and is presented here. The tusked female was sexually mature, and 18 ovarian scars (indicating pregnancies) documented a long reproductive lifespan. The complete female tusk was estimated to be between 146 and 151 cm in length. The tuskless male was sexually maturing, as indicated by body dimensions, and the double-tusked male was sexually immature, with the two tusks measuring <90 cm in length. Although narwhals exhibit extremely low levels of genetic diversity, tusk anomalies persist in the populations, perhaps facilitated by the reproductive ability of whales with tusk anomalies.

Keywords

Arctic; cetacean; marine mammal; teeth; dentition; Inuit narwhal hunt

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Abbreviations

AAR: aspartic acid racemization
CA: corpora albicans
CI: confidence interval
CL: corpora lutea
GINR: Greenland Institute of Natural Resources
GLG: growth layer group

Introduction

Narwhals (*Monodon monoceros*) are medium-sized odontocete whales endemic to the Arctic, best known for the male's elongated, spiraled tusk, which can grow up to a staggering size of nearly 3 m (Hay & Mansfield 1989). The tusk presumably grows continuously throughout the life of the whale and is most likely a secondary sexual trait used in male–male competition for hierarchical status (Best 1981; Bruemmer 1993) and possibly in female mate choice (Kelley et al. 2015; Graham et al. 2020). Narwhals are born with two elongated teeth embedded in the upper jaw. In males, the left tooth—a canine tooth (Nweeia et al. 2012)—erupts through the upper left lip, and as the whale grows older, it becomes a long, spiraled tusk. The right tooth generally remains inside the maxillae in males, and in females, both teeth usually stay embedded in the maxillae (Best 1981). Because of the general conception that the narwhal tusk is a male trait, sex determination in narwhals is typically based on the presence (male) or absence (female) of the erupted tusk. Anomalies such as females with tusks, tuskless males and double-tusked whales (whales with two erupted tusks) occur, although infrequently (Hay & Mansfield 1989). When present, the tusks of the females are likely shorter and narrower than that of males (Clark 1871; Pedersen 1931), as also reported by Inuit hunters (Nweeia 2020).

Double-tusked individuals are most likely males, but a few records suggest that females may also develop two tusks (Best 1981; Hay & Mansfield 1989), although contemporary scientific evidence is needed to support this. Other anomalies reported in the literature include a small, curved tusk (30 cm in length) protruding from the lower right jaw of an adult male that also possesses a normal sized (195 cm) left maxillary tusk (Mitchell & Kemper 1980), and a tusk emerging from the right maxilla (Hay & Mansfield 1989). Tusks can also rarely be cork-screw spiraled instead of straight, as exemplified by

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a specimen that is stored at the Natural History Museum of Denmark (Kingsley & Ramsay 1988). The spiral of the tusk, however, seems always to twist sinistrally (left-handed), even when two tusks are present (Hay & Mansfield 1989; Kingsley & Ramsay 1988), although a single female tusk with a dextrorsal (right-handed) spiral was reported by Scoresby (1823). One male 'narluga'—a hybrid between a male beluga (*Delphinapterus leucas*) and a female narwhal (Skovrind et al. 2019)—from Greenland was described as having dentition unlike that of any known cetacean, with features of the teeth analogous to those of both narwhals and belugas. The male narluga did not possess an erupted tusk (Heide-Jørgensen & Reeves 1993).

Little has been published on the frequency of tusk anomalies in narwhal populations. Hay (1984) conducted a comprehensive study of the life history of narwhals based on biological samples collected from the Inuit hunt of narwhals in northern Baffin Island in the eastern Canadian Arctic during 1963 to 1976 (n = 194) and found that 2.7% of females had an erupted tusk, 2.5% of males were tuskless and 1.2% of males had two tusks. Hay (1984) also reported on an allegedly double-tusked female, but the sex was not confirmed and was, therefore, not included in the above frequencies.

Narwhals in Greenland are subject to hunting by local Inuit hunters (Greenlanders), and catches are regulated by annual quotas (Hobbs et al. 2019). The hunt enables large-scale collections of biological samples and information from narwhal populations. In this study, we used the hunted narwhals to extract reproductive data consisting of sampled reproductive organs, the presence of a foetus and/or mammary glands, and we recorded the presence or absence of tusks, for the purpose of determining the frequency of tusk anomalies. Furthermore, we describe three narwhals with tusk anomalies—a tusked female, a tuskless male and a double-tusked male—for which we have detailed biological information.

