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Using stable isotope analysis as a tool for narwhal (<i>Monodon monoceros</i>) stock delineation	Avoir recours à l'analyse des isotopes stables pour définir les limites des zones fréquentées par le narval (<i>Monodon monoceros</i>)

Cortney A. Watt¹, Steven H. Ferguson², Aaron Fisk³, and Mads Peter Heide-Jørgensen⁴

¹Department of Biological Sciences, University of Manitoba, Winnipeg, MB, Canada, R3T 2N2 ²Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, MB, Canada, R3T 2N6 ³Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, Canada, N9B 3P4 ⁴Greenland Institute of Natural Resources, Nuuk, Greenland

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ABSTRACT

Stable isotope analysis of carbon and nitrogen was conducted on narwhal skin tissues from nine hunting areas, which included six narwhal stocks in the Canadian Arctic and Greenland: Somerset Island, Eclipse Sound, Admiralty Inlet, and East Baffin Island from the Canadian Arctic, and Melville Bay, and West Greenland from Greenland. Samples were also obtained from narwhals from the Northern Hudson Bay and East Greenland populations, and the High Arctic hunting area in Canada. Discriminant analysis, which included all six stocks, the two populations, and the High Arctic, determined if hunting areas had significantly different isotope values; however, since diet may vary seasonally and by sex, analyses that considered samples divided by the season of collection and discrimination for males and females separately was also conducted. Narwhals from East Greenland and Northern Hudson Bay are genetically and spatially segregated from the Baffin Bay stocks, and these two populations had isotope values that clearly distinguished them in spring and summer. Baffin Bay stocks were more difficult to distinguish; however, there was a significant difference between the Admiralty Inlet and Eclipse Sound stocks in the spring and summer models, and in the model that included all hunting areas regardless of season. There was also a significant difference between the West Greenland and Melville Bay stocks in winter and the Eclipse Sound and West Greenland stocks in autumn. When the model that included all hunting areas was compared to that which considered males and females independently, there was some overlap with the Melville Bay and West Greenland stocks for the females not seen in the model that combined males and females, but the discrimination among males was not significantly different from this model. The results are interpreted assuming both a short (two to three month) and long (one to two years) turnover rate. Overall, stable isotope analysis may be useful for delineating stocks, especially if used in combination with other techniques currently used for stock assignment.

RÉSUMÉ

Des chercheurs ont effectué une analyse des isotopes stables de l'azote et du carbone prélevés sur les tissus cutanés de narvals capturés dans neuf zones de chasse, y compris six stocks de narvals de l'Arctique canadien et du Groenland (île Somerset, détroit d'Éclipse, inlet de l'Amirauté et est de l'île de Baffin dans l'Arctique canadien de même que dans la baie de Melville et à l'ouest du Groenland, au Groenland). Des échantillons ont également été prélevés sur des narvals des zones de chasse situées au nord de la baie d'Hudson, à l'est du Groenland et dans le Haut-Arctique canadien. Une analyse discriminante des six stocks, des deux populations et du Haut-Arctique, a permis de déterminer si les zones de chasse présentaient des concentrations d'isotopes extrêmement différentes. Or, puisque l'alimentation diffère en fonction des saisons et du sexe, on a également mené des analyses sur des échantillons classés en fonction de ces catégories. On a constaté que les populations de narvals de l'est du Groenland et au nord de la baie d'Hudson étaient différentes des stocks de la baie de Baffin sur le plan génétique et spatial. Ces deux populations présentaient des concentrations d'isotopes qui permettaient de les distinguer clairement au printemps et en été. Les stocks de la baie de Baffin étaient plus difficiles à distinguer. On note cependant une différence importante entre les populations de l'inlet de l'Amirauté et du détroit d'Éclipse dans les modèles du printemps et de l'été ainsi que dans le modèle incluant toutes les zones de chasse peu importe la saison. On note également une différence considérable entre les stocks de l'ouest du Groenland et de la baie de Melville en hiver. C'est également le cas des stocks du détroit d'Éclipse et de l'ouest du Groenland en automne. En comparant le modèle qui englobe toutes les zones de chasse à celui qui classe les données selon le sexe, on constate que les données sur les femelles se recoupent entre les stocks de la baie de Melville et de l'ouest du Groenland, mais que ce n'est pas le cas lorsqu'on les compare au modèle qui combine les mâles et les femelles. Les données sur les mâles ne sont pas nettement différentes du présent modèle. Les résultats sont interprétés en fonction d'une période de renouvellement des stocks courte (de deux à trois mois) ou longue (de un à deux ans). De manière générale, l'analyse des isotopes stables peut servir à définir les limites des aires de répartition, surtout si elle est combinée à d'autres techniques utilisées pour désigner les stocks.

INTRODUCTION

Narwhals (*Monodon monoceros*) are socially and culturally important for northern communities, are part of the subsistent hunt in Canada and Greenland, and make up a large proportion of the dietary needs of the Inuit living in these communities. Stocks are defined as a unit group of animals that are subject to hunting (DFO 2010a). An understanding of narwhal movement and spatial distribution is needed to define narwhals to specific stocks and for providing management advice to ensure subsistence harvests are sustainable.

The first step to managing stocks is to determine how many stocks exist and how many individuals comprise a stock. Fisheries and Oceans Canada (DFO) identifies two populations of narwhals in Canada, Northern Hudson Bay and Baffin Bay narwhals. Current knowledge of narwhal stocks in Canada suggests that the Baffin Bay narwhal population is composed of at least four narwhal summering stocks: Somerset Island, Admiralty Inlet, Eclipse Sound, and East Baffin Island. There are also narwhals found elsewhere in the Canadian high Arctic (DFO 2010b; Richard 2010) but their relationship to the four summering stocks is unknown. For this report these are referred to as High Arctic narwhals. In Greenland there are two defined stocks with a third and fourth stock probable (Heide-Jørgensen pers. comm.). Evidence for current stock identity comes from genetic studies (Brown Gladden et al. 1997; Palsbøll et al. 1997; Riget et al. 2002; de March et al. 2003), contaminant analyses (Riget et al. 2002; de March and Stern 2003: Dietz et al. 2004), and satellite tracking methods (Richard 1991: Dietz and Heide-Jørgensen 1995; Dietz et al. 2001; Heide-Jørgensen et al. 2002; 2003). Satellite telemetry studies have enhanced our understanding of narwhal summer aggregations, but they are extremely expensive, only provide data on a small sub-set of the population, and few tags last a complete annual cycle. Genetic analyses are useful for defining stocks; however, this technique has provided only weak evidence for stock assignment in narwhals because of their low genetic diversity (de March et al. 2003; Petersen et al. 2011). As a result, another method for defining narwhal stocks is needed.

