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Fractals, sea-ice landscape and spatial patterns of polar bears

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Abstract. Periodic landscape transformations can give rise to macroevolutionary changes such as speciation, whereas more constant microevolutionary differences can lead to population differentiation within a species. The most recent major macroevolutionary change occurred 2.5 mya when an abrupt increase in the scale of glacial cycles in the northern hemisphere resulted in the formation of the arctic sea-ice ecosystem. An initial burst of diversity occurred and sometime later polar bears evolved from brown bears as a marine mammal predator of seals living among the sea ice landscape. We tested the hypothesis that the distribution of sea ice creates a spatial patterning in the present groupings of polar bears (i.e. populations). We compared the spatial attributes of sea ice and polar bear characteristics in the Canadian Arctic. The winter and spring seasons, before and during mating, respectively, best described groupings of polar bears based on separate cluster analyses of ice and bears. A relationship between polar bear fractal movement patterns and the fractal dimension of sea ice indicated a possible mechanism linking geography and population structure. Sea ice dominates as a structuring agent and the hierarchical spatial groupings of polar bears within a circumpolar metapopulation related to the fractal pattern of annual sea ice created by the interspersion of Arctic islands. Once a new sea-ice environment formed, directional selection resulted in allopatric speciation whereas stabilizing selection maintains present groupings due to exchanges among populations at the time of breeding.

Key words. Allopatric speciation, cluster analysis, evolution, metapopulation, movement pathway, *Ursus maritimus*.

INTRODUCTION

Evolutionary patterns result from forces acting across a hierarchy of time and space (Eldredge, 1985; DiMichele, 1994; Grantham, 1995). Biogeographical patterns of individuals within a species reflect the present and past biology of an organism and the history of the physical environment of an organism (Graham & Grimm, 1990; Haydon *et al.*, 1994). How a species evolves is still controversial (Mayr, 1988; Gibbons, 1996; Morell, 1996), as is defining a species (Cracraft, 1987; Williams, 1992; Mallet, 1993). One process of species evolution, allopatric speciation, begins as a result of geological changes in the physical structure of the earth (Connell, 1978; Wright, 1978; Vrba, 1985; Morrone & Crisci, 1995). Organisms adapt to changes in their physical environment, or, in the absence of gene flow, sometimes diverge into new species and develop new trophic interactions. The formation of two species from a single ancestral one must be the result of an interaction between the ecological and biogeographic setting and the evolutionary processes that cause genetic differentiation (Brown, 1995). Implicit in this process is the history of geological transformations for that environment and the evolutionary response of the species to that history. In particular, characteristics of a specific environment often limit and structure the distribution and abundance of populations within a species.

We used the polar bear (*Ursus maritimus*) to assess this process of speciation, and to consider how their phylogenetic history (i.e. contingent and preadaptive biological attributes) and the geophysical nature of their habitat interact. The timing of Arctic Ocean freezing, although controversial (Barry, 1989), has been estimated to have occurred 2.4 mya (Flohn, 1982; Burton *et al.*, 1997). At this time, the scale of glacial cycles in the northern hemisphere began to increase (Uchida, 1996). Permanent arctic sea ice likely formed as a result of the final closure of the Panama Isthmus (Maier-Reimer *et al.*, 1990; Burton *et al.*, 1997) and a renewed link between the Mediterranean Sea and the North Atlantic (Shackleton *et al.*, 1988; Barry, 1989; Vrba *et al.*, 1989). Polar bears evolved from brown bears (*Ursus arctos*) after the formation of the arctic ice (Kurtén, 1964; Wozencraft & Hoffmann, 1993; Talbot & Shields, 1996a). Polar bears evolved and adapted to a marine habitat considerably different from the terrestrial habitat of their phylogenetic history. Here, we ask how has this new habitat influenced the spatial structure of groups of polar bears?

A species can be defined according to the biological

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attributes of their phylogenetic history, which for polar bears includes large size, homeothermy, carnivory, terrestrial locomotion, and physiological adaptations to seasonal shortages in food. The expansion of the sea ice in the Arctic provided a new ecological niche for the evolution of polar bears as the primary predator of ringed seals (*Phoca hispida*; Smith & Stirling, 1975; Stirling & Archibald, 1977; Smith, 1980; Kingsley, 1990). Polar bear distribution is limited to the annual sea ice conditions that shelter the smallest and most abundant of the northern phocids during most of the arctic year (Smith *et al.*, 1991; Furgal *et al.*, 1996). The polar bear evolved from a 'terrestrial brown bear' as a marine predator of seals living on the terrestrial-like platform of sea ice (Kurtén, 1988; Ramsay & Stirling, 1988; Stirling & Derocher, 1990).

A species can also be defined according to the physical characteristics of its present and past environment, which in the case of polar bears is sea ice. The Arctic is predictably unpredictable (Ferguson & Messier, 1996) and as a result annual sea ice is seasonally transformed and fractured with considerable variation (Jacobs & Newell, 1979; Mysak *et al.*, 1990; Brown & Cote, 1992). This transmutable nature of sea ice results in spatial and temporal variability in access to food for polar bears (Stirling & McEwan, 1975; Smith, 1980; Ramsay & Stirling, 1986; Ramsay & Stirling, 1988). As sea ice defines the spatial distribution of polar bears, we tested whether a hierarchical organization of groups of polar bears matches the spatial and seasonal patterns of sea ice interspersed among large arctic islands. Our primary goal in this research was to develop and describe a hierarchical connection between spatial effects in geography and spatial effects in the evolution of a metapopulation structure for a large mammal (see Cantrell & Cosner, 1994).

METHODS

Study area

The Canadian Arctic waters we investigated included the coastal waters of the Eastern Beaufort, Arctic Ocean, Baffin Bay, and the channels and passages of the Canadian Arctic Archipelago (Fig. 1). All of this area supports a more or less continuous mantle of sea ice for at least 6 months of the year. More open water occurs in the Baffin Bay-Davis Strait area than other regions. Summer disintegration of sea ice in the Archipelago shows a predictable pattern (Collin & Dunbar, 1964). The Arctic region is dominated by a cycle of almost total ice cover in late winter and minimum ice extent in September. The sea ice effectively insulates the atmosphere from the water of the Arctic Ocean (Barry, 1989). Sea ice is a mixture of young and old floes of highly variable thickness as a result of a complex annual cycle of growth and decay of ice. Winter snow accumulates on arctic ice, and drifts around hummocks and ridges. Interannual variation in ice extent are primarily regional in occurrence and related to interannual changes in atmospheric conditions (Jacobs & Newell, 1979; Walsh & Johnson, 1979; Johnson, 1980; Kelly *et al.*, 1982). In particular, the distribution of sea ice and the chronology of freeze-up and break-up are determined by marine currents, wind, temperature, and short-and long-term climatic changes.

