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# Fractal analysis of narwhal space use patterns

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# Abstract

Quantifying animal movement in response to a spatially and temporally heterogeneous environment is critical to understanding the structural and functional landscape influences on population viability. Generalities of landscape structure can easily be extended to the marine environment, as marine predators inhabit a patchy, dynamic system, which influences animal choice and behavior. An innovative use of the fractal measure of complexity, indexing the linearity of movement paths over replicate temporal scales, was applied to satellite tracking data collected from narwhals (Monodon monoceros) (n = 20) in West Greenland and the eastern Canadian high Arctic. Daily movements of individuals were obtained using polar orbiting satellites via the ARGOS data location and collection system. Geographic positions were filtered to obtain a daily good quality position for each whale. The length of total pathway was measured over seven different temporal length scales (step lengths), ranging from one day to one week, and a seasonal mean was calculated. Fractal dimension (D) was significantly different between seasons, highest during summer (D = 1.61, SE 0.04) and winter (D = 1.69, SE 0.06) when whales made convoluted movements in focal areas. Fractal dimension was lowest during fall (D = 1.34, SE 0.03) when whales were migrating south ahead of the forming sea ice. There were no significant effects of size category or sex on fractal dimension by season. The greater linearity of movement during the migration period suggests individuals do not intensively forage on patchy resources until they arrive at summer or winter sites. The highly convoluted movements observed during summer and winter suggest foraging or searching efforts in localized areas. Significant differences between the fractal dimensions on two separate wintering grounds in Baffin Bay suggest differential movement patterns in response to the dynamics of sea ice. © 2004 Elsevier GmbH. All rights reserved.

Keywords: Animal movement; Arctic; Fractal; Narwhal; Satellite tracking

# Introduction

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In predictably changing habitats, animals often alternate space use patterns in a predictable way. For habitat changes on a seasonal scale, responses often

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include switching between localized resource utilization and large-scale movements driven by migration. Behavioral changes resulting in differential movement patterns have been suggested as an effort to control environmental heterogeneity and create more stable life history responses to external perturbations (Ferguson et al., 1998a).

The narwhal (Monodon monoceros) is a high Arctic cetacean species whose annual movement patterns are strongly influenced by predictable seasonal changes in their environment. Narwhals have high site fidelity to summering and wintering grounds, yet their movements are also influenced by the spatial pattern of sea ice acting as a structuring agent. Narwhals spend the summer in the sheltered bays and fjords of the Canadian Arctic archipelago and West Greenland. They migrate south in the fall before sea ice forms and spend the winter in Baffin Bay and North Davis Strait in restricted areas covered by dense offshore pack ice. In spring they return to summering grounds following the receding sea ice edge. The annual round trip distance of the migration is up to three thousand kilometers (Heide-Jørgensen et al., 2002a). Detailed seasonal movement patterns of narwhals have been described for three separate subpopulations thought to be isolated based on satellite tracking and genetic studies (Dietz and Heide-Jørgensen, 1995; Dietz et al., 2001; Heide-Jørgensen et al., 2002a). These sub-populations occupy two different wintering grounds in the Baffin Bay/Davis Strait area (Heide-Jørgensen et al., 2002a, 2003), where they show population-specific dive behavior and foraging preference (Laidre et al., 2003). There is a high degree of spatial and temporal variability in Arctic marine habitats. Changes in climate, coupled with extreme seasonality in sea ice, influence primary and secondary production processes and ultimately the distribution and abundance of top predators (Ferguson and Messier, 1996; Parkinson, 2000a, b; Mauritzen et al., 2001; Root et al., 2003). In the case of Arctic cetaceans, the long-term effects of this variation are unknown both on local and global scales (Tynan and DeMaster, 1997). A first step in understanding this link lies in quantitatively describing cetacean behavioral patterns and relating them to environmental heterogeneity in the context of seasonal changes.