Defining narwhal stocks is difficult, and determining what stock a particular community is harvesting is even more complicated. Many harvests occur when narwhals are migrating past a particular community and that community may not be within the summer range of the narwhal stock. For instance, narwhals that are part of the Somerset Island stock migrate past Pond Inlet and Arctic Bay on the way to their summer regions and these communities likely hunt some of these narwhals; however, the number of narwhals taken from this stock is unknown (DFO 2010b). As a result, catches are attributed to stocks close to the community where they occur (DFO 2010b), which can be problematic if the hunted narwhal actually belongs to a different summer stock. Thus, it is important to be able to determine what summer aggregation a narwhal that is hunted during its migration is ultimately from. Stable isotope analysis may be able to provide information on migratory animals if isotope values vary among stocks.

Stable isotopes are variations of elements with a different number of neutrons, and therefore a different atomic mass and there is natural, and often predictable, variation in the ratio of the heavy to light isotopes in the environment. In predator tissues, the stable isotope ratios of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) are directly related to the ratios found in their prey (Peterson and Fry 1987) and vary with geography (Graham et al. 2010). For instance, within the geographic range of narwhals, contour plots of isotope values show there is a 1 % change in $\delta^{15}N$ in zooplankton from Hudson Bay to the Davis Strait and there is a significant increase of approximately 5 ‰ and 1 ‰ in $\delta^{13}C$ for plankton in the Canadian high Arctic compared to East Greenland and Hudson Bay, respectively (Graham et al. 2010). Therefore, isotope ratios can

give detailed information regarding the integrated dietary and geographic information of a species (Best and Schell 1996; Hobson and Schell 1998; Das et al. 2004; Crawford et al. 2008).

Few studies investigating marine mammal stocks have utilized isotopes as a defining factor for stock assignment; however, fatty acids, which, similar to stable isotopes are primarily influenced by diet. have been shown to act as natural markers for stock identification for many fish species (Grahl-Nielsen 2005). Dietz et al. (2004) used $\delta^{15}N$ and $\delta^{13}C$ in muscle to distinguish narwhal from two presumed distinct populations from western Greenland, which suggested narwhals from the two populations may feed at different trophic levels and/or on different prey items. It is thought that narwhals from west Greenland gain most of their fat reserves in the winter by consuming large proportions of Greenland halibut (Reinhardtius hippoglossoides) (Laidre and Heide-Jørgensen 2005). In Canada, however, a study conducted by Hay (1984) showed that the condition index (maximum girth/body length) peaks in August in male narwhals and declines after that. Female narwhals, on the other hand, have shown very little seasonal change in condition index (Hay 1984) or have had a decrease in body condition over the summer months, which may have been a result of increased demands placed on calving females (Finley and Gibb 1982). Since the period of fat gain may differ between narwhal summering aggregations, this may indicate that the importance of different prey items and/or the season when prey is consumed by narwhals differs. Stable carbon and nitrogen isotopes in narwhals of the Canadian Arctic have not been previously investigated or compared to Greenland narwhal summer aggregations, and no study has compared isotopic values among different marine mammal stocks.

This study investigates differences in stable isotope values among six narwhal stocks in Canada and Greenland, the Northern Hudson Bay and East Greenland populations, and narwhals sampled from the Canadian High Arctic hunting area. Narwhal skin samples, which are also used for genetic investigations, are easily collected by hunters during the annual subsistent hunt, and can also be collected from live individuals non-invasively, are used for the analysis. If stable isotope values are distinct for defined narwhal hunting areas, this analysis may provide a financially feasible approach to determine assignment for individual narwhals. The technique may be particularly useful for deciphering stock assignment when harvests occur during the migratory period. The objective of our study was to analyze narwhal skin samples from six previously defined narwhal stocks, the Northern Hudson Bay and East Greenland populations, and the Canadian High Arctic hunting area (Figure 1) and determine if isotopic values vary, in order to identify whether stable isotope analysis can be used as another tool for defining narwhal stocks.

METHODS

Inuit hunters and researchers have collected narwhal skin samples from Greenland and Canada since the 1980s. Samples were collected from the communities of Pond Inlet, Arctic Bay, Grise Fiord, Pangnirtung, Resolute Bay, and Repulse Bay in Nunavut, Canada (Table 1; Figure 1). Samples from Greenland came from Ittoqqortormiut, Scorebysund, Savissivik, Uummannaq, and Qaersut (Table 1; Figure 1). These communities span six previously identified narwhal stocks, two narwhal populations, and the Canadian High Arctic hunting area (Heide-Jørgensen pers. comm.; DFO 2010b; Table 1). Narwhal skin samples collected from each community were defined as belonging to the hunting area the community typically encounters and skin samples collected during the migratory period were assigned to areas close to the community where catches are reported (DFO 2010b). To investigate the utility of stable isotopes for defining narwhal hunting areas, a multiple discriminant analysis was used to determine if narwhals previously defined as belonging to a specific hunting area could be distinguished based on their

isotopic values. Stable isotope values are impacted by diet, and diet may vary seasonally; thus, discrimination among hunting areas was considered on a seasonal basis. Samples collected in December-March were defined as winter samples, those from May-July as spring, August-September as summer, and October-November as autumn. Seasonal analysis limited the sample size and resulted in only two stocks being compared for both autumn and winter seasons so a discrimination analysis of all communities regardless of the date of catch was also performed. Since males and females may exhibit different diet habits and diet may change over time, discriminant analysis was also used to determine if stable isotope values were significantly different between male and female narwhals within each hunting area.

Narwhal skin tissue was sub-sectioned and a 0.5 q piece of skin was diced, freeze-dried for 48 hours and further homogenized with a glass mortar and pestle. To extract lipids, tissues were vortexed with ~5 ml of 2:1 chloroform:methanol for 30 s, placed in a water bath (30°C) for 24 hours, decanted and the process repeated. Lipid extracted samples were placed in a fumehood for 24 hours to dry. Four hundred to 600 µg of tissue was weighed into tin capsules and a continuous flow isotope ratio mass spectrometer (IRMS, Finnigan MAT Deltaplus, Thermo Finnigan, San Jose, CA, USA) was used to determine δ^{13} C, δ^{15} N and % C and N. The standard reference material was Pee Dee Belemnite carbonate for CO₂ and atmospheric nitrogen N₂. Every 12th sample was run as a triplicate to assess precision; the mean standard deviation of these samples was 0.11 ‰ for δ^{13} C and 0.12 ‰ for δ^{15} N. Internal lab and National Institute of Standards and Technology (NIST) standards were analyzed after every 12 samples for quantification of samples and to assess analytical precision. The analytical precision (standard deviation) for NIST standard 8414 (bovine muscle, n=152) and an internal lab standard (tilapia muscle, n = 152) for δ^{13} C was 0.07 and 0.09, respectively, and for δ^{15} N was 0.15 and 0.19, respectively. To assess accuracy, certified NIST standards were analyzed during the analysis of samples. For δ^{13} C, the mean value for NIST 8542 (-10.48 ± 0.03; n = 10) was within 0.01 of the certified value of -10.47 and for NIST 8573 (-26.26 \pm 0.04; n = 10) was within 0.13 of the certified value of -26.39. For δ^{15} N, the mean value for NIST 8542 (4.58 ± 0.11; n = 10) was within 0.12 of the certified value of 4.70 and for NIST 8548 (20.11 \pm 0.38; n = 9) was within 0.30 of the certified value of 20.41.