Data analyses

Delineation of polar bear populations have been based on evidence for spatial separation of individual bears (Bethke *et al.*, 1996). For species with a large geographical range, we can expect a hierarchy of clumping of individuals. For polar bears, the species' range can be considered a metapopulation as this range is continuous and circumpolar. Within this metapopulation, 'populations' exist (Bethke *et al.*, 1996) and within each population 'subpopulations' may be present (see Wells & Richmond, 1995). We are interested in the hierarchical pattern of polar bear groups within the Canadian Arctic, and the factors responsible for this pattern. We are not describing a method of population delineation as Bethke *et al.* (1996) have already formulated an appropriate technique.

Two sets of attributes were used in cluster analysis, one based on information from satellite-collared polar bears, and the other from the spatial pattern of sea ice. Four biological seasons were delineated according to seasonal changes in activity level and mobility (Messier *et al.*, 1992) and ecological considerations: winter (1 Nov. – 15 March), spring (16 March – 31 May), summer (1 June – 15 August), and autumn (16 August – 31 October).

Cluster analysis was used to group objects (polar bears or sea ice) according to similarity (Romesburg, 1984). The standardized data matrix of objects (e.g. polar bears) and attributes (e.g. seasonal range) were used to compute the values of the Euclidean distance or resemblance coefficient. Average linkage clustering method (UPGMA) processed the values of the resemblance coefficient to create a dendrogram that shows the hierarchy of similarities among all pairs of objects. The dendrogram was divided into clusters for each of four seasons. The interpretation of clusters was based on a hierarchical separation into a small number of well defined groups ($n = 5$–8).

Polar bears

We used the radio locations of polar bears captured in the eastern Beaufort and western Arctic Archipelago (forty-five bears successfully tracked, 5003 locations 1989–93; Messier *et al.*, 1992) and those captured in the eastern Arctic Archipelago and Baffin Bay (111 polar bears, 8632 locations 1991–95; see Ferguson *et al.*, 1997) for a total of 608 bear-seasons. The radio-collars had a 4–6 day duty cycle and provided ten to twenty locations per season. We did not use location data from females while in dens or shelters.

Three variables were calculated for individual polar bears for each season. First, we determined the median easting and northing for all locations of each polar bear within each season. We transformed the decimal latitude-longitude coordinate system to Universal Transverse Mercator coordinates using SPANS^{TM} GIS (Intera Tydac Technologies, Inc. 1991). Second, the seasonal range (> nine

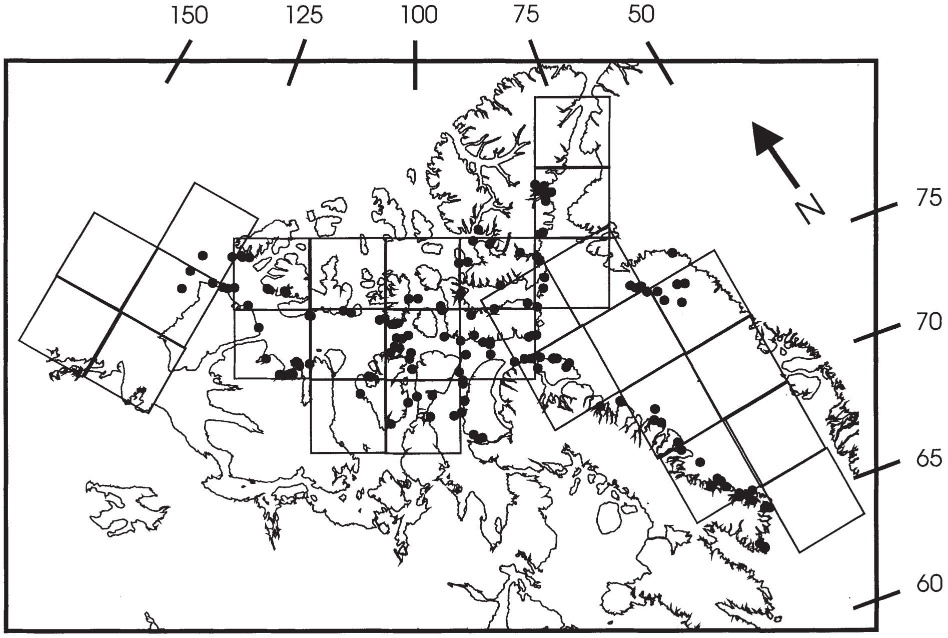

FIG. 1. Map of the study area in the Canadian Arctic with original capture locations (solid dots) of radio-tracked polar bears and the layout of 90,000 km^2 blocks used to study sea ice characteristics (see methods).

locations) was calculated as the 100% minimum convex polygon using a SAS^{TM} program written by White & Garrott (1990). Third, the fractal dimension of seasonal movements was calculated using the line segment method (Hastings & Sugihara, 1993; Ferguson, Rettie & Messier, 1998). The fractal dimension, D, of a movement pathway is a quantifiable measure of roughness or irregularity and varies between 1 and 2 (Fig. 2). We spatially and temporally restrict our calculations of fractal dimension to polar bears within the study area and for each season to avoid the problem of scale dependence of movement pathways (Turchin, 1996).

We performed two cluster analyses for polar bear classifications. First, we used all four variables: the fractal dimension of polar bear movement pathways, seasonal range, and x-y-median location. Because of the reduced sample size of fractal dimension of movement pathways (28–57 *v.* 98–178; four seasons) we chose to only show the results of our second cluster analysis which used three variables (excluding fractal dimension). The groupings (76–93% match) and topology ($r = 0.61$–0.87, $P = 0.001$–0.01, $n = 10$–21) of the two classifications were similar.

Sea ice

To assess the spatial pattern of sea ice, we selected 28, 300 × 300 km blocks (90,000 km^2) across the study area (Fig. 1). The size of these blocks approximated the mean annual home range of an adult female polar bear (99, 000 km^2, $n = 96$; data on file). Five blocks were located in the Eastern Beaufort, thirteen in the Arctic Archipelago and ten in Baffin Bay. Firstly, we considered the spatial nature of sea ice within each block. We divided blocks into 100 × 100 km cells and used the centre of each cell for point sampling (total $n = 252$). Only points that were on ice or within 5 km of sea-ice were used in the analysis ($n = 186$). We took the 10-year ice normals from the Ice Centre (Ice Climatology Notes, 1990) to select sampling points for each season.

