

**Ice, tropics and the Hooded seal: evidence of panmixia or recent gene flow
that hides past populations.**

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**This thesis submitted in partial fulfillment of the requirements for the
Biologist degree**

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Abstract

Hooded seals breed synchronously in four main breeding sites along the Atlantic region of the Arctic Ocean. Each of these sites might represent a different subpopulation. However, genetic studies reveal high genetic diversity coupled with an absence of population structure among breeding sites. Additionally, there has been an increasing number of wandering events of individuals out of their home range. We used the mitochondrial control region sequences from 114 individuals belonging to the four breeding sites and 11 from individuals that were found wandering out of their normal range, to test for genetic differentiation related to the wandering behavior. Moreover, we modeled the ecological niche of this species to find which places outside their normal range had viable environmental conditions for a seal to wander. Additionally, we used a phylogenetic approach based on coalescence coupled to a molecular clock to try to understand the genetic diversity that Hooded seals appear to have. We found no genetic differentiation between the individuals that wander outside of their normal range and those who do not. We also found that the East Coast of Europe provides good environmental conditions for Hooded seals to live while the Caribbean region doesn't. Finally, our phylogenetical analyses suggest that the Hooded seals diversity may have arisen during the Pleistocene period and that the lack of genetic structure seen today is probably caused by lack of time following a colonization event after the last glacial maxima. We therefore suggest the breeding herds to be currently in a divergence process for what it will be prudent to continue managing the stocks separately.

Introduction:

The pattern by which a species or a population is phylogenetically assembled in the present is a remnant of its history. Such phylogenetic pattern may be caused by several microevolutionary processes, such as mutations, changes in the quantity of the gene flow, genetic drift and the direction of natural selection, leaving genetic marks in a species population (Bolnick *et al.* 2002; Manel *et al.* 2003) or individual (Bolnick *et al.* 2002). When studied these marks may act, within an environmental framework, as clues for understanding the history and predicting future processes that a species might have or will experience (O'Corry-Crowe 2008).

One of the most common pattern by which genomes acquire variability relies on the idea of an environmental barrier that separates a population in two or more groups preventing gene flow (Dobzhansky 1936). Eventually, these allopatric subgroups will be exposed to different environmental conditions that may cause an increase in the variance of those genomes. Such environmental separation can result in phylogenetical splits which might ultimately result in speciation (Barracough & Vogler 2000). Associating the phylogenetical splits with the environmental changes that occurred in the past, including geological processes and climate changes, may give insights of how diversity is produced.

Shifts in the earth's temperature produce abrupt environmental changes that usually lead genomes to vary. The loss of some environments and the creation of new ones due to climatic change had been associated with speciation events, adaptive radiation, extinction and variation among individuals (Johnson &

Cicero 2004; Monasterio & Sarmiento 1991; Weider & Hobæk 2000). The earth's climate has been subjected to constant shifts in the last million years. During the Pliocene (5.33 to 2.58 MYA) the earth's temperature was relatively higher than it is in present days (Haywood & Valdes 2004). Furthermore, during the mid-Pliocene (3.3 to 3 MYA) the oceans heated from 1 to 5°C in both hemispheres to a depth of 2000 m causing a great sea ice cover reduction (50% on Greenland and 33% on Antarctica), an increase in the sea level and changes in water temperature and sea currents producing abrupt alterations in the environmental conditions, specially in high latitudes where the effects are more intense (Chandler *et al.* 2008). Additionally, an increase in the temperature of the earth is thought to have affected productivity and the entire web of life especially in polar and subpolar waters (Smetacek & Nicol 2005). It has been proposed that this temperature increase likely isolated small, geographically distinct populations of Arctic marine mammals at the southern boundaries of the species range causing a variation in the genomic diversity of the populations (O'Corry-Crowe 2008).

Afterwards, there was a transition from the warm Pliocene climates to cooler ones during the Pleistocene (2.588 MYA to 12000 years). During this period there were four major times of formation and expansion of ice sheets covering about 30% of the land area separated by three interglacials with temperatures a little bit above those in present times (Hewitt 2000). As ice grew, species must have went extinct from their native range, dispersed to new locations or may have survived in southern refugia. Thereafter, during interglacial periods, species must have expanded their range favoring high diversification rates. (Avice *et al.* 1998; Johnson & Cicero 2004). As this process happened repeatedly, genomic diversity should have increased (Fedorov & Goropashnaya 1999). In this type of events, the abiotic characteristics of the geographical location of an organism determine the amount and rate of genetic differentiation. In this sense, the history of each region in the world causes a unique rate and pattern of genome diversification in a determined species (Hewitt 2000). For example, climatic changes are much stronger in high latitude regions and the polar and subpolar species, including marine mammals, are exposed to extremely high diversification rates (O'Corry-Crowe 2008; O'Corry-Crowe *et al.* 1997; Palo 2003).