The burning of fossil fuels emits anthropogenic CO_2 that is depleted in ¹³C resulting in a more depleted carbon isotope value, which is known as the "Suess effect" (Körtzinger and Quay 2003). As a result, carbon isotope values were corrected for the Suess effect by applying a correction. A value of 0.02 ‰ (an average between mean values reported by Körtzinger and Quay (2003) and Sonnerup et al. (1999)) per year beyond 1982 (the oldest sample included in the data set) was added to the δ^{13} C value.

RESULTS

First, we tested for differences among narwhal hunting areas according to the season of the hunt. Linear discriminant analysis (LDA) found there was a significant difference between winter samples from Melville Bay and West Greenland (Wilk's Lambda = 0.8459, $F_{2,67}$ = 6.1032, p = 0.0037) and correctly classified 81 % of narwhals to their winter stocks. Twelve of 64 narwhals from Melville Bay were misclassified as West Greenland narwhals, and one of six narwhals from West Greenland was assigned to the Melville Bay stock (Table 2). Multiple discriminant analysis (MDA) for spring samples collected from Admiralty Inlet, Northern Hudson Bay, High Arctic, East Baffin Island, and Eclipse Sound showed there were significant differences among some hunting areas (Figure 2A) (Wilk's Lambda = 0.1679, $F_{8,272}$ = 48.9651, p < 0.0001) and the analysis was able to correctly classify 67 % of narwhals to their correct summering area. Typically, misclassified narwhals were assigned to two or three other hunting areas, with

approximately equal probability (Table 3A). Only one of 51 narwhals from Northern Hudson Bay was misclassified (Table 3B). Summer samples from Admiralty Inlet, East Greenland, High Arctic, Eclipse Sound, Somerset Island, and Northern Hudson Bay could also be discriminated (Wilk's Lambda = 0.1392, $F_{10,414}$ = 69.5450, p < 0.0001), but only 51 % of the narwhals were correctly classified to their putative hunting area (Figure 2B; Table 4A), with most of the misclassification occurring among the narwhals sampled from the High Arctic and Eclipse Sound (Table 4B). Autumn samples from Eclipse Sound and West Greenland were significantly different (LDA: Wilk's Lambda = 0.8550, $F_{2,101}$ = 8.5644, p = 0.0004) and were correctly classified 90 % of the time. Only 10 of 102 narwhals from West Greenland were misclassified as being from Eclipse Sound and all narwhals from Eclipse Sound were correctly assigned (Table 5).

Next, we combined seasons and assessed differences among narwhal hunting areas. Multiple discriminant analysis of narwhals from the six stocks, the Northern Hudson Bay and East Greenland populations, and the High Arctic hunting area indicated there were significant differences between isotope values (Wilk's Lambda = 0.1522, $F_{16,1040}$ = 101.6337, p < 0.0001) (Figure 3). Most notably, narwhal stable isotope values were significantly different for the Northern Hudson Bay and East Greenland populations; these populations are spatially segregated from narwhals in other areas with no known geographic overlap, and narwhals from these populations were classified to the correct population 88 and 93 % of the time, respectively (Table 6). There were also significant differences, based on 95 % confidence circles, between the Melville Bay and West Greenland stocks. Narwhals from Admiralty Inlet also had isotope values that were distinct from other stocks. Confidence intervals were large for the Somerset Island and East Baffin Island narwhal stocks as a result of the small sample sizes (n=13 and 12. respectively). Despite the large confidence limits, narwhals from East Baffin Island do appear to have a relatively distinct isotope value that may be useful for defining the stock. Considering we had such a small sample size, 25 % of narwhals from the East Baffin Island stock were classified correctly, compared to only 8 % of narwhals from the Somerset Island stock (Table 6). Narwhals from Eclipse Sound and the High Arctic have similar isotope values, and Somerset Island isotope ratios overlap these hunting areas as well as the two stocks from west Greenland (Melville Bay and West Greenland). Narwhals from the High Arctic were misclassified most frequently at 93 % (Table 6).

Male and female narwhals displayed significantly different isotope signatures within the Melville Bay (Wilk's Lambda = 0.7607, $F_{2,61}$ = 9.5960, p = 0.0002), West Greenland (Wilk's Lambda = 0.8393, $F_{2,98}$ =, p = 0.0002), Eclipse Sound (Wilk's Lambda = 0.9146, $F_{2,127}$ = 5.9313, p = 0.0034) stocks, and the High Arctic hunting area (Wilk's Lambda = 0.7734, $F_{2,41}$ = 6.0059, p = 0.0052) (Table 1). Since these differences spanned many hunting areas (Table 1), a discrimination test for all hunting areas was conducted separately for each sex. Multiple discriminant analysis of female narwhals from all hunting areas except East Baffin Island, because we only had male samples, and male narwhals from all nine hunting areas indicated there were significant differences between isotope values (Wilk's Lambda = 0.1272, $F_{14,338}$ =, p < 0.0001; Wilk's Lambda = 0.1479, $F_{16,650}$ = 64.9937, p < 0.0001) (Figure 4; Table 7). The discrimination model that only included females was similar to that for all narwhals together, other than the Melville Bay and West Greenland stocks were no longer distinct from one another and overlapped significantly more with narwhals from the High Arctic (Figure 4A). The discrimination model for male narwhals was not significantly different from the model with all narwhals together (Figure 4B).

DISCUSSION

Stable carbon and nitrogen isotopes varied significantly among most narwhal hunting areas, and the technique was able to statistically distinguish among narwhal populations that exhibit no overlap in their home ranges in summer or winter. The method was also able to discriminate among some stocks that summer in areas in the same geographical region and thus may be useful for stock definitions.

Narwhal skin samples from Canada are primarily collected in the summer months, from June to early September. Samples from Greenland, on the other hand, are more often than not collected in the winter months. Differences in the season of collection complicate comparisons of isotope values between Greenland and Canadian narwhals because diet likely differs between summer and winter and the influence this may have on the interpretation of the results depends on tissue turnover rates. There is relatively little known about how guickly stable isotopes are incorporated into large marine mammal tissues and nothing is currently known regarding turnover rates in narwhal skin; however, there are studies on epidermal movement rates in beluga (Delphinapterus leucas) (St. Aubin et al. 1990) and dolphin (Tursiops truncatus) (Brown et al. 1983; Hicks et al. 1985), as well as a diet-switching experiment conducted in alpaca (Lamo pacos) muscle (Sponheimer et al. (2006). These studies found different rates and the implications of these turnover rates on discrimination among the Baffin Bay stocks is not trivial and thus will be discussed independently. The East Greenland and Northern Hudson Bay populations are not considered in the following turnover discussion because we find good isotope discrimination among these groups across all seasons since they are geographically segregated from the Baffin Bay population at all times of the year.