Secondly, for each block, the percentage of the area covered by sea ice (i.e. available habitat) was assessed using composite sea ice maps prepared by Environment Canada, Ice Centre and digitized using SPANS^{TM} GIS. Only areas > 20% ice cover were included in this analysis as polar bears seldom used thinly distributed pack ice (data on file). For those areas and seasons (usually autumn) with < 20% ice cover, the coastline was used as a measure of available habitat. Here, we summed the available land within 5 km of the shoreline as 99% of polar bear capture locations were within 5 km of the coast (Ferguson *et al.*, 1997).

Thirdly, we calculated the fractal dimension of ice cover for each block using the following procedure. We recorded the presence of sea ice for each season to create a black (ice) and white (land and open water) picture (Fig. 3). For the autumn season, the shoreline was included as a black line as polar bears in some areas were forced onto land during the periods when sea ice melts. We used the box counting method (Morse *et al.*, 1985; FDC program for Macintosh computers, Paul D. Bourke, University of Auckland, New Zealand) to calculate the fractal dimension of available sea ice (and land for some blocks in autumn) for these pictures (28 blocks·4 seasons·4.25 years = 476 pictures). We averaged each season over years (1991–95) to obtain a mean measure of percentage ice cover and its fractal dimension for each block. Then, these values were assigned to the sampling points (above) specific to each block.

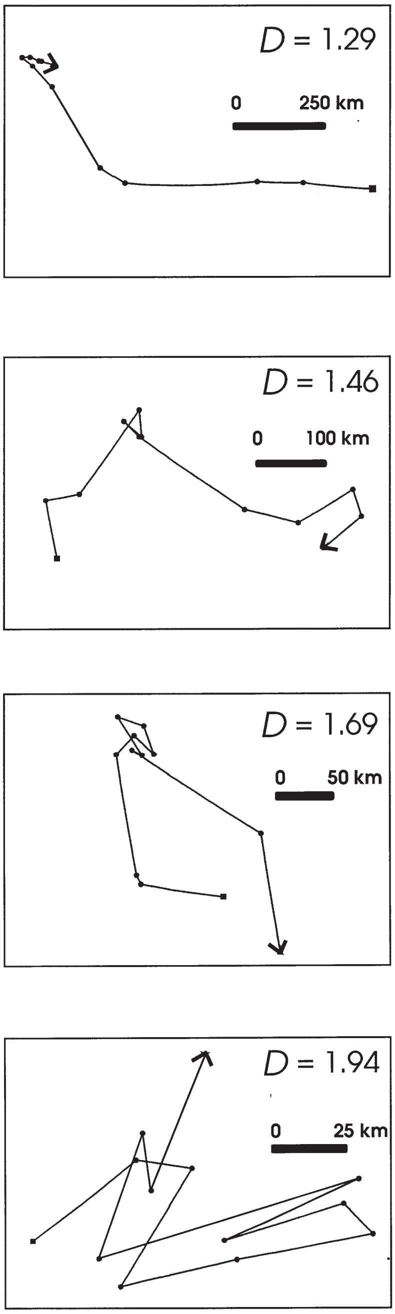

FIG. 2. Example showing how fractal dimension (*D*) changes with the degree of tortuosity of polar bear movement pathways.

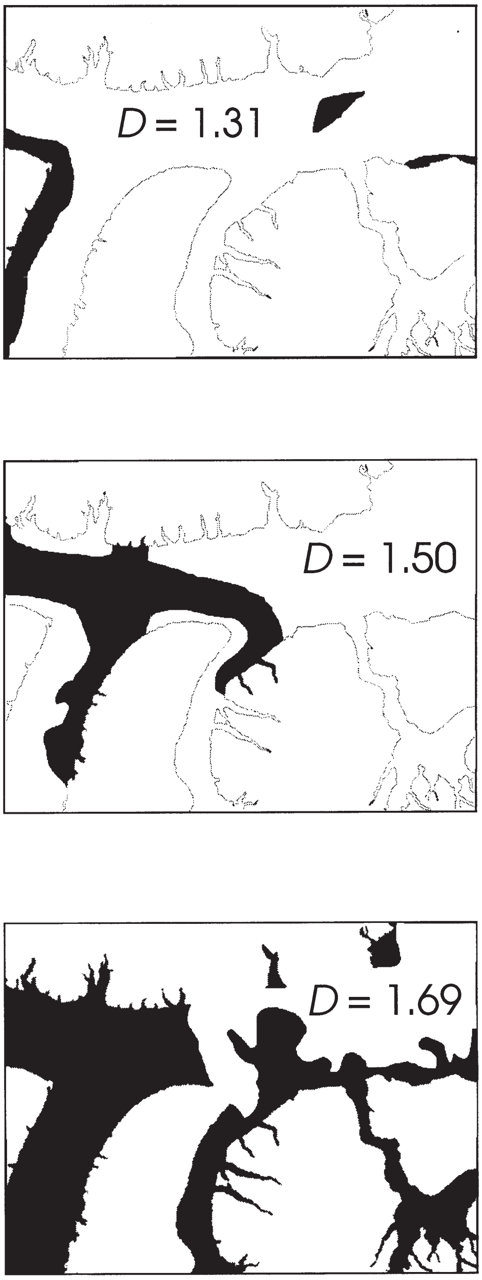

FIG. 3. Example illustrating how fractal dimension (*D*) increases with increasing irregularity in the distribution of sea ice and increasing ice cover.

Statistical analyses

ANOVAs, correlation and regression analyses (Sokal & Rohlf, 1969) and cluster analyses were performed using SAS statistical packages (SAS, 1990). We used log-likelihood ratio tests to compare frequencies of polar bear membership between a clustering by bear characteristics and by sea-ice characteristics (i.e. a significant difference indicated an association between the two classifications). To investigate the relationship among variables and perform the cluster analysis for sea ice characteristics, we took the average of 4–5 years of data for each season (above). We also averaged bear movement data within each block and season for regression analysis to derive partial regression coefficients (r_p). For all multiple regressions, we used the forward step-wise selection method for entry of independent variables.