Other possible effects of environmental changes on populations could be the raise in interspecific competition due to a loss in habitat resources or habitat availability, decreasing the probability of two sympatric species to coexist. As a consequence, species that are subject to strong interspecific competition are thought to become extinct or evolve to change their habitat resource use to overcome competition (Connell 1961). In addition, the effects of competition can also be noticeable at the intraspecific level. Rare individuals that can reduce the effect of competition are more likely to survive driving populations to intraspecific variation (Burger & Gimelfarb 2004), trophic polymorphism (Smith & Skúlason 1996) or even speciation (Burger *et al.* 2006). Accordingly, an individual can extend its niche range affecting profoundly a population's ecology and evolutionary dynamics (Bolnick *et al.* 2002). Alternatively, species can evolve a migratory behavior in order to locate and capture food in suitable empty

habitats. These migrations are considered to be an important strategy for the survival of a species (Bergman *et al.* 2000). Therefore, competition triggers intraspecific variation in movement behaviors as a tactic for the individuals inside a population to maximize its fitness or survival (Austin *et al.* 2004).

The hooded seal (*Cystophoracristata*) is a large, deep diving, pelagic pinniped inhabiting the Atlantic region of the Arctic Ocean as well as high latitudes in the North Atlantic (Sergeant 1974). Strictly, its habitat range goes from the west coast of Norway in Bear Island to the Labrador Peninsula including Jan Mayen Island, Iceland and Greenland. Hooded seals are known to breed synchronously during mid to late March in four pack ice areas: 1) around Jan Mayen island referred to as "West Ice", 2) Northeast of Newfoundland and/or southern Labrador known as "The Front", 3) in the Gulf of St. Lawrence "The Gulf" and 4) in Davis Strait between west Greenland and Baffin Island (Folkow *et al.* 1996). It has been thought that the Hooded seals whelping in the West Ice near Jan Mayen constitute the Northeast Atlantic population while the other three herds conform the Northwest Atlantic population (Hammill & Stenson 2006). The Northeast population is thought to be composed by approximately 70,000 to 90,000 individuals, however these estimates are uncertain due to paucity of data and limited understanding of whelping areas (Anonymous 2006). The Northwest population is thought to have approximately 600,000 individuals with 90% of them whelping at The Front (Stenson *et al.* 1996). The Northeast population whelping in Jan Mayen seems to disperse to the sea after breeding, thereafter molting North from there in July. The Northwest population leaves to the sea after breeding to feed and then they seem to return to a molting patch located southeast of Greenland (Stenson & Kavanagh 1994). After the molting period, the individuals seem to disperse to the sea to feed, gaining weight in preparation for the next whelping and breeding season. The Northeast population is thought to remain in ice-covered waters off Greenland with some migrations to Faroe Islands, Bear Island (Norway), Iceland and the United Kingdom (Folkow, Mårtensson *et al.* 1996). In the other side, the Northwest population stays along the continental shelf in Davis Strait and Baffin Bay where they also feed until the following breeding season (Andersen *et al.* 2009).

In reference to these two putative populations, Coltman *et al.* (2007) carried out a population genetics analysis using mitochondrial DNA and microsatellites finding that although the east Greenland population was genetically dissimilar from the Northwest Atlantic ones, the difference was not statistically significant. His conclusion was that the world's Hooded seals belong to a unique panmictic population, suggesting an overcrossing between the two above mentioned putative populations. However, the genetic structure showed in the present by the Hooded seals can be a remnant of its past history. Geographic changes across the species distribution due to environmental factors could have led the species to conquer new habitats, evolve new lineages and increase diversity. Hence, the seals may have recolonized the modern range recently and either insufficient time or enough gene flow would have prevented genetic differentiation to arise (Coltman *et al.* 2007).

Additionally, in recent times a trend has been noticed for the hooded seals to

wander out of their normal habitat range There have been reports of individuals in the Northern Gulf of Main, Nova Scotia (Canada), New England (USA)(Mcalpine *et al.* 1999), the western coast of Europe(Van Bree 1997) the Mediterranean coast of Spain (Bellido *et al.* 2007), and in the Caribbean where, in the year 2001, 130 individuals were reported stranded across Antigua, Puerto Rico and the Canary islands (Mignucci-Giannoni & Haddow 2002). Most Hooded seals that expand their home range (94.2 %) are young individuals less than three years old (Lucas & Daoust 2002). The majority of these show conditions of extreme sickness due probably to starvation, including gastric impaction with abnormal ingesta, hemorrhagic diathesis possibly induced by parasitic migration and secondary vasculitis, and stomatitis (Lucas *et al.* 2003). There may be two important reasons that explain why the Hooded seals are expanding their habitat range in the last years: 1) The Hooded seals have increased their population numbers due to law enforcement prohibiting hunt of this seals since the 70s and/or 2) the fish stocks have been reduced greatly due to over fishing causing a shortage on food for seals (Mcalpine *et al.* 1999).