TURNOVER ~ 2-3 MONTHS

St. Aubin et al. (1990) found that tissue turnover in beluga whales was on the order of 70-75 days (approximately 2-3 months). If we assume this rate is the same for the beluga's closest relative, the narwhal, then samples collected in summer (August-September) represent diet from June, when narwhals are travelling to their summering regions, to August-September, when narwhals have reached their summer destination (Heide-Jørgensen et al. 2003). We expect relatively little isotope discrimination among the stocks during the migratory period; however, we expect larger distinction when they are at their summering regions. There is a significant difference between the Admiralty Inlet and Eclipse Sound stocks at this time. In addition, the Somerset Island stock, had there been a larger sample size, may have been distinct during this time frame. Samples collected in autumn (October-November) represent dietary intake from August to October-November when narwhals are in their summer regions and begin their migration to the Davis Strait. We expect large discrimination at this time; unfortunately, there are only two stocks for comparison from autumn (Eclipse Sound and West Greenland), but there was large discriminatory power among those stocks. Samples collected in spring (May-July) represent March to May-July dietary intake when narwhals are in the wintering area at the Davis Strait and start their migration toward the summer regions. At this time we would expect relatively little discrimination among stocks, but we actually see distinction between the Admiralty Inlet and Eclipse Sound stocks. Samples collected in winter (December-March) represent October to December-March when narwhals have started migrating back to the Davis Strait and at this time we would expect very little variation in isotope signatures, although we do see a difference in the only two stocks we can compare, West Greenland and Melville Bay.

This turnover rate determined by St. Aubin et al. (1990) was calculated on a beluga whale, penned in an estuary in July 1985 for 42 days where they measured epidermal turnover by

charting the migration of labeled cells; however, at 42 days the cells had not fully migrated out of the skin and thus they assumed a constant rate and calculated 70-75 days as the estimated tissue turnover (St. Aubin et al. 1990). Unfortunately, belugas undergo an unusual molting process by moving into warm estuaries and physically sloughing off skin, which is not seen in any other cetaceans, including narwhals. St. Aubin et al. (1990) warn the rate they calculated comes from only one whale, at a time of maximal proliferation, and may be unique to beluga whales. In addition, the assumption of constant rate may only be applicable during the molting season; St. Aubin et al. (1990) suggest the sloughing rate is relatively slow during the 8-10 months that belugas spend in water of 5 °C, although they were not able to quantify this rate. Labeled cells migrated through the epidermis at a rate of 0.13 mm/day in beluga skin and this rate was six times higher than that reported for the bottlenose dolphin (*Tursiops truncatus*) (Brown et al. 1983; Hicks et al. 1985). The bottlenose dolphin studies were also conducted using labeled cells measured at specified time intervals in captive dolphins that were held in sea water in floating pens at the Naval Ocean Systems Center's laboratory at Kaneohe Bay, Hawaii and then moved to the New England Aquarium (Brown et al. 1983; Hicks et al. 1985). They calculated an epidermal migration rate of 0.019 mm/day (Brown et al. 1983; Hicks et al. 1985). If this rate applies to narwhals, which have an average skin thickness of 13.6 mm (Wagemann and Kozlowska 2005), it would take almost 2 years for full skin turnover. Sponheimer et al. (2006) used diet-switching experiments to measure turnover rates in a large mammal, the alpaca. Diet-switching experiments are the best method for measuring turnover rates because these studies are ultimately investigating the phenomena of interest, how quickly diet is incorporated into tissues. Typically these studies find much longer turnover times than artificial labeling studies. Sponheimer et al. (2006) fed alpacas a C₃ grass diet on a small pasture at Brigham Young University, Utah for a year and then switched the diet to C₄ grass. Although they did not measure turnover rates in skin, their rates for muscle turnover suggest it would take well over a year to incorporate 90 % of a new dietary signal into the tissue (Sponheimer et al. 2006). Given these circumstances it is possible that narwhals experience a much longer turnover rate, perhaps on the order of 1-2 years.

TURNOVER ~ 1-2 YEARS

If narwhal epidermal migration rates are similar to those determined for bottlenose dolphins (Brown et al. 1983; Hicks et al. 1985), narwhal samples collected in August-September (summer) would reflect an average dietary signal from the previous two years and if we assume rates are similar to alpaca muscle, an average of the previous year. Regardless of whether the rate is one or two years, if we assume diet changes significantly with season but not annually, the interpretations are the same. Tissues would reflect an integrated signal from diet across all seasons and all samples, regardless of the season of collection, can be directly compared. In this case, if we ignore Somerset Island and East Baffin Island, for which we have small sample sizes, we see distinction among all of the hunting areas, except Eclipse Sound and the High Arctic, which overlap significantly.

CONCLUSION

If we assume a short turnover rate, we still see some differences among hunting areas in times when we would expect little variation, such as when all whales that make up the Baffin Bay population are in the Davis Strait, which may provide evidence for a much longer turnover rate. When we expected differences to be maximized we had few hunting areas to compare, but those in which comparisons were made were significantly distinct. If we assume a longer turnover then the isotope method is able to distinguish among many hunting areas, even those that have low genetic diversity such as narwhals from the Admiralty Inlet and Eclipse Sound

stocks. Regardless of why differences in isotope values among hunting areas exist, either a result of a change in diet or geography, the technique proved it may be useful for understanding current stock definitions across all seasons and can potentially aid in delineating stocks in the future. For some of the hunting areas, narwhal assignment to their hunting area was weak, for instance for the High Arctic area individuals were often assigned to Admiralty Inlet, Eclipse Sound or Somerset Island. It is important to note that the "actual" hunting area that the whale belongs to is assumed based on where the whale was hunted; however, the whale may belong to another summer aggregation if it was hunted on the migration route to or from its summer region. This is particularly an issue for samples collected in summer and spring if we assume a 2-3 month tissue turnover rate, because these whales would be hunted while in transit to and from their summering areas, respectively. Migrating whales are not a concern if the tissues are integrating diet over the previous year because they would still contain signals that originated in their summering regions. Despite these considerations we were able to classify many narwhals to the assumed correct hunting area.