Material and methods

Samples

Reproductive organs, consisting of testes from males and ovaries from females, and/or information on the presence of a foetus or mammary glands, were collected and used to determine the sex of 173 narwhals (65 females [38%] and 108 males). The presence (or absence) of an erupted tusk was recorded for each animal. The 173 whales were taken in the Inuit hunt of narwhals in Greenland during the years of 1993 and 2010–19. Samples were collected from three different areas and time periods: in north-west Greenland, Qaanaaq (n = 44 [52% females]; 77.46632°N, −69.23114°W), in July and August 1993, and Uummannaq (n = 51 [35% females]; 70.67471°N, −52.12635°W), in November 1993; and, in south-east Greenland, Hjørnedal in the Scoresby Sound fjord (n = 78 [31% females]; 70.36795°N, −28.18713°W), in July to September 2010–19 (Table 1). To eliminate the risk of sampling error, only sampling conducted by trained biologists and scientists was used.

The frequency of narwhals with tusk anomalies was estimated as the number of females and males, respectively, with tusk anomalies relative to the number of each sex examined in each sampling area and in total.

Examination of three narwhals with tusk anomalies

A tusked female (ID #938) and a tuskless male (ID #1189) collected during the Inuit hunt of narwhals in the Scoresby Sound fjord, and a double-tusked male collected in Uummannaq, were examined in the field. The following body measurements from the three whales were recorded using standard methods (Heide-Jørgensen & Teilmann 1994; Garde et al. 2015; Garde et al. 2022): body length (cm), body mass (kg), tusk length (cm), fluke width (cm) and circumference (cm). Tusks were measured from the front edge of the upper jaw (where the

Table 1 Number and frequency of tusk anomalies of 173 narwhals from three locations in Greenland.

Year	Region[a]	Location[b]	Month	Females	Males	Sum	Females with tusk		Males without tusk		Males double-tusks	
				n	*n*	*n*	*n*	%	*n*	%	*n*	%
1993	NW	QA	July–Aug.	23	21	44	0	0.0	2	9.5	0	0.0
1993	NW	UU	Nov.	18	33	51	0	0.0	0	0.0	1	3.0
2010–19	SE	SC	July–Sept.	24	54	78	1	4.2	1	1.9	0	0.0
Total				65	108	173	1	1.5	3	2.8	1	0.9

[a]North-west (NW) and south-east (SE). [b]Qaanaaq (QA), Uummannaq (UU) and Scoresby Sound (SC).

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tusk protrudes) to the tip of the tusk. The base of the tusk (the part within the skull of the whale) was measured when the tusk was released from the skull. The stomach content of the tuskless male was examined in the field.

The complete tusk, ovaries and eyes of the tusked female were purchased from local hunters and shipped to the GINR for further analyses. In the laboratory, the tusk was sectioned in two, and the individual GLGs, consisting of a dark layer and a paler layer (Heide-Jørgensen et al. 1994), were counted by two different analysts (the authors of this study) using the procedure described by Garde et al. (2012). Three tusk measures—length (cm), mass (kg) and diameter (mm, measured at the melon front)—and the number of GLGs in the sectioned tusk were used to investigate the growth of the female tusk in relation to the growth of male tusks from west (n = 10; Garde et al. 2012) and east (n = 6; GINR database) Greenland, using linear regression. The reproductive status of the tusked female was assessed by external examination of the ovaries for the presence of ovarian corpora: the CL, the yellow body present at pregnancy, and CAs, the scars in ovaries after pregnancies (Perrin & Donovan 1984). The eyes were used for age estimation using the AAR technique; the results have been presented by Garde et al. (2022).