RESULTS

Relationships between sea ice and polar bear variables

Seasonal ranges of polar bears were related to the amount of sea ice available ($r_p = 0.20$, $P < 0.01$, $n = 79$ blocks) and the spatial pattern (fractal dimension) of sea ice ($r_p = -0.30$, $P < 0.01$, $n = 79$). Polar bears that ranged within regions with a high proportion of sea ice, for example Baffin Bay during winter (77%) and spring (75%), had large seasonal ranges (66,200 km^2). In contrast, polar bears living in the Arctic Archipelago, a region characterized by an interspersion of numerous land masses, had smaller seasonal ranges (13, 200 km^2), despite the reduced overall coverage of sea ice in the region (56%). Regions with a high proportion of sea ice also had a high fractal dimension of sea ice habitat as shown by a positive correlation between these two variables ($r = 0.86$, $P < 0.01$, $n = 112$). Partial correlation described a negative relationship (30% of variation explained) between the fractal dimension of sea ice and the seasonal range of polar bears. For example, the Arctic Archipelago is characterized by an interspersion of land resulting in a fractured pattern of sea ice available to polar bears. This pattern of sea ice accounts for the relatively small ranges observed. Although, the relative proportion of sea ice is lower in the Arctic Archipelago region, the fractal dimension of this sea ice is correspondingly high.

The fractal dimension of polar bear movement varied with both the spatial pattern of sea ice ($r_p = 0.18$, $P < 0.001$, $n = 60$) and the percentage of ice coverage ($r_p = -0.44$, $P < 0.001$, $n = 60$). Polar bears ranging within regions consisting of mostly sea ice, showed less irregular and less tortuous movement patterns as described by a smaller fractal dimension. Similarly, with greater irregularity in the spatial structure of their sea ice (higher D), polar bears responded with greater irregularity in their movement patterns.

Clustering

Spring

Clustering polar bears based on their seasonal range generally matched clusters based on the amount of ice available and the fractal dimension of sea ice ($G = 30.6$, d.f. $= 7$, $P < 0.001$, $n = 126$). 84% of the median polar bear locations ($n = 126$) grouped according to polar bear characteristics matched with the spatial classification of sea ice (eight regions; Fig. 4). For the classification based on sea ice (Fig. 5), the High Arctic and Eastern Beaufort separated as the most distinct regions and the two Baffin Bay regions grouped with the Davis Strait region. In contrast, for the classification based on polar bears (Fig. 6), Davis Strait separated out as the most distinct region and the Southern Arctic Archipelago grouped with the two Baffin Bay regions.

For the spring, the same eight regions were delineated based on polar bears as for sea ice (Fig. 4). The Eastern Beaufort (EB), Baffin Bay (NBB and CBB), and Davis Strait (DS) regions are characterized by the greatest percentage ice cover (63–87%) compared to Arctic Archipelago regions (HA, NAA, CAA, and SAA; 27–63%; Table 1). The largest polar bear seasonal ranges (69,000 km^2) and lowest fractal dimension of movement ($D = 1.52$) were recorded for the Northern Baffin Bay and Davis Strait bears. These two regions also had the largest expanse of sea ice (83%) and a correspondingly high fractal dimension for the sea ice (1.86). The lowest polar bear seasonal ranges (9100 km^2) and highest fractal dimension of movement (1.64) came from the Arctic Archipelago bears (HA, NAA, CAA, and SAA). These regions also had similar proportions of sea ice (46%) and land (54%) intermixed. Although less sea ice generally results in reduced fractal dimension, the irregular distribution of land masses in the Archipelago resulted in a relatively high fractal dimension of sea ice (i.e. more edge effect).

The spring season was the time for mating in polar bears but not all females participated. To test whether those potentially breeding females grouped differently then all females together we ran a separate cluster analysis using only solitary adult females (i.e. likely breeders, $n = 48$). The match of bears with groupings ($n = 8$) was almost identical (97%) with the clustering based on all females.

Summer

For the summer period, we found less congruence between the polar bear and sea ice clustering ($G = 16.8$, d.f. $= 6$, $P = 0.01$, $n = 172$). Sixty-three percentage of the grouped median polar bear locations matched the cluster classification of sea ice (Fig. 4). Eight regions were identified using ice characteristics (Fig. 5) and six using polar bear characteristics (Fig. 6). High Arctic and Southern Arctic Archipelago bears did not form a cluster in summer likely because of the few bears radio-collared in these regions.

As in the spring, Northern Baffin Bay and Davis Strait regions supported polar bears with the largest seasonal range (44,100 km^2) and the lowest fractal dimension of movement (1.56; Table 1). These two regions were characterized by proportionately less sea ice (33%) and a lower fractal dimension of sea ice (1.67), likely resulting from the melting sea ice and movement of ice floes south. The Eastern Beaufort region contained polar bears with the next largest summer range (18,300 km^2) and a correspondingly low fractal dimension of movement (1.62). The remaining regions consisted of the Arctic Archipelago and western Baffin Bay and were characterized by bears with small summer range (12,400 km^2) and highly irregular or tortuous pathways (high $D > 1.68$). These remaining regions generally had greater amounts of sea ice available (51%) during the summer and a correspondingly higher fractal dimension of sea ice (1.79).

Autumn

The autumn period recorded the smallest seasonal ranges (17,200 km^2) and lowest fractal dimension of polar bear movements (1.54), as well as the least amount of sea ice (38%) and the lowest measure of fractal dimension of the remaining sea ice (1.54; Table 1). Ninety percent of the median polar bear locations grouped according to polar bear characteristics matched the spatial classification based on sea ice characteristics (Fig. 4; $G = 26.1$, d.f. $= 3$, $P < 0.001$, $n = 68$). Whereas Baffin Island grouped as the most distinct