The distribution of pinnipeds is affected by physical factors, such as habitat and the type of haul-out substrate, temperature, salinity, ocean current patterns and sea depth, and ecological factors, such as the distribution and abundance of prey, predators and competitors (Deméré *et al.* 2003). Since the Hooded seals give birth in the pack ice, changes in the percentage and location of ice coverage due to recent climatic shifts affect their distribution and comprise a problem of habitat loss for many individuals (Tynan & DeMaster 1997). Additionally, climate change is likely to affect the prey availability for pinnipeds. Fish represents seventy-seven percent of the total prey consumption by Hooded seals followed by shrimps and other invertebrate species. Basically, in respect to the fish diet, Hooded seals principally consume three fish species, Capelin (*Mallotus villosus*), the Arctic Cod (*Boreogadus saida*) and Sand lance (*Ammodytes* sp.) (Hammill & Stenson 2000). The population dynamics of fish, including the above mentioned, are affected by climate variability. For cod, statistical relationships between growth, condition, maturity and distribution with atmospheric and ocean climatic indices have been observed (Ottersen, Alheit *et al.* 2004). Moreover, modern factory fleets have transform fishing into a worldwide industry in which the extraction is dominated by multinational enterprises which capacity of fish harvesting is much higher than the sustainable levels for fish populations (Hannesson 2007). Therefore, the populations of arctic cod and capelin have, and still are, subject to strong diminishment due to heavy industrial extraction which have caused starvation among predators (Hamre 1994; Hannesson 2007). As resources become less available competition for them becomes stronger. It is well known that two species don't coexist long if they use the same kind of resources (Schoener 1974). For that, every behavior that leads to a reduction in competition is favored by selection. It has been documented that animals displace individuals with lower competitive abilities into less quality resource niches. For example, older individuals of Elephant seal (*Mirounga leonina*) avoid time and spatial overlapping niches with the younger (Field *et al.* 2005). Additionally, harp and hooded seals show a resource partitioning between old and young which is likely to affect their distribution (Tucker *et al.* 2009). This type of behavior is known as the "Age structure component" of niche width and

contributes importantly to the amplitude of a species niche (Polis 1984). Consequently, the Hooded seals are under strong environmental pressures, which could be affecting their movement patterns for foraging, constituting a possible warning about newer distribution ranges.

There is still lack of clarity about the background and potential reaches of new behaviors being acquired by Hooded seals. In this study we tested for genetic differences and similarities of individuals of Hooded seals outside and inside their home range using the control region of the mitochondrial DNA to get an insight about genetic patterns of individuals that present this abnormal behavior. Additionally, we used a coalescent approach to understand the evolutionary history of the overwhelming genomic diversity that the Hooded seals appear to have. Moreover, to understand the ecological factors of the wandering behavior, it was important to understand if there are geographically associated physical characteristics that may lead seals to migrate to a specific place, or if the migration places are better explained by ecological and/or random events. For this, we modeled the potential niche of hooded seals using physical marine conditions to assess the physically suitable locations for hooded seals to live. All of these can give us clues about expected shifts in the population's ecology and evolutionary dynamics of Hooded seals when challenged to a changing environment.

Methods:

Samples:

Wandering Hooded seals sequences were provided by the Caribbean Stranding Network through S. Caballero. Samples were collected from eleven individuals of wandering hooded seals that arrived to different locations outside their normal range (Table 1). The provided sequences contained a 324-bp fragment of the control region (D-loop) of the mitochondrial DNA.

Dr David Coltmangently provided normal range seals' sequences. These contained a 900-bp fragment of the end of the cytochrome b, tRNA_{thr}, tRNA_{pro} and part of hypervariable region I (HVR I) in the control region from individuals collected at four main breeding concentrations of hooded seals in the North Atlantic: West Ice (n=53), The Front (n=19), The Gulf of St. Lawrence (n=21) and Davis Strait (n=21) (see also Coltmangent *et al.* 2007).

Data analysis

Sequences were aligned using the Muscle algorithm in Geneious 2.5 (Drummond *et al.* 2006) and confirmed by eye using Maclade version 4 (Maddison & Maddison 2000). Afterwards, the surplus parts of the sequences were cut using Geneious 2.5 for all these sequences to share the same homologous nucleotides (324-bp).

Following previous categorizations (Coltmangent *et al.* 2007), we divided the samples into four putative subpopulations, West Ice, The Front, The Gulf, Davis Strait and added another subpopulation which corresponded to the wandering individuals. Number of haplotypes, haplotypic diversity, shared haplotypes and nucleotide

diversity π were performed using ARLEQUIN 3.0 (Excoffier *et al.* 2005) for the wandering population. Additionally, pairwise F_{st} and Tajima's D tests were performed in ARLEQUIN 3.0 to compare among populations. With this data set we also generated a phylogenetic network to test for connectivity among the haplotypes using the median-joining algorithm (Bandelt *et al.* 1999) in Network V 4.51.0 (www.fluxus-engineering.com).