Results and discussion

Frequencies of tusk anomalies

Tusk anomalies in narwhals are a recognized phenomenon, but the frequency of such anomalies in narwhal populations is not well known and has been the subject of few large-scale studies. We investigated 173 narwhals, of which 2.9% (n = 5) displayed tusk anomalies: 1.5% (n = 1) of females had an erupted tusk, 2.8% (n = 3) of males were tuskless and 0.9% (n = 1) of males had double tusks (Table 1). Our finding that <3% of narwhals display tusk anomalies accords with frequencies showed for narwhals harvested in Canada (Hay 1984), although a slightly higher frequency of tusked females (2.7%; n = 3) was found in Canada compared to our result of 1.5%. The frequency of tusk anomalies per area in this study was 4.5% in Qaanaaq, 2.0% in Uummannaq and 2.6% in Scoresby Sound (Table 1). Our results show that tusk anomalies occur sporadically and may vary in different narwhal populations. The difference in frequencies of tusked females observed in this study and in Hay's (1984) study likewise indicates a geographical variation.

Tusked females and tuskless males will not always be identified in the catches, for example, if the reproductive organs are not inspected and (early) pregnancy not detected during flensing. Conversely, catches of the spectacular double-tusked whales often garner public attention and are, therefore, frequently (but not always) reported in the Greenlandic media, although the sex of the whales is rarely noted. Since 2007, double-tusked whales appeared four times in the two Greenlandic online media (www.Sermitsiaq.ag and www.Knr.gl): in 2007 two double-tusked whales were taken in the catches in spring (May) and summer (August) in Kangersuatsiaq (in the Upernavik district) and in Qaanaaq, respectively. The tusks of the former were nearly 2 m in length, and the latter had tusks of 206 and 185 cm in length. In October 2020, a double-tusked whale taken north of Kullorsuaq (in the Upernavik district) had tusks of 200 cm (right) and 186 cm (left). Both tusks had broken tips. In late June 2021, a double-tusked narwhal was sighted from a drone near Qaanaaq and from visual inspection of the whale; both tusks seemed complete, with the right being longer than the left (Fig. 1a).

Biological information from narwhals with tusk anomalies

The tusked female (ID #938; Fig. 2) was caught in the Inuit hunt at the location Hjørnedal in the Scoresby Sound fjord, on 22 August 2017. The female was sexually mature and within the normal range of female growth (Table 2; Garde et al. 2022). The external part of the tusk was 109 cm in length and the part within the skull was 32 cm. The tusk had a broken tip of an estimated length of 5–10 cm; the complete length of the intact tusk was estimated to be 146–151 cm. The length of the female tusk corresponds to lengths of male tusks of similar body lengths (figure 7 in Hay 1984; figure 5 in Garde et al. 2015). The tusk weighed 2.4 kg, with a diameter measured at the melon front of 45 mm (Garde et al. 2012), and 44 GLGs were counted in the sectioned tusk. Growth of the female tusk was assessed by comparison with the growth of male tusks: male tusk length, mass and diameter were expressed by linear regressions, where length against mass was expressed as: $y = 0.035 \times -2.76$ (n = 16; r = 0.88; 95% CI: 0.024–0.045; $p < 0.001$), and length against diameter was expressed as: $y = 0.245 \times +4.94$ (n = 16; r = 0.94; 95% CI: 33.67–48.92; $p < 0.001$). The female tusk fitted well within the 95% CI for both regressions, indicating that the growth of the female tusk follows that of male tusks. The female tusk was considerably more occluded; as annual dentine layers occlude the pulp cavity with time (Watt et al. 2020; Fig. 2b), this indicates that the female tusk was older than male tusks of similar length. We tested this by linear regressions of male tusk length against number of GLGs, $y = 0.254 \times -12.03$ (n = 16; r = 0.83; 95% CI: 11.19–40.34; $p < 0.001$), and male