A relatively new approach for assessing animal movement involves calculating the fractal dimension of paths, which describes variation in animal movement at a range of spatial scales across time (Mandelbrot, 1983; Milne, 1991; Turchin, 1998). Fractals have been linked to animal movement and terrestrial landscape structure for a wide range of species, from invertebrates (Crist et al., 1992; With, 1994; Wiens et al., 1995) to large mammals (Bascompte and Vilà, 1997; Ferguson et al., 1998a, b, Mouillot and Viale, 2001). The fractal dimension (D) indexes the overall complexity of a movement

path using a scale-independent measure of movement. The index of fractal dimension ranges from D = 1 if an animal is moving along a perfectly linear path to D = 2 if movement is extremely convoluted and essentially all points in two-dimensional space are visited (analogous to "Brownian-like" or random walk paths) (Wiens et al., 1995). Fractal dimensions lie somewhere between these two extremes, with values for insects generally <1.5 and values for large mammals generally >1.5 (Ferguson et al., 1998b).

Recent advances in satellite tracking technology and the miniaturization of transmitters have enabled the collection of large amounts of movement data from species inhabiting remote or inaccessible environments. In the case of marine predators such as the narwhal, extending landscape-based pattern metrics to the marine environment can identify important foraging zones, potentially even elucidating areas with unique or important oceanography. This study applied concepts of fractal geometry to quantify space-time related differences in the linearity of seasonal movement patterns of narwhals. Differences in sub-population specific movements were investigated across seasons and discussed in the context of causal factors or potential environmental heterogeneity encountered in the high Arctic.

### Materials and methods

### Location data

Satellite location data were collected from three narwhal sub-populations in the eastern Canadian high Arctic and West Greenland. Studies were conducted in Melville Bay, West Greenland in August 1993–1994 (Dietz and Heide-Jørgensen, 1995; Heide-Jørgensen and Dietz, 1995), in Tremblay Sound, Baffin Island, Canada in August 1997–1999 (Dietz et al., 2001; Heide-Jørgensen et al., 2002a), and in Creswell Bay, Somerset Island, Canada in August 2000 (Heide-Jørgensen et al., 2003) (Fig. 1). Narwhals were captured using nets set perpendicular to the shoreline (details on capturing and handling described in Dietz et al., 2001; Dietz and Heide-Jørgensen, 1995; Heide-Jørgensen et al., 2002a).

Two types of tags were used: Telonics (Mesa, AZ) and Seimac (Canada) satellite-linked time depth recorders with approximately 0.5 W power output, programmed and cast in epoxy by Wildlife Computers (Redmond, WA). Transmitters were attached to female whales on the dorsal ridge with two or three 5–8 mm polyethylene pins. Transmitters were attached to the tusk of males using two stainless-steel bands (Seimac SSC3 or the Telonics ST-6 transmitter unit programmed and cast by Wildlife Computers). Whale movements were obtained



Fig. 1. Movement paths of 20 narwhals obtained from satellite tracking studies at three summering localities (Creswell Bay, Tremblay Sound, and Melville Bay) in the eastern Canadian high Arctic and West Greenland.

using the ARGOS Data Location and Collection System (Harris et al., 1990). Tags transmitted ultra-high frequency messages, which were received by National Oceanic and Atmospheric Administration (NOAA) polar orbiting satellites. Locations were determined by ARGOS from the Doppler shift of the tag signal frequency that occurs during the satellite pass overhead (Harris et al., 1990). Only location classes 1, 2 and 3 (LC 1–3), which have a predicted standard error of 1.0, 0.35, and 0.15 km, respectively, were used in this analysis. None of the transmitters were duty-cycled.

Sex was determined by the presence or absence of a tusk. Whales were classified into one of four size categories (category 1 = length < 375 cm, category 2 = 375-424 cm, category 3 = 425-474 cm, and category  $4 \ge 475 \text{ cm}$ ), one of three summering sub-populations (Melville Bay, Tremblay Sound, and Creswell Bay) based on tagging site, and one of two wintering grounds (Southern Wintering Ground and Northern Wintering Ground; Fig. 1) based on wintering ground selection.

The time series of data for each whale were divided into three seasons: summer period (tagging date to September 15), migration period (September 16-October 31), and winter period (November 1 to end of tag transmissions).

Autocorrelation error, introduced by using pseudoreplicated locations in the analysis resulting from satellite passage and whale surfacing behavior, was addressed by selecting one good quality location from each 24-h period. The daily position was selected by first visually examining the total number of positions for quantity and quality during each hour of the day for each whale. A 5h time span was identified where position quality and quantity were highest from all tags. The mean minimum absolute difference was calculated between each hour in that time span and all ARGOS positions received for each individual. The hour with the smallest absolute difference, when averaged across all individual whales, was selected as the temporal point at which the daily position was selected.