We used a coalescent-based inference method coupled with a Uncorrelated Lognormal relaxed molecular clock to enable population genetics parameters of seal's population structure in BEAST V 1.5.1 (Drummond & Rambaut 2007). For the phylogenetic analysis and the calibration of the molecular clock we used, aside of all the sequences from hooded seals mentioned above, twelve other mitochondrial sequences from seven Pinniped species acquired from GenBank (Table 2). For the coalescent inference we used a GTR + G model determined using MRMODELTEST V 2.3 (Nylander 2004). Additionally we set BEAST to estimate the base frequencies. We used a coalescent: constant size tree prior. To calibrate the clock we used the taxa time divergence among five nodes based on the molecular estimates of pinniped divergence in Arnason *et al.* (2006). The first node used for the calibration was the divergence between Phocidae and Odobenidae \approx 33 Myr. The second, the divergence point between Phocidae and Phocinae \approx 22 Myr. Third, the node that separates *Erignathus* from *Cystophora*/Phocini \approx 17 Myr. The fourth was the node in which *Cystophora* diverges from Phocini \approx 13 Myr. Finally, we used the divergence node between the ribbon and harp seals (*Histriophocina*) and a branch (Phocina) that contains the remaining Phocini species among the sample (harbor and ringed seals) \approx 9 Myr. The number of steps of the Markov Chain Monte Carlo (MCMC) was set to 20000000 generations. We used Tracer V 1.4.1 (Drummond & Rambaut 2007) to check up that the results had effective sample sizes. To test for the demographic behavior of the seal's population through time, we performed a Bayesian Skyline Plot and a Lineage through time analyses using the ape package (Paradis *et al.* 2004) in R (R_Development_Core_Team 2005).

After inferring the phylogenetic structure of the hooded seals with BEAST, we performed an AMOVA to test for significant genetic differentiation among phylogenetic groups. To do so, we divided the samples into three groups according to the monophyletic clades formed by the hooded seal's haplotypes in the tree. We then performed a pairwise F_{st} to test whether a significant difference among the phylogenetic haplotype groups was noticeable using ARLEQUIN 3.0 (Excoffier 2005).

Finally to get insight about the possible causes and predict the wandering hooded seals movement, we performed a niche modeling using the maximum entropy algorithm implemented by Maxent V.3.1 (<http://www.cs.princeton.edu/~schapire/maxent/>; (Phillips *et al.* 2006; Phillips *et al.* 2004) to understand the physical characteristics of hooded seal's niche and know other geographical locations with similar variables. We acquired 1-degree grid cell layers from the National Oceanographic Data Center (NODC) containing temperature, salinity, dissolved oxygen, percent oxygen saturation, apparent oxygen utilization, phosphate, silicate and nitrate variables. On the

other hand, we used Google Earth to obtain 15 points randomly chosen but restricted to the four putative population locations where Coltman (2007) acquired the samples. These points shall give insight of the physical niche characteristics of hooded seal's normal range. Afterwards, we used a discriminant analysis using SPSS V.16 to evaluate statistically climatic differences between the hooded seals normal range and the conditions in reported wandering sites.

Results:

From 125 individuals belonging to all five putative subpopulations, only ten haplotypes were found more than once. However for the wandering seals all individuals had unique haplotypes (Table 4). Every subpopulation shared at least one haplotype with every other except for the wandering. The wandering subpopulation had 11 haplotypes, determined by 33 polymorphic sites and two haplotypes were shared with the Davis Strait subpopulation; NEPST 520 from Virgin Islands and NEPST 636 from Bahamas. The F_{st} calculated for the wandering population, showed no significant differences when compared to all other subpopulations (Table 3). In addition, the wandering seal's haplotype and nucleotide diversities are presented in table Table 4. Most of the Tajima's D calculated for each population, were negative which suggests that most are under positive selection or population size expansion. However none of these values were significantly different from a model of neutral evolution (Table 4).

The evolutionary relationships of the haplotypes resulting from the phylogenetic network show a pattern of relatedness that cannot be explained by the geographical origin of the samples (Fig-1). Moreover, the haplotypes of the wandering subpopulation don't show a closer relationship to any specific subpopulation.