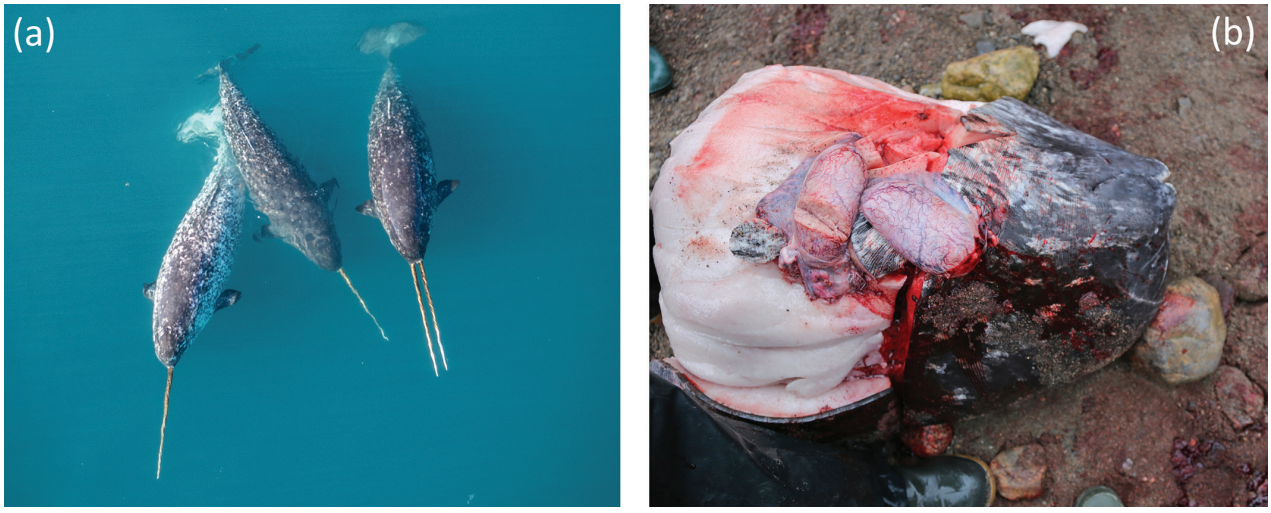

Fig. 1 (a) Double-tusked narwhal filmed from a drone near Qaanaaq on June 2021 (Photo: Jens Ascanius). (b) The head of the tuskless male (#1189) after harvest, with testicles placed on top of the animal.

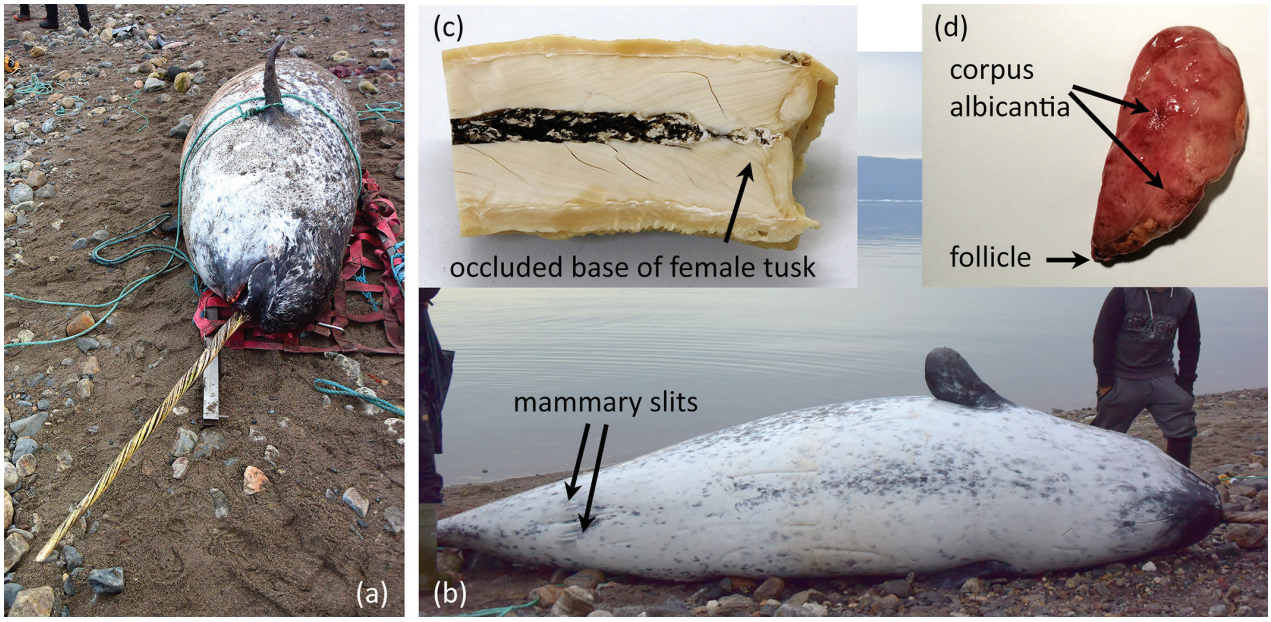

Fig. 2 (a) The tusked female (#938) towed up on the beach at the location Hjørnedal in the Scoresby Sound fjord, south-east Greenland. (b) The ventral side of the tusked female with visible mammary slits. Insets show the occluded base of the female tusk (left) and an ovary from the tusked female with visible ovarian scars (*Corpus albicantia*) and a follicle (arrows indicate the positions of two ovarian scars and the follicle).