## Calculation of fractal dimension

Interest in behavioral changes by week and season provided the basis for selecting pathway length measurements and resulting in fractal dimension calculations. The total pathway length was measured over seven different step lengths or measurement scales (in kilometers). Spatial step lengths were calculated incrementally for temporal step lengths of 1 day (using every sequential daily position) to 7 days (every 7th position or one per week). With increasing temporal step length an increasing number of starting points for total distance calculations (different days) were available (e.g., for a step length of four, there were four different potential starting points for the calculation). For each of these cases (step lengths 2–7), total length measurements were calculated for all starting point options and the mean value for that temporal step length was used for each season. We spatially and temporally restricted our calculations of fractal dimension to narwhals within the study area for each season, with no more than a 7-day step length, to avoid the problem of scale dependence of movement pathways (Turchin, 1996).

The fractal dimension (D) was derived by regressing the log of the measured length of pathway (L) on the log of the measurement scale (or step length) ( $\delta$ ) based on the power-law function  $L(\delta) = K \delta^{1-D}$ , where K is the standardized length of movement pathways (km). The fractal dimension indexed the irregularity of movement paths over the range of measurement scales and K indexed the standard measure of pathway length. Fractal dimension and pathway length were calculated for individual whales for each of the three seasons. Data from each individual were pooled among years to assess overall seasonal patterns and data were then grouped based on sub-population, sex, size, or wintering ground to examine differences at the sub-population level. Fractal dimension was tested for normality and analyzed using two-way linear models in SPSS Version 11.0 with a significance level <0.05.

## Results

Twenty narwhals (8 M and 12 F) were used in the analysis: four whales (3 M and 1 F) from Melville Bay, West Greenland, 10 whales (5 M and 5 F) from Tremblay Sound, and 6 whales (6 F) from Creswell Bay (Table 1, Fig. 1). Sixty-five percent of the whales were in size category 2 (375–424 cm), 15% in size category 3 (425–474 cm), and 10% in each of the size categories 1 (<375 cm) and 4 (>475 cm). ARGOS position quantity and quality, on average, peaked between the hours of 12:00 and 18:00 (local time). The

Table 1. Fractal dimensions (D) for paths of individual narwhals in three seasons for three sub-populations in Melville Bay, Tremblay Sound, and Creswell Bay. Length is standard body length in cm

Sub-population	Whale ID-Year	Sex	Length	Summer D	Migration D	Winter D
Melville Bay	3960-93	М	>400	1.93	1.42	1.55
	20162-93	Μ	475	1.81	_	
	20167-94	Μ	405	1.92	1.59	1.48
	20690-94	F	>400	1.81	_	
All Melville Bay whales $(N = 4, 2, 2)$				1.86 (0.05)	1.50 (0.08)	1.51 (0.08)
Tremblay Sound	6335-97	Μ	440	1.80	1.32	_
	3961-98	Μ	500	1.64	1.37	
	20162-98	Μ	475	1.55	1.30	1.58
	20696-98	F	380	1.80	1.52	
	3964-99	Μ	410	1.62	1.43	1.68
	20688-99	F	415	1.46	1.33	
	20689-99	F	405	1.63	1.33	
	20687-99	F	390	1.70	1.31	
	20168-99	Μ	440	1.53	1.36	
	20691-99	F	350	1.36	_	
All Tremblay Sound whales $(N = 10, 9, 2)$				1.60 (0.03)	1.36 (0.03)	1.63 (0.07)
Creswell Bay	20690-00	F	398	1.53	1.23	_ `
	20689-00	F	397	1.38	1.28	1.91
	20688-00	F	402	1.56	1.34	1.78
	20683-00	F	390	1.17	1.23	
	7927-00	F	390	1.56	1.15	1.87
	7928-00	F	370	1.47	_	
All Creswell Bay whales $(N = 6, 5, 3)$				1.44 (0.04)	1.24 (0.05)	1.85 (0.06)
All tracked whales $(N = 20, 16, 7)$				1.61 (0.04)	1.34 (0.03)	1.69 (0.06)



**Fig. 2.** Regression between step length (day) and length of path (km) for a narwhal tagged in summer in Melville Bay, West Greenland in 1993 (ID 3960). The fractal dimension D = 1-exponent of x and K is the y-intercept. Fractal dimensions for this animal were D = 1.93 (summer), D = 1.42 (migration), and D = 1.55 (winter). Note the longest path length was recorded during the migration period. The data for each step length by season are solid squares for summer, solid circles for migration, and open triangles for winter. Similar regressions were conducted for each season for each individual whale.

mean minimum absolute time difference was found between all positions received by the satellite and the hour of 15:00 (local time). Therefore, this hour was selected as the time at which the daily best quality position (LC 1–3) was determined for each whale. Daily positions for all whales deviated from 15:00 to 2.04 h (SD 0.9).