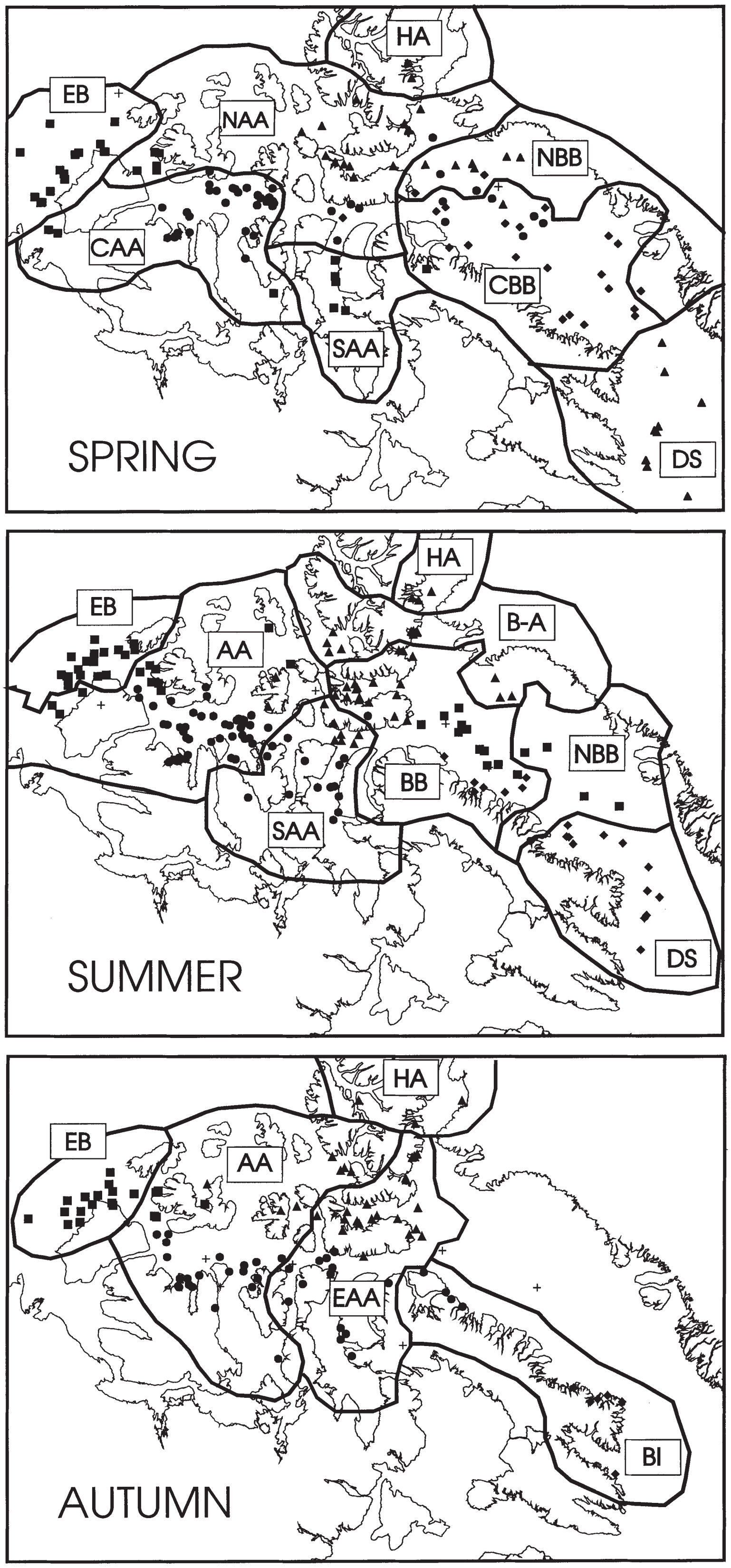
HA
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FIG. 4.
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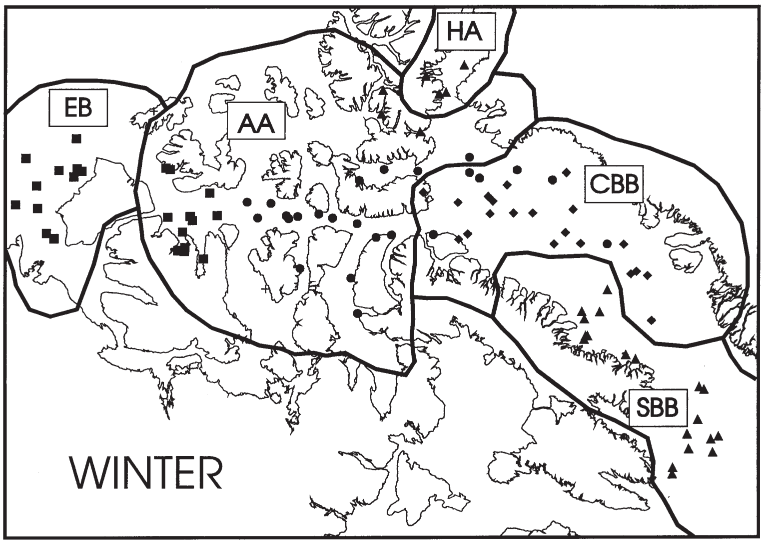

FIG. 4. Map of sea-ice regions by season (see Table 1) as revealed by clustering of sea-ice characteristics. Symbols denote separate clustering of polar bears based on range size and geographical location.

region for polar bears (Fig. 6), the sea-ice classification grouped the two regions with the least amount of sea ice together, Baffin Island (5%) with the Eastern Arctic Archipelago (19%; Fig. 5). The autumn period was also noteworthy in how the Arctic Archipelago subdivided. Based on information from polar bears, northern and southern regions grouped separately. In contrast, eastern and western regions grouped according to sea ice characteristics.

In autumn, polar bears in Baffin Bay are forced onto land with the disappearance of sea ice. One consequence of living on land is small home ranges (800 km^2) and low fractal dimensions of movement (1.47; Table 1). This pattern likely resulted from the removal of any significant sea-ice cover (5%) for the autumn period. In contrast, the bears of the Arctic Archipelago showed fewer differences in seasonal range and fractal dimension of movement between summer and fall seasons. The Archipelago regions did show a reduction in the amount of sea ice available and the fractal dimension of this sea ice. In particular the Eastern Archipelago recorded considerable loss of sea ice in the autumn period that also corresponded with a decreased fractal dimension. Polar bears that lived within the High Arctic region displayed small seasonal range (8300 km^2) and low fractal dimension of movements (1.42) which were likely related to the relatively smaller area of sea ice available (26%) and the correspondingly low fractal dimension of this ice (1.66).

Winter

The winter period was characterized by the maximum extent of sea ice (68%) and highest fractal dimension of sea ice (1.81; Table 1). Polar bears recorded their largest seasonal ranges (46,800 km^2) and one of their lowest fractal dimensions of movement pathways (1.55). The two classifications were very similar with 79% of grouped polar bear locations matching the spatial grouping of sea ice (Fig. 4; $G=31.2$, d.f.$=4$, $P<0.001$, $n=95$).