One issue with adding this technique to the repertoire of currently used methods is that it requires a reasonable sample size. East Baffin Island and Somerset Island both displayed large 95 % confidence intervals around the mean because of the small sample size, which made it difficult to distinguish these stocks; however, in addition to hunter collections, samples can be collected non-invasively through biopsies, which would allow a much greater proportion of the population to be sampled. Stable isotope analysis is a cost effective method, samples can easily be obtained in conjunction with samples collected for genetic investigations, no chemical preservation is required, and a very small amount of tissue is required, which suggests it may be beneficial for stock delineation. Stable isotope analysis could be added as another tool for stock assignment, and in conjunction with the other approaches currently being used, may result in more detailed stock discreetness knowledge, which can improve management decisions.

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Table 1. Summary information on narwhal skin samples collected from 11 communities, which comprised six narwhal stocks, the Northern Hudson Bay and East Greenland populations, and narwhals hunted in the High Arctic area (Heide-Jørgensen pers. comm.; DFO 2010b). The year and month samples were collected along with sample sizes indicating the number of male and female samples is presented. Total sample size includes narwhals that have not been genetically sexed.

Community	Hunting area	Year	Month/Season	Total	Males	Females	Significant
	assignment		sampled	sample			sex
				size			differences?
Ittoqqortormiut	East Greenland	1995	Summer	26	6	6	No
Scoresbysund	East Greenland	1994	Summer	17	15	2	No
Savissivik	Melville Bay	1994	Feb	64	40	24	Yes
Uummannaq	West Greenland	1993	Mar and Nov	45	27	13	Yes
Qaersut	West Greenland	1992	Nov - Dec	63	44	17	Yes
Repulse Bay	Northern Hudson Bay	1993-2009	June - Aug	73	40	23	No
Pond Inlet	Eclipse Sound	1982-2009	May - Oct	159	72	58	Yes
Arctic Bay	Admiralty Inlet	1999-2009	June - Sept	76	43	27	No
Grise Fiord	High Arctic	2000-2007	July - Sept	45	38	6	Yes
Pangnirtung	East Baffin Island	1990-2004	May - Aug	12	2	0	NA
Resolute Bay	Somerset Island	2002-2009	Aug - Sept	13	7	3	No

Table 2. Winter narwhal skin samples from the Melville Bay and West Greenland stocks showing A) the misclassified narwhals and what stock they were assigned and B) the numbers of narwhals assigned to the actual versus predicted stock.

A) Actual stock	Stock assignment	Probability of	Probability of
	by discriminant	assignment to	assignment to
	analysis	actual stock	incorrect stock
Melville Bay	West Greenland	0.34	0.66
Melville Bay	West Greenland	0.43	0.57
Melville Bay	West Greenland	0.29	0.71
Melville Bay	West Greenland	0.27	0.73
Melville Bay	West Greenland	0.42	0.58
Melville Bay	West Greenland	0.29	0.71
Melville Bay	West Greenland	0.36	0.64
Melville Bay	West Greenland	0.45	0.55
Melville Bay	West Greenland	0.36	0.64
Melville Bay	West Greenland	0.11	0.89
Melville Bay	West Greenland	0.45	0.55
Melville Bay	West Greenland	0.07	0.93
West Greenland	Melville Bay	0.45	0.55

B) Predicted stock⇒	Melville	West
Actual stock ↓	Bay	Greenland
Melville Bay	52	12
West Greenland	1	5

Table 3. Spring narwhal skin samples from the Canadian narwhal hunting areas showing A) the misclassified narwhals and what hunting area they were assigned and B) the numbers of narwhals assigned to the actual versus predicted hunting area (EBI=Eastern Baffin Island, HA=High Arctic, ES=Eclipse Sound, AI=Admiralty Inlet, NHB=Northern Hudson Bay).

A) Actual hunting area	Hunting area assignment by discriminant analysis	Probability of assignment to correct hunting area	Probability of assignment to incorrect hunting area
Admiralty Inlet	EBI, HA, ES	0.29	0.32, 0.23, 0.16
Admiralty Inlet	EBI, HA, ES	0.29	0.29, 0.24, 0.19
Admiralty Inlet	EBI, HA	0.27	0.45, 0.23
Admiralty Inlet	ES	0.16	0.52, 0.27
Admiralty Inlet	EBI, HA, ES	0.29	0.33, 0.22, 0.16
Admiralty Inlet	ES, HA, EBI	0.23	0.35, 0.29, 0.12
Admiralty Inlet	EBI, HA, ES	0.29	0.37, 0.21, 0.13
Admiralty Inlet	EBI, HA, ES	0.29	0.30, 0.25, 0.16
Admiralty Inlet	HA, EBI, ES	0.24	0.32, 0.14, 0.30
Admiralty Inlet	EBI, HA, ES	0.29	0.32, 0.22, 0.17
Admiralty Inlet	EBI, HA, ES	0.29	0.30, 0.26, 0.16
Admiralty Inlet	EBI, HA, ES	0.29	0.30, 0.26, 0.16
Admiralty Inlet	EBI, HA, ES	0.29	0.31, 0.23, 0.17
Admiralty Inlet	ES, HA, EBI	0.23	0.35, 0.31, 0.11
Admiralty Inlet	HA, EBI, ES	0.27	0.29, 0.22, 0.22
High Arctic	ES, AI, EBI	0.27	0.34, 0.24, 0.15
High Arctic	ES, AI, EBI	0.28	0.33, 0.24, 0.15
High Arctic	EBI, AI, ES	0.20	0.37, 0.29, 0.14
High Arctic	EBI, AI, ES	0.20	0.36, 0.29, 0.15
High Arctic	ES, AI, EBI	0.29	0.33, 0.24, 0.14
High Arctic	ES, AI	0.31	0.41, 0.20
High Arctic	ES, AI	0.35	0.38, 0.19

A) Actual hunting area	Hunting area assignment by discriminant analysis	Probability of assignment to correct hunting area	Probability of assignment to incorrect hunting area
High Arctic	AI, EBI, ES	0.27	0.28, 0.27, 0.18
High Arctic	AI, EBI, ES	0.26	0.28, 0.24, 0.23
High Arctic	EBI, AI, ES	0.22	0.35, 0.29, 0.15
East Baffin Island	ES, AI, HA	0.09	0.37, 0.21, 0.32
Eclipse Sound	AI, HA, EBI	0.19	0.28, 0.28, 0.25
Eclipse Sound	AI, HA, EBI	0.21	0.28, 0.25, 0.26
Eclipse Sound	AI, HA, EBI	0.22	0.28, 0.23, 0.27
Eclipse Sound	AI, HA, EBI	0.18	0.28, 0.28, 0.26
Eclipse Sound	HA, AI, EBI	0.33	0.34, 0.23, 0.11
Eclipse Sound	HA, AI, EBI	0.26	0.28, 0.27, 0.19
Eclipse Sound	HA, AI, EBI	0.20	0.30, 0.28, 0.23
Eclipse Sound	HA, AI, EBI	0.21	0.36, 0.26, 0.17
Eclipse Sound	HA, AI, EBI	0.24	0.27, 0.27, 0.21
Eclipse Sound	HA, AI, EBI	0.26	0.28, 0.27, 0.19
Eclipse Sound	HA, AI, EBI	0.18	0.33, 0.28, 0.22
Eclipse Sound	HA, AI	0.35	0.39, 0.19
Eclipse Sound	EBI, AI, HA	0.09	0.47, 0.27, 0.17
Eclipse Sound	EBI, AI, HA	0.16	0.34, 0.29, 0.21
Eclipse Sound	EBI, AI, HA	0.20	0.30, 0.28, 0.21
Eclipse Sound	EBI, AI, HA	0.02	0.66, 0.21, 0.11
Eclipse Sound	EBI, AI, HA	0.17	0.33, 0.29, 0.21
Eclipse Sound	EBI, AI, HA	0.05	0.48, 0.27, 0.20
Eclipse Sound	EBI, AI, HA	0.11	0.39, 0.29, 0.22