The first noticeable event inferred from the tree is the grouping of three different monophyletic clades, referred to in the tree as Group 1, Group 2 and Group 3 (Fig 2). The haplotypes in each of the clades are not grouped according to their geographical origin. However, only Group 2 shows a posterior probability above 0.5 in the most basal node. Still, Group 1 has a posterior probability of 0.43. Moreover, there is a node that separates Group 1 from Group 2 and 3, with a posterior probability of 1 which occurred \approx 5.25 MYA. Going to the present in the time scale, there is a high lineage sorting beginning approximately 2.8 MYA and being the last lineage divergence 3000 years ago. However, these events take place mainly around 1 MYA and 100,000 years. The lineage through time plot estimates an accumulation of lineages in recent times (Fig 3-A). Additionally, the Bayesian Skyline Plot estimates a repeated pattern of expansions and contractions of the effective population size in recent times (Fig 3-B).

The ecological niche model showed low presence probability in stranding places located in the Caribbean Sea as well as the East coast of United States and Canary islands. However, the probability increases in reported stranding places in the West coast of Europe (Fig 4). The discriminant analysis didn't show significant

differences in climatic conditions between the normal range and the wandering sites (Wilk's Lambda = 0.740, $p = 0.051$).

Discussion

Our mitochondrial DNA analysis indicate high haplotypic diversity among the wandering individuals. Additionally, although there is insight to suggest that the wandering haplotypes may be migrating from the Davies Strait subpopulation, the results show non-significant differentiation among the mtDNA of these individuals and those from the four different subpopulations, indicating that this behavior is not associated to any specific location. Accordingly, the phylogenetic network confirms that the individuals that wander out from their normal range may come randomly from any of the four subpopulations. Similar to Coltman's (2007) results our findings also show a lack of genetic structure and considerable intermixing among the hooded seals subpopulations and we enlarge this deduction to the possible wandering subpopulation.

However, the phylogenetic analysis based on coalescence shows that the pattern of high genetic intermixing was probably not the case along the complete history of this species. The ancestor's lines in the tree suggest that in the early Pliocene there was a distinction between individuals that may have belong to two different populations (Fig-2). As is the case of other animal species, shifts in the temperature of the earth have a strong part determining the structure of the populations (Johnson & Cicero 2004). As the earth's temperature increased the habitat changed, especially for species inhabiting high latitudes as the Arctic region. Previous ice barriers sorting out individuals belonging to different populations disappeared due to ice melting, and for ice breeding species the amount of possible places to gather for reproduction decreased, therefore, increasing the encounter probability of individuals from different populations. As a result, gene flow would reduce genetic differentiation forming large panmictic populations. Still, as the water level increased and covered some portions of land, there were little, but new open niches for a few to conquer. As the phylogenetic tree shows, ≈ 5.2 MYA there was a separation between two groups maintained until the Pleistocene epoch. The divergence of these two groups may be a consequence of the environmental shifts due to the climatic changes that were described above. In this sense, the first population, represented by Group 1 (see Fig 2), might be a small population isolated by land masses probably in the southern margin of the species range and the second (represented by Groups 2 and 3; see Fig 2) a large population produced by the possibility of high gene flow among individuals lacking barriers in the high Arctic region.

Furthermore, the phylogenetic tree shows a considerable amount of lineages appearing during the Pleistocene. This finding is confirmed by the increasing accumulation of lineages in recent times showed in the Lineage Through Time plot. The appearance of these new lineages is probably due to the repeated glaciations of the Pleistocene epoch. During a glacial maximum, Arctic species are forced to move out of their normal range due to ice coverage, which forms large populations and increase the probability for interbreeding in southerly

glacial refugia. Conversely, during interglacial periods, the ice sheets retreat and the species are allowed to move north colonizing newly created marine habitats. Consequently, the once big southern populations divide into several smaller ones, likely specializing in newly open habitats and evolving different ecological and behavior adaptations which may result in a high accumulation of lineages. In addition, because species gain genetic diversity in a rate inversely proportional to the population size (Frankham 1996) the recent repeated contractions of the populations (Fig 3-B) could result in the currently observed high genetic variability in the Hooded seals mtDNA, suggesting that such variability was originated during the Pleistocene period. Therefore, it is likely that in the last glaciation event (≈ 9500 MYA) the hooded seal individuals from different populations have mixed in southern refugia, and they have recently recolonized the habitat range that is currently observed. So, genetically similar individuals might now be members of different populations because, individuals belonging to the same population before the last glacial maximum, could have randomly dispersed to different locations after the ice melted. This phenomenon might result in non-significant differentiation among present populations because they have had insufficient time for us to molecularly see the divergence among them.