The Baffin Bay regions recorded large ranges (85,800 km^2) and low fractal dimension of movement (1.50; Table 1). Polar bears of the Eastern Beaufort region recorded small range (9300 km^2) even though this region as well as the two Baffin Bay regions were characterized by the most sea ice (79%) and the highest fractal dimension of sea ice (1.85).

Polar bears in the High Arctic region recorded the smallest seasonal range (6700 km^2) in winter. However, seasonal range did not vary among seasons for this region and remained small year round (6700–8300 km^2). In fact, all parameters for this region remained relatively constant throughout the seasons (Table 1).

Hierarchy of groupings

Regions occurred within a hierarchical structure (Figs 5 and 6). During the winter and spring periods, the High Arctic and Eastern Beaufort were the most distinct regions based on sea-ice characteristics. The Arctic Archipelago and Baffin Bay-Davis Strait separated next as two large regions. In contrast, for the same winter and spring periods, groupings based on characteristics of the polar bears, showed the Davis Strait group as the most distinct whereas the Eastern Beaufort grouped with the Arctic Archipelago as one group, and the Southern Arctic Archipelago grouped with the Baffin Bay bears (Fig. 4). These patterns broke down during the summer and fall periods with the ablation of sea ice. Still, relationships among regions for both sea ice and polar bear groupings are evident (Figs 5 and 6): Davis Strait clustered with Baffin Bay, Eastern Beaufort clustered with Arctic Archipelago, and the High Arctic generally remained distinct.

DISCUSSION

The spatial arrangement of resources, habitat, and barriers affects the location, movement patterns, foraging dynamics,

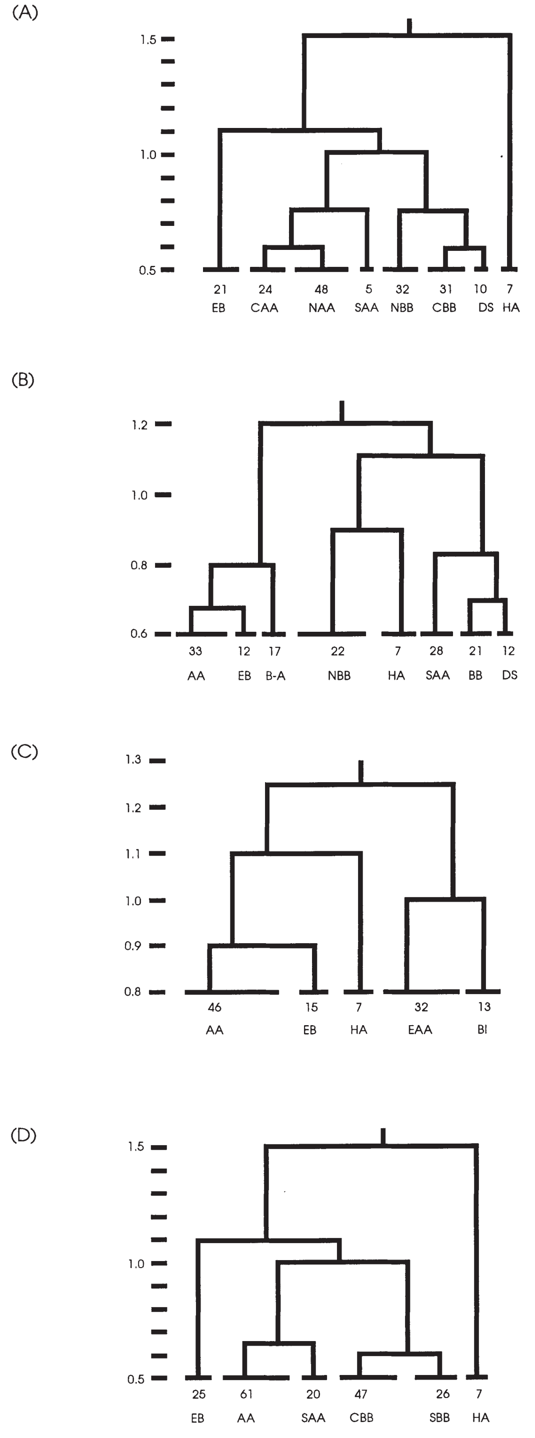

FIG. 5. Cluster analysis dendrograms based on sea ice characteristics from 186 sampling points (100 km apart) for the Canadian Arctic: (A) Spring season (16 March to 31 May) (B) Summer season (1 June to 15 August) (C) Autumn season (16 August to 31 October), and (D) Winter (1 Nov. to 15 March).

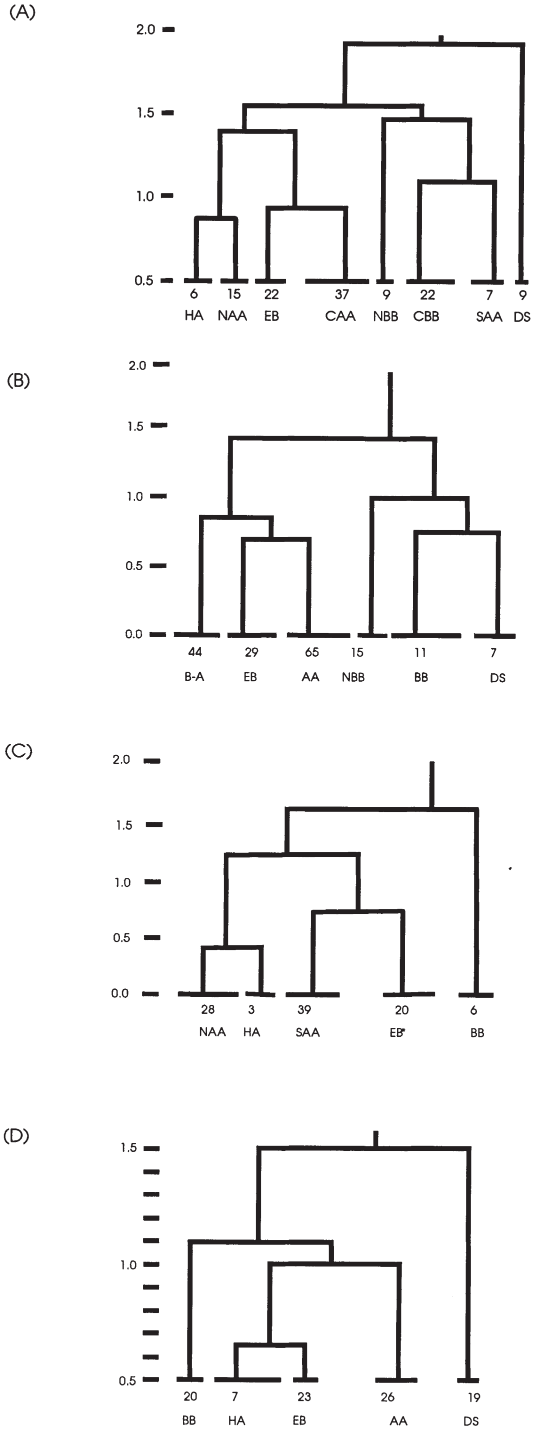

FIG. 6. Cluster analysis dendrograms based on movement data of polar bears ($n = 156$) by season: median telemetry location, and seasonal range size. (A) Spring season (16 March to 31 May) (B) Summer season (1 June to 15 August) (C) Autumn season (16 August to 31 October), and (D) Winter (1 Nov. to 15 March).