A) Actual hunting area	Hunting area assignment by discriminant analysis	y assigr	bility of ment to t hunting	Probability of assignment t incorrect hur area	0
Eclipse Sound Eclipse Sound Northern Hudson Bay	EBI, AI, HA NHB, HA ES, AI, HA, EB		0.17 0.37 0.00	0.32, 0.2 0.4 0.37, 0.2	4, 0.12
B) Predicted hunting area ⇒ Actual hunting area∜	Admiralty Inlet	High Arctic	East Baffin Island	Eclipse Sound	Northern Hudson Bay
Admiralty Inlet	10	2	9	3	0
High Arctic	2	2	3	5	0
East Baffin Island	0	0	4	1	0
Eclipse Sound	4	8	8	29	1
Northern Hudson Bay	0	0	0	1	50

A) Actual hunting area	Hunting area assignment by discriminant analysis	Probability of assignment to correct hunting area	Probability of assignment to incorrect hunting area
Admiralty Inlet	HA, ES, SI	0.26	0.28, 0.25, 0.21
Admiralty Inlet	HA, ES, SI	0.22	0.27, 0.26, 0.25
Admiralty Inlet	HA, ES, SI	0.28	0.29, 0.27, 0.16
Admiralty Inlet	ES, HA, SI	0.11	0.37, 0.31, 0.19
Admiralty Inlet	ES, HA, SI	0.13	0.36, 0.31, 0.19
Admiralty Inlet	ES, HA, SI	0.22	0.33, 0.31, 0.13
Admiralty Inlet	ES, HA, SI	0.17	0.33, 0.31, 0.19
Admiralty Inlet	SI, HA, ES	0.25	0.31, 0.24, 0.21
Admiralty Inlet	SI, HA, ES	0.32	0.39, 0.17, 0.12
Admiralty Inlet	SI, HA, ES	0.27	0.34, 0.21 0.17
Admiralty Inlet	SI, HA, ES	0.31	0.34, 0.20, 0.15
Admiralty Inlet	SI, HA, ES	0.24	0.27, 0.26, 0.23
Admiralty Inlet	SI, HA, ES	0.32	0.36, 0.18, 0.14
Admiralty Inlet	SI, HA, ES	0.35	0.37, 0.17, 0.12
Admiralty Inlet	SI, HA, ES	0.27	0.42, 0.18, 0.13
Admiralty Inlet	NHB, HA, ES	0.05	0.36, 0.22, 0.30
East Greenland	ES, AI HA, SI	0.00	0.36, 0.18, 0.33 0.13
East Greenland	SI, AI	0.11	0.52, 0.22
East Greenland	SI, AI, HA	0.00	0.45, 0.33, 0.13
High Arctic	AI, ES, SI	0.26	0.26, 0.23, 0.25

A) Actual hunting	Hunting area	Probability of	Probability of
area	assignment by	assignment to	assignment to
	discriminant	correct hunting	incorrect hunting
	analysis	area	area
High Arctic	AI, ES, SI	0.27	0.33, 0.23, 0.17
High Arctic	AI, ES, SI	0.25	0.29, 0.22, 0.24
High Arctic	AI, ES, SI	0.25	0.31, 0.21, 0.23
High Arctic	AI, ES, SI	0.25	0.36, 0.21, 0.18
High Arctic	AI, ES, SI	0.25	0.40, 0.20, 0.15
High Arctic	AI, ES, SI	0.22	0.33, 0.18, 0.27
High Arctic	AI, ES, SI	0.20	0.35, 0.15, 0.29
High Arctic	AI, ES, SI	0.27	0.34, 0.24, 0.15
High Arctic	ES, SI	0.31	0.38, 0.20
High Arctic	ES, AI, SI	0.31	0.33, 0.19, 0.17
High Arctic	ES, AI, SI	0.30	0.32, 0.20, 0.18
High Arctic	ES, AI, SI	0.29	0.30, 0.20, 0.21
High Arctic	SI, NHB	0.22	0.35, 0.15, 0.25
High Arctic	SI, AI, ES	0.24	0.35, 0.15, 0.25
High Arctic	SI, AI, ES	0.26	0.27, 0.24, 0.24
High Arctic	SI, AI, ES	0.26	0.27, 0.23, 0.24
High Arctic	SI, AI, ES	0.24	0.33, 0.20, 0.22
High Arctic	SI, AI, ES	0.27	0.31, 0.13, 0.29
High Arctic	SI, AI, ES	0.25	0.34, 0.18, 0.23
High Arctic	SI, AI, ES	0.25	0.35, 0.15, 0.24
High Arctic	SI, ES	0.26	0.33, 0.32
High Arctic	SI, AI, ES	0.25	0.36, 0.15, 0.24
High Arctic	SI, AI, ES	0.25	0.36, 0.14, 0.25

A) Actual hunting area	Hunting area assignment by discriminant analysis	Probability of assignment to correct hunting area	Probability of assignment to incorrect hunting area
	-	1	
High Arctic	NHB, ES	0.07	0.77, 0.12
Eclipse Sound	AI, HA, SI	0.23	0.36, 0.27, 0.14
Eclipse Sound	AI, HA, SI	0.10	0.39, 0.15, 0.35
Eclipse Sound	AI, HA	0.05	0.68, 0.18
Eclipse Sound	AI, HA, SI	0.25	0.30, 0.27, 0.18
Eclipse Sound	AI, HA	0.26	0.37, 0.28
Eclipse Sound	AI, HA, SI	0.25	0.35, 0.27, 0.13
Eclipse Sound	AI, HA, SI	0.12	0.42, 0.18, 0.28
Eclipse Sound	AI, HA, SI	0.22	0.39, 0.26, 0.13
Eclipse Sound	AI, HA, SI	0.21	0.28, 0.25, 0.26
Eclipse Sound	AI, HA, SI	0.14	0.39, 0.19, 0.28
Eclipse Sound	AI, HA, SI	0.14	0.48, 0.20, 0.18
Eclipse Sound	AI, HA, SI	0.24	0.29, 0.27, 0.19
Eclipse Sound	AI, HA, SI	0.22	0.31, 0.26, 0.21
Eclipse Sound	AI, HA, SI	0.21	0.38, 0.25, 0.16
Eclipse Sound	AI, HA, SI	0.24	0.38, 0.27, 0.11
Eclipse Sound	EG	0.02	0.86
Eclipse Sound	HA, AI, SI	0.27	0.28, 0.25, 0.20
Eclipse Sound	HA, AI, SI	0.28	0.29, 0.29, 0.13
Eclipse Sound	HA, AI, SI	0.25	0.27, 0.26, 0.22
Eclipse Sound	HA, AI, SI	0.28	0.29, 0.28, 0.16
Eclipse Sound	HA, AI, SI	0.26	0.27, 0.23, 0.24
Eclipse Sound	HA, AI, SI	0.26	0.27, 0.21, 0.26