The phenomenon of genetic intermixing between possible populations is not the case only for Hooded seals. Harp seals, which have a similar geographical distribution and life history in comparison to the Hooded seals, show no genetic differentiation between two northwest Atlantic populations or between two Northeast Atlantic populations (Perry *et al.* 2000). This pattern is at some extent also true for hooded seals, where, although there are no significant differences, individuals from the Eastern population are more distinct from individuals that belong to western populations than they are from each other (Coltman *et al.* 2007). Furthermore, pack-ice breeding Antarctic species (e.g. Ross seals, Crabeater seals and leopard seals) show no genetic differentiation (Davis 2004) while land-breeding pinnipeds (e.g. Harbor seals) do (Westlake & O'Corry-Crowe 2009). Based on these observations, the presence of genetic structure has been associated to the natal fidelity that can be displayed based on the type of breeding land. However, based on these predictions Davies *et al.* (2007) tested for genetic differentiation of Pack-ice breeding species compared to that breeding in stable portions of ice attached to land or prevented from moving known as Fast-ice. They found that some species of Pack and Fast ice breeding Pinnipeds showed presence of genetic structure but some did not. These results suggested that the development of genetic structure in Phocid seals may not only be consequence of the type of breeding substrate or amount of natal fidelity but also can be an effect of the ecological and historical phylogenetical features of each species. Specifically, as our results suggest, shifts in the earth temperature played an important role in determining the population dynamics of Hooded seals. The modern populational characteristics that they exhibit today is not only a consequence of their breeding habits and life history but is also strongly related to the landscape changes caused by climatic variation during the Pliocene and Pleistocene periods. This scenario might also be applicable to several other northern pinnipeds that breed in Fast or Pack Ice patches and show no population genetic differentiation.

As for the rare migrational behavior that some individuals of Hooded seals perform, the ecological niche model predicts low probability of presence in stranding sites in the Caribbean as well as along the East coast of United States. This means that the ecological habitat of these places is different, in relation to the variables measured here, from that present in the natural habitat range of the Hooded seals. The hooded seals individuals are migrating to a probably harmful environment for them, what has resulted in health impoverishment of these individuals (Lucas *et al.* 2003). Therefore, this type of behavior is forced by an increase in the living cost for some individuals due to resource competition in their natural habitats (Mcalpine *et al.* 1999). If this is the case, there are two main reasons that may explain the southwards movement. 1) Resource competition can lead to increased diet variation among members of a single population (Svanbäck & Bolnick 2007), for which the latitudinal gradient of species diversity will favor a southward migration or 2) fast oceanic currents that flow southwards of the hooded seal's natural range, could be an elected track for seals to wander in search for food (Gaspar *et al.* 2006).

However, despite of the low presence probability predicted by the model in the Caribbean, the discriminant analysis was not able to distinguish statistically between places in their migration sites and places in their natural ranges. These non-statistical differences may be influenced by places where the ecological niche model predicts higher probability of presence such as stranding places of the West coast of Europe as well as the Canary Islands. Individuals affected by resource competition in their natural range, may be finding a much healthier ecological habitat in these places than in the Caribbean region by a niche tracking process. It is therefore possible that these places gather more individuals as the environment continues to change which may turn into an expansion of the habitat range or even the appearance of new populations.

In summary, the genetic structure as well as the high diversity observed in Hooded seals may be an effect of the past climatic changes. Additionally, our results may be extrapolated to other species in terms of that the genetic structure of species that share behaviors and life histories could be understood by analyzing the phylogenetic history in an environmental framework. Therefore, the genetic structure present in Hooded seals using mitochondrial DNA may be misleading when not coupled with the interpretation of the geological and environmental changes across evolutionary time. Then, our results suggest that it would be reasonable to consider the breeding sites as separate subpopulations given the demographic history of the hooded seals proposed here. Additionally, as the earth's temperature continues increasing, the Hooded seals populations are likely to follow a similar pattern to that suggested by our data during the Pliocene. Moreover, as gene flow increases due to loss of ecological or geographical barriers, populations may become just few panmictic populations with high number of individuals, homogenizing their genetic variability. This process may be either positive or negative at the same time. In a positive sense, it will be expected an increase in the level of heterozygosity, which may raise the vigor of individuals for counteracting the effects of climatic change (Barton 2001). On the opposite, the genetic variability would be reduced causing many probable specific adaptations to be lost reducing the capacity of the

species to adapt to new environments (O'Corry-Growe 2008). Finally, the effect of competition is likely to be forcing individuals to migrate (McAlpine *et al.* 1999). Although the individuals that reduce competition by this means are not genetically different from the individuals that do not migrate, this behavior may produce either temporal or behavioral reproductive isolation, especially in individuals that migrate to places with suitable environmental conditions (e.g. West Coast of Europe and Canary Islands). If this tendency is coupled with strong assortment and sexual selection, genetic differentiation may arise in several generations (Orr & Smith 1998).