Fractal dimension was normally distributed (Shapiro-Wilk statistic, W = 0.96, p = 0.15) and parametric statistics were used. The fractal dimension on measurement scales from 1 to 7 days showed self-similarity within the range of step lengths (Fig. 2) and indicated that this range was acceptable for the assumption of scale-independence (Turchin, 1996). Fractal dimension for individual whales ranged from a minimum of 1.15 (calculated during migration) to a maximum of 1.93 (calculated during summer) (Table 1).

#### Seasonal and annual differences

Estimated fractal dimensions for pooled individuals were 1.61 in the summer (SE 0.04, n = 20), 1.34 during migration (SE 0.03, n = 16), and 1.69 in the winter (SE 0.06, n = 7), varying significantly across seasons ( $F_{2,40} = 15.92$ , p < 0.001). Tukey HSD post-hoc tests indicated this difference was due to the low fractal dimension during the migration period. The general pattern of seasonal movement and the seasonal fractal dimensions (Fig. 2) were similar for almost all whales. Fractal dimension was significantly highest during the summer period, indicating the most irregular and random movements. Fractal dimension was significantly lowest during the migration period, indicating the most directed, linear movements. Fractal dimension increased significantly again in winter when whales reduced travel speed and remained in localized areas in the pack ice, to a value similar to but not as high, as the summer (Fig. 3). Standardized path lengths could only be compared between individuals for summer and migration seasons, since tags that failed during the winter period did not record the entire movement path length for that season. The mean path length K for the summer season was 767 km (SD 496), less than half the mean path length for the migration period (1801 km, SD 343).

Significant differences were found between the fractal dimensions of year and season ( $F_{9,26} = 5.38$ , p < 0.001), with post-hoc tests indicating differences occurring in summer and migration. Post-hoc analyses could not be conducted between all years or seasons because in 1997 there was only a sample of one. When Tukey post-hoc analyses were conducted for summers excluding the year 1997, significant differences were found for the fractal dimension in summer between both 1993 and 2000 and 1994 and 2000.

#### Sex and size category differences

There were no significant effects of size category or sex on the fractal dimension by season. The effect of size category in summer was, however, just above 0.05 (p = 0.07). This was due to two individuals in size class 1 which deviated from the observed general pattern for all other whales (ID 20691-99 and 7928-00). These two whales were the smallest in the sample (370 and 350 cm standard length), and presumably the youngest. They were tagged and tracked from two different summering grounds in 1999 and 2000. Both individuals had a delayed migration exploring alternative regions that were not visited by the rest of the population.

#### Sub-population and wintering ground differences

There were large differences in the fractal dimensions of movement between sub-populations across seasons (Table 1). For whales from Melville Bay, the most convoluted path (D = 1.86) was found during the summer and movement patterns became more linear in the fall and winter (D = 1.50 and 1.51, respectively). Conversely, for whales from Creswell Bay the most convoluted path was found during the winter (D = 1.85) and fractal dimension was lowest during migration (D = 1.24) (Table 1). Tremblay Sound whales exhibited the least variation in fractal dimension across seasons, with high fractal dimensions on both the summer and wintering grounds (D = 1.60/1.63) and lowest during migration (D = 1.36).



Fig. 3. Entire movement pathway of narwhal ID 20689, tagged in Creswell Bay in 2000, shown with daily positions as black markers. Seasonal fractal dimensions for each pathway were (a) summer (D = 1.38), (b) migration (D = 1.28), and (c) winter (D = 1.91). Note that data are shown on an unprojected scale and are intended to illustrate movement behavior in different seasons.