A) Actual hunting area	Hunting area assignment by discriminant analysis	Probability of assignment to correct hunting area	Probability of assignment to incorrect hunting area
Eclipse Sound	HA, AI, SI	0.29	0.30, 0.28, 0.13
Eclipse Sound	HA, AI, SI	0.26	0.27, 0.21, 0.26
Eclipse Sound	HA, AI, SI	0.26	0.27, 0.22, 0.25
Eclipse Sound	HA, AI, SI	0.26	0.28, 0.26, 0.20
Eclipse Sound	SI, AI, HA	0.22	0.29, 0.23, 0.25
Eclipse Sound	SI, AI, HA	0.23	0.37, 0.16, 0.24
Eclipse Sound	SI, AI, HA	0.27	0.32, 0.14, 0.27
Eclipse Sound	SI, AI, HA	0.28	0.31, 0.14, 0.27
Eclipse Sound	SI, AI, HA	0.15	0.48, 0.15, 0.18
Eclipse Sound	SI, AI, HA	0.26	0.28, 0.18, 0.27
Eclipse Sound	SI, AI, HA	0.26	0.30, 0.18, 0.27
Eclipse Sound	SI, AI, HA	0.23	0.41, 0.13, 0.23
Eclipse Sound	SI, HA	0.32	0.32, 0.27
Eclipse Sound	SI, AI, HA	0.24	0.31, 0.20, 0.26
Eclipse Sound	SI, AI, HA	0.30	0.30, 0.12, 0.27
Eclipse Sound	SI, AI, HA	0.16	0.32, 0.30, 0.21
Eclipse Sound	SI, AI, HA	0.25	0.29, 0.19, 0.26
Eclipse Sound	SI, AI, HA	0.20	0.39. 0.19, 0.22
Eclipse Sound	SI, AI, HA	0.24	0.27, 0.22, 0.26
Eclipse Sound	SI, AI, HA	0.18	0.41, 0.21, 0.21
Eclipse Sound	SI, AI, HA	0.23	0.32, 0.20, 0.25
Eclipse Sound	SI, AI, HA	0.15	0.43, 0.22, 0.19
Eclipse Sound	SI, AI, HA	0.23	0.36, 0.17, 0.24

A) Actual hunting area	Hunting area assignment by discriminant	Probability of assignment to correct hunting	Probability of assignment to incorrect hunting
	analysis	area	area
Eclipse Sound	SI, AI, HA	0.11	0.50, 0.23, 0.15
Eclipse Sound	SI, AI, HA	0.16	0.47, 0.16, 0.19
Eclipse Sound	SI, AI, HA	0.25	0.36, 0.14, 0.25
Eclipse Sound	SI, AI, HA	0.29	0.30, 0.14, 0.27
Eclipse Sound	NHB, HA	0.29	0.40, 0.20
Eclipse Sound	NHB	0.04	0.93
Eclipse Sound	NHB, HA, SI	0.32	0.33, 0.21, 0.12
Eclipse Sound	NHB, HA	0.19	0.60, 0.13
Eclipse Sound	NHB, HA	0.27	0.44, 0.17
Eclipse Sound	NHB, HA	0.30	0.38, 0.20
Somerset Island	AI, HA	0.28	0.47, 0.15
Somerset Island	HA, AI, ES	0.25	0.28, 0.20, 0.27
Somerset Island	HA, AI, ES	0.24	0.28, 0.20, 0.28
Somerset Island	HA, AI, ES	0.26	0.27, 0.22, 0.25
Somerset Island	ES, HA, NHB	0.10	0.36, 0.26, 0.21
Somerset Island	ES, AI, HA	0.27	0.34, 0.10, 0.29
Northern Hudson Bay	ES, HA, SI	0.26	0.34, 0.23, 0.12

B) Predicted hunting

area⇒ Actual hunting area ↓	Admiralty Inlet	East Greenland	High Arctic	Eclipse Sound	Somerset Island	Northern Hudson Bay
Admiralty Inlet	22	0	3	4	8	1
East Greenland	0	28	0	1	2	0
High Arctic	9	0	6	5	10	1
Eclipse Sound	15	1	10	33	23	6
Somerset Island	1	0	3	2	6	0
Northern Hudson Bay	0	0	0	1	0	13

Table 5. Autumn narwhal skin samples from Eclipse Sound and West Greenland stocks showing A) the misclassified narwhals and what stock they were assigned and B) the numbers of narwhals assigned to the actual versus predicted stock.

Actual stock	Stock assignment by discriminant analysis	Probability of assignment to correct stock	Probability of assignment to incorrect stock
West Greenland	Eclipse Sound	0.28	0.72
West Greenland	Eclipse Sound	0.38	0.62
West Greenland	Eclipse Sound	0.48	0.52
West Greenland	Eclipse Sound	0.38	0.62
West Greenland	Eclipse Sound	0.22	0.78
West Greenland	Eclipse Sound	0.49	0.51
West Greenland	Eclipse Sound	0.22	0.78
West Greenland	Eclipse Sound	0.34	0.66
West Greenland	Eclipse Sound	0.46	0.54
West Greenland	Eclipse Sound	0.11	0.89

B) Predicted stock \Rightarrow

Eclipse Sound

I West Greenland

Eclipse Sound	2	0
West Greenland	10	92

Table 6. Misclassified narwhal samples from all nine hunting areas, irrespective of season.

Predicted hunting area⇒ Actual hunting area∜	Admiralty Inlet	East Greenland	High Arctic	Melville Bay	East Baffin Island	Eclipse Sound	Somerset Island	Northern Hudson Bay	West Greenland
Admiralty Inlet	40	0	2	4	18	3	1	0	8
East Greenland	0	38	0	1	3	1	0	0	0
High Arctic	14	0	3	9	1	10	1	1	6
Melville Bay	4	1	4	28	10	5	5	0	7
East Baffin Island	4	0	0	2	3	1	0	0	2
Eclipse Sound	31	2	13	16	12	36	6	5	38
Somerset Island	2	0	2	2	2	1	1	1	2
Northern Hudson Bay	0	0	0	0	0	1	1	68	3
West Greenland	5	0	3	21	4	22	5	0	48

Table 7. Misclassified female narwhal samples, from eight hunting areas (A), and male narwhals from all nine hunting areas (B), irrespective of season.