Figures:

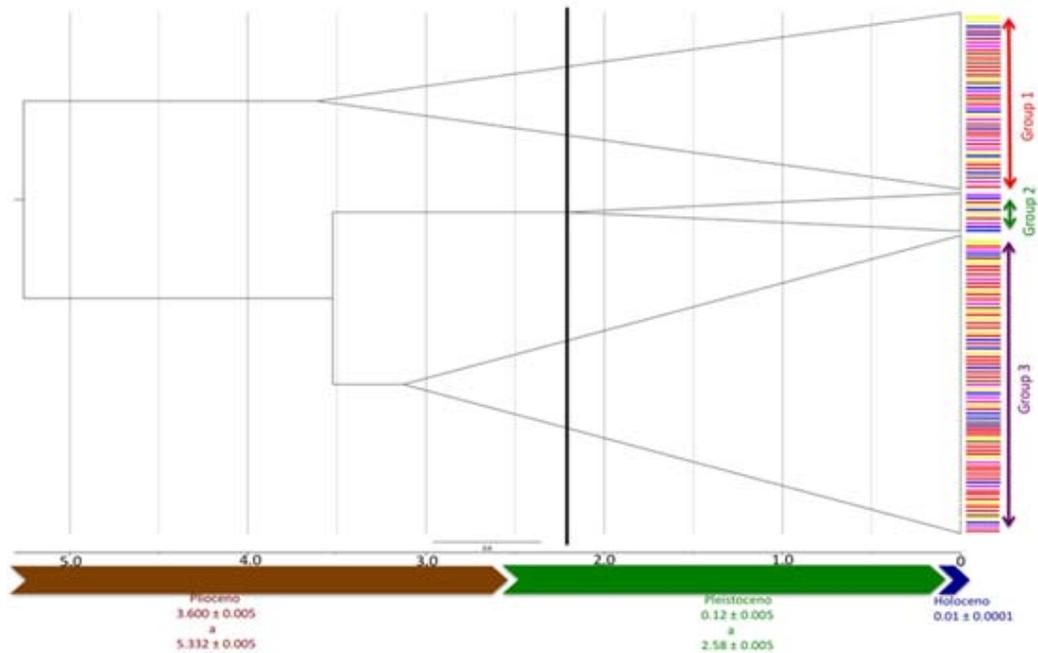


Fig-1 Phylogenetic tree based on coalescence coupled to a relaxed molecular clock, which shows three different clades grouping randomly haplotypes of hooded seals individuals from 4 different subpopulations plus the haplotypes of the migratory individuals. The location from each of the haplotypes is represented with a different color: red-West Ice, yellow- The Gulf, purple-The front, blue-Davis Strait and brown- Migratory individuals. The line shows the possible time when most of the lineages may have originated.

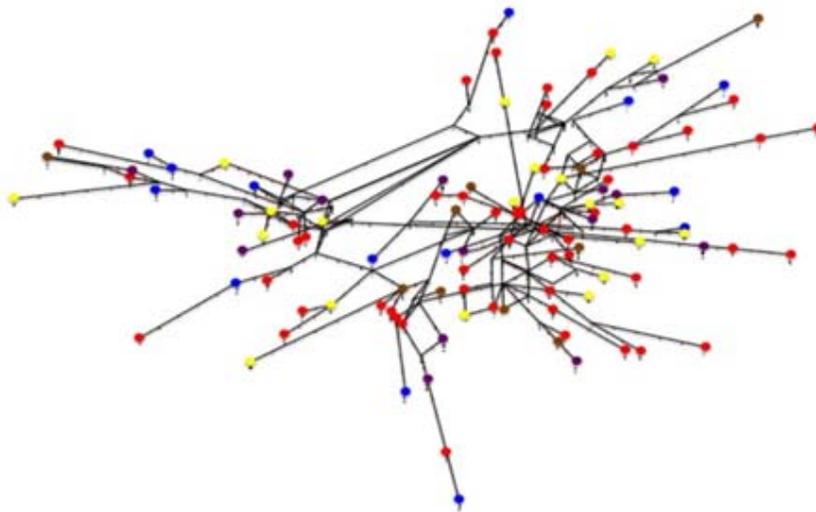


Fig-2 Phylogenetic network performed with the median-joining algorithm showing the connectivity between the haplotypes of the 4 different subpopulations plus the haplotypes of the migratory individuals. The location from each of the haplotypes is represented with a different color: red-West Ice, yellow- The Gulf, purple-The Front, blue-Davis Strait and brown- Migratory individuals