tusk diameter against number of GLGs, $y = 0.995 \times -15.14$ ($n = 16$; $r = 0.85$; 95% CI: 10.24–39.07; $p < 0.001$). We found, however, that although the female tusk seemed smaller (shorter and narrower) compared to male tusks with a similar number of annual GLGs, the female tusk fitted within the 95% CI for the male tusks. The growth and size of the female tusk likely reflects the general smaller body size of female narwhals compared to males.

The AAR age of the tusked female was estimated to be 84 ± 6 years (Garde et al. 2022). In most cetacean species, growth layers form annually (Hohn 2008), which has also been established in the conical teeth of beluga whales, the closest relative of narwhals (Stewart et al. 2006; Waugh et al. 2018), and it is reasonable to assume that one GLG is deposited annually in the tusks of narwhals (Hay 1984; Watt et al. 2020; Zhao et al. 2021). The discrepancy between the AAR age estimate and the

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number of annual GLGs (44) in the female tusk is probably a result of occlusion of the pulp cavity for further dentine deposition (Fig. 2b). This has been established for the embedded tusk in both male and female narwhals, where the maximum number of GLGs deposited is in the early 20s, resulting in minimum age estimates (Hay 1984; Watt et al. 2020).

Nine ovarian scars (CAs) were present in each of the ovaries of the tusked female, possibly representing 18 pregnancies (Fig. 2b). Two of the scars appeared recent: they were larger in size, had prominent surface wrinkling and bulged from the ovary. Old and regressed CAs are smaller in size, have an orange–brown colour and are flattened parallel to the ovarian surface (see Hay [1984] for an extended description of ovarian structures). Two follicles were present in one of the ovaries and four in the other, all <5 mm in diameter. In general, CAs regress with age, and in older females, it is expected that a proportion of the CAs has disappeared completely due to this regression (Dabin et al. 2008), resulting in a minimum estimate of CAs in the ovaries of older females. The tusked female could, therefore, potentially have gone through >18 pregnancies. The presence of multiple follicles and two recent looking CAs indicated that the female was still reproductively active. Female narwhals become sexually mature at nine years, and with an average birth rate of one calf every third year (Garde et al. 2022), the tusked female would have been at least 63 years. The examined eye lens was yellow and big (0.59 g); these are also signs of old age (Hood et al. 1999). Based on body dimensions, age, reproductive information and general appearance, we assume that in spite of her age, the tusked female was in good health and perhaps even still reproductively active. Hay (1984) reported on two pregnant females with tusks; carrying a tusk is apparently not in conflict with reproductive success in female narwhals. Additional analyses of tusks from females are needed to learn more about the growth of the female tusk.

The tuskless male (#1189) was collected from the local Inuit hunt at Hjørnedal, in the Scoresby Sound fjord, on 14 August 2014. The body was 440 cm long and weighed 940 kg, with a circumference of 304 cm, which is within the normal range of male growth (Table 1; Garde et al. 2022). Dissection of the tuskless male revealed a pair of testicles 15 cm in length (Fig. 1b). The mass of the testicles was not recorded. In the previous year, on 13 August 2013, the tuskless male was tagged with a satellite transmitter (#3965), measured to have a body length of 420 cm, and erroneously noted as being female because of the lack of a tusk (Heide-Jørgensen et al. 2017). When the tuskless male was dissected in 2014, the stomach contents were examined. They consisted of polar cod (*Boreogadus saida*) and squid remains, characteristic for the diet of narwhals in Scoresby Sound (Heide-Jørgensen et al. 2014; Garde et al. 2022). Subsequent analyses of the dive data (duration and depth) from the satellite transmitter attached in 2013 revealed typical narwhal dive patterns (Ngô et al. 2019). On the basis of body dimensions (length and mass) and testicle size (normal for a male of similar body length [Garde et al. 2015]), the tuskless male was assumed to be sexually maturing, but not yet fully grown (Garde et al. 2022). The lack of a tusk could possibly have hindered his future ability to establish a high rank among other males (Graham et al. 2020), attract females and engage in mating rituals, in which case he might never have had the chance to mate and sire calves. That tuskless males persist in narwhal populations could conceivably be explained by their ability to establish a hierarchy based solely on a large body size and aggressive and/or dominant behaviour, even in the absence of a tusk. The mating system of narwhals is not well known but is possibly polygynous, with one male mating with several females (Kelley et al. 2015). In a population of another tusked animal with a polygynous mating system, the Asian elephant (*Elephas maximus*), it has been observed that of the three male–male signals (musth, body size and tusk possession), musth and body size can override tusk possession. Musth and body size are, thus, stronger determinants of dominance than tusk possession in this particular population of Asian elephants (Chelliah & Sukumar 2013). The presence of scars left on the skin by the teeth of conspecifics also indicate intra-specific aggression in beluga whales (Ham et al. 2021), and a clear correlation between size and dominance, with larger animals most often more dominant to smaller animals, regardless of sex, was found in a study of captive beluga whales (Lomac-Macnair et al. 2015).