Significant differences were found between seasons and sub-populations ( $F_{4,34} = 10.60, p < 0.001$ ). During summer narwhal movements on the summering ground in Melville Bay were significantly more convoluted than those of whales in both Tremblay Sound (p = 0.01) and Creswell Bay (p < 0.001). The difference between Tremblay Sound and Creswell Bay was not significant during summer (p = 0.07). Differences in D were also found for the migration period. Melville Bay and Tremblay Sound had significantly lower fractal dimensions than Creswell Bay (p = 0.003 and 0.04, respectively), while Melville Bay and Tremblay Sound showed no significant difference. During winter, when the two sub-populations from Melville Bay and Tremblay Sound share a wintering ground, their fractal dimensions were similar and not significantly different from one another. Both of these sub-populations had significantly lower fractal dimensions than the sub-population of whales from Creswell Bay wintering in an area further north (p = 0.01 and 0.04, respectively).

When whales occupying the two wintering grounds were pooled and examined for differences, fractal dimension was significantly different ( $F_{1,5} = 22.05$ , p = 0.005). The fractal dimension on the Northern Wintering Ground (whales from Creswell Bay) was higher (D = 1.85, SE 0.07) than the fractal dimension on the Southern Wintering Ground (whales from Melville Bay and Tremblay Sound) (D = 1.56, SE 0.06).

## Discussion

Meaningful quantitative descriptions of spatial patterns are important in ecology. Pattern metrics are frequently used methods to describe, simplify, or group complex spatial data into categories that are more easily understood or analyzed. It is, however, important that pattern analysis is not merely subjective but that the observed differences are quantified. Even though individual movement path parameters can easily be indexed (i.e., speed, distance, bearing), the mechanisms responsible for variation may not be easily understood and subjective behavioral grouping can confound the interpretation of results.

Turchin (1996) suggests that fractal theory is not applicable to movement data due to a lack of selfsimilarity. Clearly, animal paths do not follow the pure definition of fractals, as clusters or breaks tend to define multiple realms of self-similarity in nature (Ferguson et al., 1998b). Studies have documented the hierarchical nature of marine species' response to patch structure using spatial autocorrelation indices (Fauchald et al., 2000) indicating that organisms may be responding to prey distribution or density on a range of nested scales. In this study, the range of measurement scales was restricted to one to seven days and temporal scales were investigated on the order of seasons. This is the range of scales over which fractal dimension would reflect shortterm behavior and where patterns and causation are both recurring and predictable.

The fractal dimensions for seasonal narwhal movements are consistent with descriptions of behavior, yet provide metric values for the qualitative patterns. Narwhals tend to have high fractal measures of movement during the summer when they occupy restricted localities. This correlates well with summer behavioral descriptions of high site fidelity to coastal bays and fjords, with minimal to no long-distance exchange between sub-populations (Heide-Jørgensen et al., 2003). The lowest fractal dimension (least complex behavior) was found during the migration period. The literature describing narwhal migration reports a substantial increase in daily travel distances and speed, together with a substantial decrease in the amount of time spent stationary in a single area (Dietz et al., 2001). In winter the increase in fractal dimension was due to occupation of the wintering grounds, where whales remain stationary for up to 6 months during the continuous buildup of consolidated pack-ice. This also correlates well with winter studies of localized horizontal and vertical ranging behavior (Laidre et al., 2003).

The convoluted summer and winter pathways suggest that narwhals are interacting with environmental heterogeneity on a finer scale (Wiens et al., 1995). The similarity in tortuosity, however, is likely driven by different factors during these seasons. The reasons for high summer site fidelity to localized bays and fjords are not completely understood. The summering grounds do not appear to afford large quantities of prey and intense feeding behavior has not been observed (Finley and Gibb, 1982; Heide-Jørgensen et al., 1994; Laidre et al., 2002). These localized movements may be important for calves or may be a remnant of matrilineal site-specific behavior, similar to the beluga (*Delphinapterus leucas*), a close phylogenetic relative.

During migration the linearity of movement paths suggests individuals are not searching for highly clumped resources and are moving in a directed manner. The migratory period of narwhals is well-defined; they leave their summering grounds in early to mid-September (prior to ice formation) and move in specific corridors towards offshore areas (Dietz et al., 2001; Heide-Jørgensen et al., 2002a). The timing of this migration is very specific, with whales moving out of the same areas on the same dates each year. Because of this strict schedule, narwhals have most likely adapted to a course that leaves little time for exploration of alternative regions along the way. There was some subpopulation variation in the fractal dimension observed during the migration period, likely reflecting different paths (coastal or offshore) narwhals take towards their wintering grounds.