A) Predicted hunting area \Rightarrow	Admiralty	East	High	Melville	Eclipse	Somerset	Northern	West
Actual hunting area∜	Inlet	Greenland	Arctic	Вау	Sound	Island	Hudson Bay	Greenland
Admiralty Inlet	20	0	1	3	0	2	0	0
East Greenland	0	8	0	0	0	0	0	0
High Arctic	0	0	2	2	1	1	0	0
Melville Bay	1	0	4	14	2	1	0	2
Eclipse Sound	16	0	5	10	8	15	2	2
Somerset Island	1	0	0	1	0	1	0	0
Northern Hudson Bay	0	0	1	0	1	1	20	0
West Greenland	3	0	12	7	2	5	0	1

Table 7 continued. Misclassified female narwhal samples, from eight hunting areas (A), and male narwhals from all nine hunting areas (B), irrespective of season.

B) Predicted hunting group⇒ Actual hunting group∜	Admiralty Inlet	East Greenland	High Arctic	Melville Bay	East Baffin Island	Eclipse Sound	Somerset Island	Northern Hudson Bay	West Greenland
Admiralty Inlet	17	0	2	4	13	2	1	0	5
East Greenland	0	17	0	3	0	1	0	0	0
High Arctic	10	0	6	3	2	7	5	1	4
Melville Bay	2	2	6	`8	1	3	6	0	2
East Baffin Island	0	0	0	0	2	0	0	0	0
Eclipse Sound	12	1	6	7	4	17	2	1	22
Somerset Island	0	0	3	1	1	0	0	0	2
Northern Hudson Bay	0	0	0	0	0	0	0	39	1
West Greenland	1	0	2	14	0	17	5	0	32



Figure 1. Map indicating the communities in Canada and Greenland from which narwhal skin samples were collected and analyzed for stable isotopes. Colors indicate the approximate summer distribution of the hunting areas assessed, except for Uummanaaq where red indicates the winter hunting area.

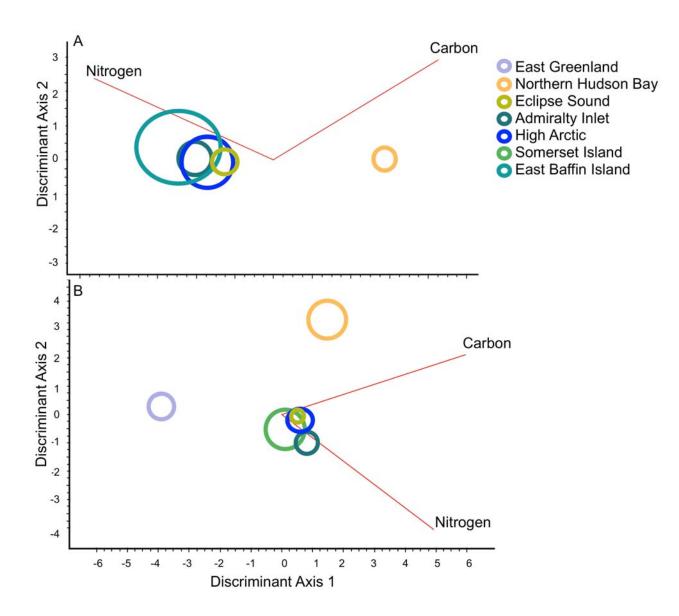


Figure 2. Multiple discriminant analysis indicating 95 % confidence intervals around the mean for the defined narwhal hunting areas in spring (A) and summer (B). Nitrogen and carbon axes are shown relative to the discriminant axes. Non-overlapping circles indicate a significant difference among hunting areas.

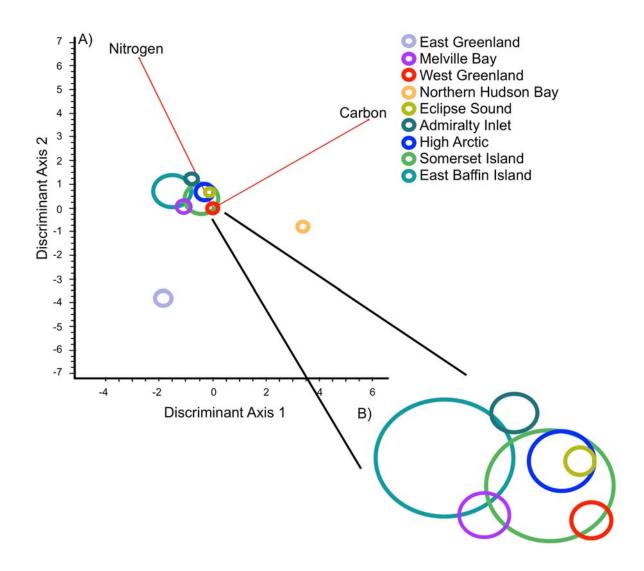


Figure 3. Multiple discriminant analysis indicating 95 % confidence intervals around the mean for each defined narwhal hunting area (A) and an insert showing the relationship among the Baffin Bay hunting areas (B). Nitrogen and carbon axes are shown relative to the discriminant axes. Non-overlapping circles indicate a significant difference among hunting areas.

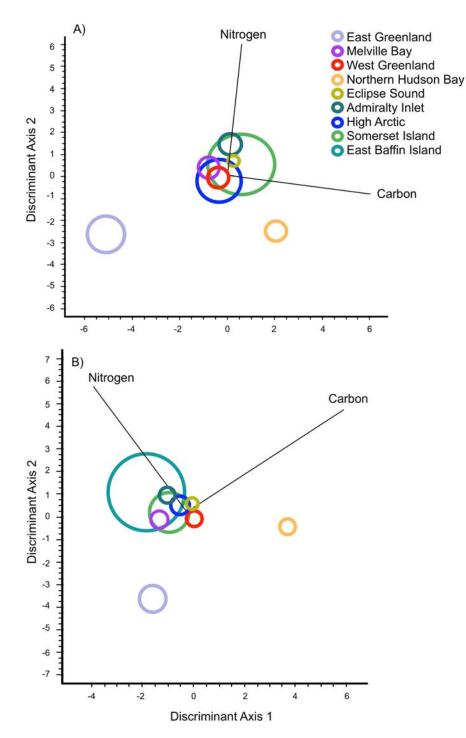


Figure 4. Multiple discriminant analysis indicating 95 % confidence intervals around the mean for each defined narwhal hunting area for females (A) and males (B). Nitrogen and carbon axes are shown relative to the discriminant axes. Non-overlapping circles indicate a significant difference among hunting areas.

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