and persistence of organisms (Kareiva, 1990; Danielson, 1991; Pulliam *et al.*, 1992; Turner *et al.*, 1995). We tested whether patterns in the sea ice related to the hierarchical organization of groups in polar bears within the Canadian Arctic. Our results indicate that spatial characteristics of the sea-ice landscape does link to the hierarchical pattern of polar bear groupings. We have not identified the mechanism of spatial patterning although water currents

TABLE 1. Statistics for season range, fractal dimension (*D*) of polar bear movements, percentage sea-ice cover, and fractal dimension (*D*) of sea ice (x ± SE (*n*)) for various regions of the Canadian Arctic. Data are presented by biological season pooled across years 1991–95.

		Polar bear		Ice	
Season*	Cluster†	Range (km^2)	*D* of movement	Percent ice cover	*D* of sea ice
Spring	CAA	7900 ± 1486 (37)	1.72 ± 0.035 (10)	58.7 ± 1.01 (24)	1.80 ± 0.0030 (24)
	EB	11300 ± 1930 (22)	1.60 ± 0.068 (4)	86.6 ± 2.16 (21)	1.86 ± 0.0044 (24)
	NAA	8791 ± 1618 (15)	1.60 ± 0.064 (2)	54.2 ± 1.20 (48)	1.76 ± 0.0030 (48)
	CBB	26312 ± 2621 (22)	1.71 ± 0.066 (6)	62.9 ± 1.01 (31)	1.81 ± 0.0028 (31)
	NBB	66826 ± 3992 (9)	1.48 ± 0.0059 (2)	87.0 ± 1.10 (32)	1.87 ± 0.0034 (32)
	SAA	11877 ± 4309 (7)	1.56 (1)	45.6 ± 0.04 (13)	1.71 ± 0.0014 (13)
	DS	71413 ± 17856 (9)	1.55 (1)	76.6 ± 0.00 (10)	1.85 ± 0.0000 (10)
	HA	7963 ± 1325 (6)	1.67 (1)	27.3 ± 0.00 (7)	1.66 ± 0.0000 (7)
	All	22469 ± 2620 (129)	1.64 ± 0.028 (28)	65.1 ± 1.28 (186)	1.80 ± 0.0043 (186)
Summer	AA	14608 ± 1700 (65)	1.72 ± 0.040 (21)	60.8 ± 0.75 (38)	1.80 ± 0.0019 (38)
	EB	18349 ± 2273 (29)	1.62 ± 0.049 (18)	84.4 ± 0.72 (12)	1.85 ± 0.0035 (12)
	B-A	8588 ± 1161 (44)	1.68 ± 0.032 (5)	54.1 ± 0.98 (17)	1.79 ± 0.0096 (17)
	NBB	49320 ± 3661 (15)	1.56 ± 0.064 (7)	23.0 ± 1.28 (22)	1.63 ± 0.0046 (22)
	BB	14233 ± 2277 (11)	1.77 ± 0.058 (4)	39.0 ± 0.93 (21)	1.77 ± 0.0092 (21)
	DS	38972 ± 6193 (8)	NA	43.8 ± 0.59 (12)	1.70 ± 0.0023 (12)
	SAA	NA	NA	46.5 ± 1.00 (28)	1.73 ± 0.0059 (28)
	HA	NA	NA	20.5 ± 0.00 (7)	1.60 ± 0.0000 (7)
	All	20945 ± 1790 (178)	1.65 ± 0.025 (57)	47.9 ± 1.38 (158)	1.74 ± 0.0060 (158)
Autumn	SAA	13387 ± 1672 (39)	1.53 ± 0.036 (17)	NA	NA
	NAA	11433 ± 2230 (28)	1.70 ± 0.040 (5)	NA	NA
	AA	NA	NA	47.1 ± 1.07 (46)	1.74 ± 0.0062 (46)
	EAA	NA	NA	19.3 ± 0.82 (32)	1.47 ± 0.0176 (32)
	EB	15661 ± 2692 (20)	1.54 ± 0.044 (12)	82.7 ± 2.38 (15)	1.85 ± 0.0016 (15)
	BI	843 ± 347 (6)	1.47 (1)	5.2 ± 0.36 (13)	1.19 ± 0.0000 (13)
	HA	8252 ± 3297 (3)	1.42 (1)	26.2 ± 0.00 (7)	1.66 ± 0.0000 (7)
	All	17237 ± 2111 (104)	1.54 ± 0.025 (37)	37.9 ± 2.25 (113)	1.61 ± 0.0199 (113)
Winter	AA	18122 ± 2853 (26)	1.63 ± 0.036 (19)	57.7 ± 0.84 (61)	1.77 ± 0.0028 (61)
	EB	9255 ± 1889 (23)	1.67 ± 0.110 (4)	83.8 ± 2.53 (25)	1.86 ± 0.0040 (25)
	SBB	63271 ± 11052 (19)	1.52 ± 0.041 (13)	67.6 ± 2.25 (26)	1.83 ± 0.0041 (26)
	CBB	108398 ± 12699 (20)	1.47 ± 0.031 (18)	86.1 ± 1.15 (47)	1.87 ± 0.0053 (47)
	HA	6698 ± 2315 (7)	1.62 ± 0.137 (3)	28.1 ± 0.00 (7)	1.67 ± 0.0000 (7)
	SAA	NA	NA	49.0 ± 0.99 (20)	1.74 ± 0.0073 (20)
	All	46791 ± 5789 (98)	1.55 ± 0.022 (59)	67.7 ± 1.31 (186)	1.81 ± 0.0045 (186)

* Seasons: spring (16 March – 31 May), summer (1 June – 15 August), autumn (16 August – 31 October), and winter (1 Nov. – 15 March).
† Clusters (see Figs 5 and 6): CAA, Central Arctic Archipelago; EB, Eastern Beaufort; NAA, Northern Arctic Archipelago; CBB, Central Baffin Bay; NBB, Northern Baffin Bay; SAA, Southern Arctic Archipelago; DS, Davis Strait; HA, High Arctic; All, Combined regions; AA, Arctic Archipelago; B-A, Baffin-Archipelago; BB, Baffin Bay; EAA, Eastern Arctic Archipelago; BI, Baffin Island.

and barriers to movement likely influence areas of den use, hence bear groups.