The two tuskless males collected in Qaanaaq in July–August 1993 were both physically mature, with body lengths of 489 and 490 cm, but both had undeveloped testes (<100 g; GINR database) compared to tusked males of similar body size (Garde et al. 2015). The absence of tusks in some male narwhals could perhaps be linked to disorders in the hormonal system inhibiting growth of the testes. Hay (1984) reported that embedded in the maxillae of two young tuskless males (336 and 338 cm in body length) were the two teeth characteristic of females. It was not recorded whether the embedded teeth were present in the maxillae of the three tuskless males in this study, although we assume they were.

We have limited information on the double-tusked male (#547) collected in November 1993 in Uummannaq. The body was 385 cm in length with a body mass of 838 kg, a fluke width of 90 cm and tusk lengths of 68 cm (right) and 88 cm (left; Table 2). Based on these body

Table 2 Collection date, location and body measurements from the tusked female (#938), tuskless male (#1189) and two-tusked male (ID #547).

ID no.	Year	Month	Day	Region[a]	Location[b]	Sex	Body length (cm)	Body mass (kg)	Tusk length, external (cm)	Fluke width (cm)	Circumference (cm)
938	2017	8	22	SE	SC	F	390	1000	109[c]	-	-
1189	2014	8	14	SE	SC	M	440	940	-	102	304
547	1993	11	18	NW	UU	M	385	838	68; 88	90	-

[a]South-east (SE) and north-west (NW). [b]Scoresby Sound (SC) and Uummannaq (UU). [c]The part of the tusk within the skull was 32 cm. The tusk had a broken tip of an estimated length of 5–10 cm. The complete length of the tusk was estimated to be 146–151 cm.

dimensions, it was assessed that the double-tusked male was a sub-adult that had not yet attained full sexual maturity (Garde et al. 2015; Garde et al. 2022). Another double-tusked whale was caught in the Scoresby Sound fjord in September 2009. Biological information about the whale originates from the sample record provided by the Inuit hunter who caught the whale. The whale was male, measuring 420 cm in length, with a fluke width of 100 cm and tusks of 83 and 56 cm. This male was not included in the frequency of double-tusked males because it was not part of a sampling scheme collected by trained biologists. There was no information on the testes. It was previously reported that the right tusk of double-tusked whales is nearly always shorter and less robust than the left (Porsild 1922; Fraser 1938); the shorter length of the right tusk of the double-tusked male (#547) in this study supports this observation.

Conclusion

Our study shows that although relatively uncommon, tusk anomalies in narwhals persist. The biological mechanisms behind tusk anomalies and how they persevere in a species as genetically homogeneous as the narwhal (Palsbøll et al. 1997; Westbury et al. 2019) are unknown. Further studies of tusk development, including genetic and hormonal studies, would increase our understanding of the growth of the narwhal tusk and the persistence of tusk anomalies. For future investigations of tusk anomalies, institution and museum collections of narwhal tusks could provide additional insights into tusk anomalies. Also, specimens of double-tusked whales could be genetically sexed to determine if female narwhals are also represented.

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Disclosure statement

The authors report no conflict of interest.

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