In winter, the localized movements can be primarily attributed to dense sea ice. Narwhals inhabiting pack ice are at the mercy of reliable leads and cracks for breathing as they are entirely dependent upon the physical structure of the ice and cannot break breathing holes (Siegstad and Heide-Jørgensen, 1994; Heide-Jørgensen et al., 2002b). This restricts narwhal movements to areas that are not completely closed and at the same time requires that the whales shift with the movement of leads. Localized movements on the wintering grounds are also likely influenced by foraging behavior (Laidre et al., 2003). Narwhals from West Greenland and the eastern Canadian high Arctic have a sympatric winter distribution with deep-water Greenland halibut (*Reinhardtius hippoglossoides*) in Baffin Bay, and there is evidence of significant and consistent predation on these halibut during winter (Laidre et al., 2004). The narwhals on the wintering grounds have limited options for long-distance movements to search for schools of squid or pelagic fish species because they are confined to small open water regions. Locations of high-density benthic prey on the wintering ground may enforce restricted horizontal movement and may be reflected in the fractal dimension.

The two smallest, and probably youngest, female whales were responsible for the deviations from the general fractal patterns or pathway lengths. When the standard date (September 15) for the end of summer was used for whale 20691-99 (tagged in Tremblay Sound, Baffin Island), it resulted in an exceptionally low fractal dimension (D = 1.18). This was due to a delayed migration, with this whale traveling west to Admiralty Inlet, and then performing localized movements until October 4 (see Heide-Jørgensen et al., 2002a). When this delayed migration was accounted for and the summer date extended, the fractal dimension rose to D = 1.36. Another whale (7928-00, tagged in Creswell Bay, Somerset Island) traveled through Peel Sound following other whales from the sub-population in late August. However, in September it turned south and explored bays and fjords in Franklin Strait for another three weeks, while the rest of the sub-population from Creswell Bay migrated out through Lancaster Sound (see Heide-Jørgensen et al., 2003). Standardized pathway lengths for this individual were nearly identical during summer and migration due to the exceptionally long exploratory period (1141 km vs. 1161 km). Both of these behavioral deviations detected by using fractals were qualitatively identified in the literature (Heide-Jørgensen et al., 2002a, 2003). These deviations may be due to foraging inexperience or increased exploratory tendencies of younger individuals, who have not yet developed strict fidelity to movement paths and departure timing.

The differences in fractal dimension between wintering grounds offer insights into movement patterns in response to sea ice. The whales occupying the Northern Wintering Ground displayed more convoluted and tortuous paths than the whales occupying the Southern Wintering Ground. The effect of sea ice (concentration, shifting leads and cracks, and flow size) is not uniform across Baffin Bay and conditions experienced by whales on different wintering grounds vary. A wider range of sea ice concentrations and larger fractions of open water have been detected on the Southern Wintering Ground based on analysis of remotely sensed microwave sea ice data between 1978 and 2001 (Laidre, 2003). This may be due to the closer location of the Southern Wintering Ground to the pack ice edge, where conditions are more dynamic and offer whales greater freedom of movement. Narwhals may need to travel greater distances to keep

up with shifting leads and cracks, which is reflected in a lower fractal dimension in this area (Laidre, 2003).

Observing how an organism responds to the structural complexity of the environment and how this response is modified on different time scales can provide information on the mechanisms of interaction with landscape structure and the spatial response of a population to dynamic processes (With, 1994; Wiens et al., 1995). The application of fractal dimension to examine movement data for a marine mammal is a nontraditional method and can be extended to comparative analyses or interpretations of life history patterns. The method offers an objective means for using behavior to identify areas of particular geographic interest (i.e., foraging, breeding). The major prospect for fractal analysis of movements lies in the comparative nature of the metric data for identifying changes over time between species, populations, or smaller groups inhabiting similar habitats. The fractal dimension can be viewed as the species' or population's strategy for dealing with spatial and temporal changes or as a response to environmental heterogeneity. Comparison between narwhals and other Arctic marine mammals will provide insight into the dynamics of the Arctic environment and strategies that determine viability of species under the influence of climatic change.

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