Classifications based on sea ice characteristics are difficult because spatial patterns of sea ice changes continually throughout seasons and among years. Still, at longer time scales geological activity has remained relatively constant over the past interglacial period (10 kya to present; Bartlein & Prentice, 1989; Dyke *et al.*, 1996) and sea-ice history has successfully distinguished populations of bowhead whales (*Balaena mysticetus*; Dyke *et al.*, 1996) and beluga whales (*Delphinapterus leucas*; O'Corry-Crowe *et al.*, 1997). We propose that by extending our methods, polar bears could be grouped within their entire circumpolar range by a clustering based only on the distribution and pattern of sea ice and islands. For the Canadian Arctic region, we identified four or five major groupings of polar bears based on landscape pattern: the Eastern Beaufort, Arctic Archipelago, High Arctic, Baffin Bay, and possibly Davis Strait. The winter and spring seasons provided the most parsimonious groupings of polar bears, likely due to the occurrence of mating in spring (Ramsay & Stirling, 1988) and relatively constant sea-ice landscape over winter (January through April). Bethke *et al.* (1996) determined similar groupings of polar bears for the western portion of our study area. For the spring and winter periods, our EB (Eastern Beaufort) region matched their NB (Northern Beaufort; Fig. 6 in Bethke *et al.*, 1996) with only two of twenty-seven polar bear locations differing between the two classifications. Similarly, our classification decisions resulted in combining their VM and PC populations into an AA (Arctic Archipelago) region (Fig. 5 in Bethke *et al.'s* 1996) and results in a 96% matching of the two classifications. Taylor & Lee (1995; Fig. 2) reported a 4% exchange rate of marked polar bears among Arctic populations. Low rates of exchange can prevent genetic isolation while maintaining population discreteness.

Two approaches can be used to explain the existence of populations: characteristics intrinsic to the population may define differences among populations (sympatry), or geophysical characteristics of the extrinsic environment can result in separation of groups of animals (allopatry). To understand adaptation and speciation (diversity) we delineate the spatial hierarchy of polar bear populations relative to their major landscape-structuring agent, sea ice. Polar bears are spatially composed of local populations that likely show genetic, morphologic, or behavioural distinctions due to selection, mutation, emigration, and immigration. However, these differences among populations are unlikely to lead to reproductive isolation. Natural selection has resulted in the evolutionary origin of polar bears as a species during a period of rapid geological change due to intense directional selection. Under present conditions, natural selection serves as a stabilizing force during a period of stasis due to stabilizing or normalizing selection.

Controversy exists concerning the role of geography in speciation (Ridley, 1993; Coyne, 1994; McPeek, 1996; Wilson, 1996). The freezing of the Arctic sea was a significant event that resulted in the evolution of a number of new species (Riddle, 1996). Kurtén (1964) postulated that a population of brown bears, possibly from Siberia, became geographically isolated from other brown bears as a result of the advance of glaciers. Natural selection for features adaptive to hunting seals on sea ice led to the gradual divergence of the original species of brown bears and the emerging population of polar bears (Zhang & Ryder, 1994; Talbot & Shields, 1996a). The subsequent development of biological differences (genetical, morphological, behavioural) between the two populations distinguishes them as distinct species (Talbot & Shields, 1996b; Slattery & O'Brien, 1995) and are based on differences in geography (land *v.* ice). Therefore, for polar bears, a geological event (short evolutionary time) resulted in speciation (diversity) whereas the formed sea-ice landscape now results in a spatial structuring of populations that stabilizes diversity (long evolutionary time).

Movement pathways are strongly influenced by environmental structure (Burrough, 1981; Palmer, 1988; DeCola, 1989; Milne, 1992) and therefore measuring fractal dimension may help to understand how conspecific groupings relate to landscape patterns. Wiens and coworkers (Wiens & Milne, 1989; Crist *et al*., 1992; Crist & Wiens, 1994; With, 1994; With & Crist, 1995) compared the fractal measures of movement pathways among insect taxa and found variations related to the spatial heterogeneity of the landscape (Wiens *et al*., 1995). Our results for polar bears (Table 1) also indicate a link between fractal movements and fractal landscape, suggesting that consequences of environmental heterogeneity probably result from similar processes for insects (Wiens *et al*., 1995) as for large mammals (Swihart *et al*., 1988). For example, polar bears living in the Arctic Archipelago are characterized by relatively small seasonal ranges and higher fractal dimension of movement pathways (controlling for amount of ice cover). This movement pattern is likely related to the higher fractal dimension of the ice landscape which is interspersed by numerous large islands.

The study of the temporal dynamics of a species' geographical range and the spatial distribution of populations can help to determine how the size and geometry of habitats affect both population dynamics and community structure (Cantrell & Cosner, 1994; Gaston, 1995; Uchida, 1996). Identifying and naming groups of polar bear population lineages can provide a reference point for the purposes of studying the effects of natural selection over time. The species range for polar bears persists as a metapopulation – an assemblage of local populations inhabiting a sea-ice landscape fragmented by islands. Future multidisciplinary studies that examine morphological, behavioural, and genetic variation among populations (e.g. Paetkau *et al*., 1995; O'Corry-Crowe *et al*., 1997) will provide critical information for addressing questions concerning the evolutionary biology of polar bears. Molecular phylogeography offers biogeographers and palaeoecologists one approach to examining patterns of range shift, population differentiation, speciation, and illuminating patterns of hierarchical structure of organisms in response to geological events (Riddle, 1996). Equally important, the quantitative understanding of metapopulation dynamics is critical for the successful management and conservation of a species like polar bears (Edwards *et al*., 1994; Hanski & Gilpin, 1996).

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