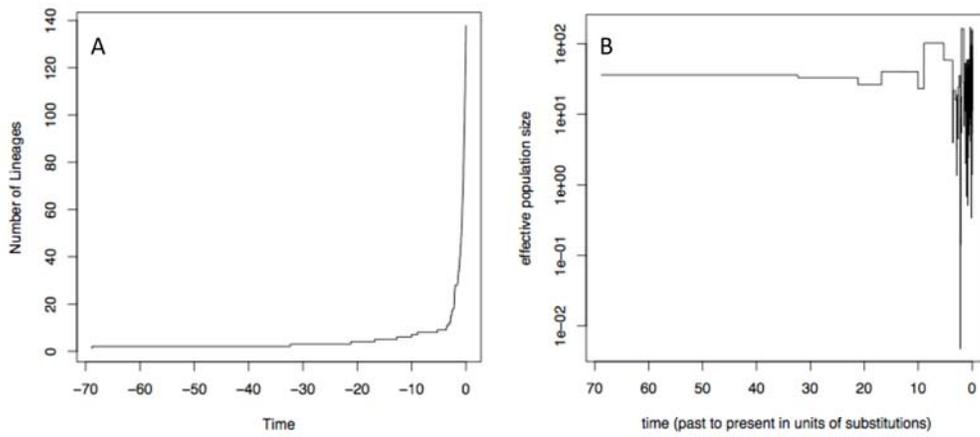


Fig-3 Estimates of past population dynamics from the phylogenetic tree. A) Lineages through time plot which graphs the minimum number of lineages through time from the phylogenetic tree. It shows an accumulation of lineages in recent times. B) Bayesian Skyline Plot estimates the effective population size through time. It shows a pattern of population expansions and contractions in recent times.

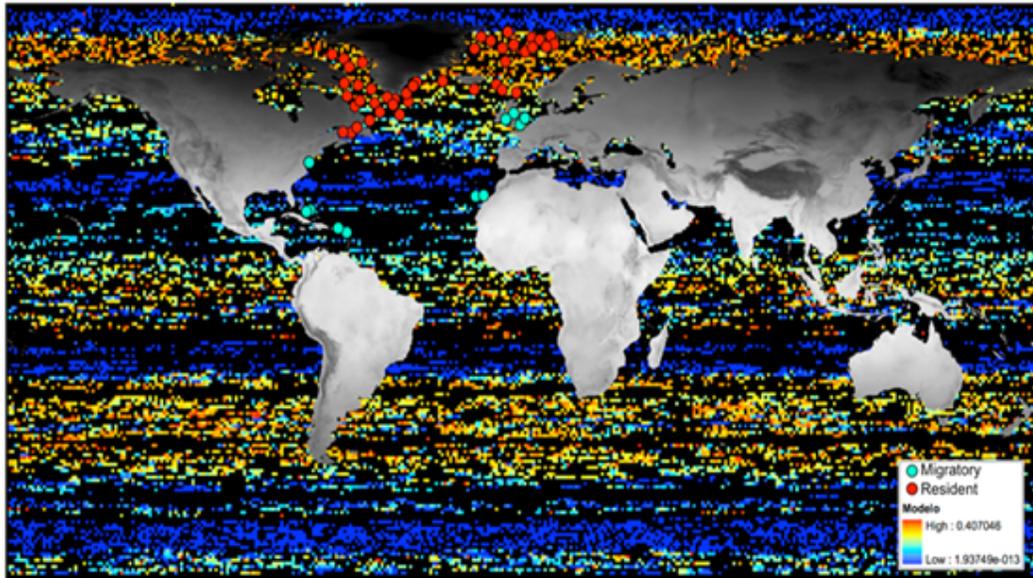


Fig 4 Ecological niche model performed with seven 1-degree grid cell layers containing information of different environmental variables. It predicted low probability of presence in stranding sites located in the East coast of United states, the Caribbean region and Canary islands. However stranding sites of the West coast of Europe have a much higher probability of presence prediction than the other ones mentioned.

Tables:

Table 1- Characteristics and location of samples of individuals of hooded seals that expanded their home range. ATG- Antigua Island, BHS-Bahamas, ESP-Spain, GBR-Great Britain, IRL-Ireland, USA-United States and VIR-Virgin Islands.

Tissue	Field No./Name	Country	Locality	Latitude	Longitude
Blood	NEPST628/Wadadli	ATG	Runaway Beach	17°06.0'N	61°50.0'W
Skin	NEPST629	BHS	San Salvador Island	24°03.5'N	74°33.0'W
Skin	NEPST636	BHS	Great Exuma Island	23°33.0'N	75°51.0'W
Blood	Guanche	ESP	Isla de Terierife	28°22.0'N	16°44.0'W
Blood	Majo	ESP	Isla de Fuerzeventura	28°40.0'N	13°54.0'W
Blood	Diamond	GBR	Cumbria	54°23.0'N	03°29.0'W
Skin	Fondue	GBR	Hampshire	50°48.0'N	01°12.0'W
Blood	Zirconia	GBR	Norfolk	52°51.0'N	00°27.0'E
Hair	Flubber	IRL	Wexford	52°31.0'N	06°14.0'W
Blood	MMS01-165	USA	New Jersey	38°55.8'N	74°54.6'W
Skin	NEPST520	VIR	St. John	18°22.0'N	64°45.0'W

Table 2- Taxa included in the phylogenetic analysis except for Hooded seals

Common Name	Scientific Name	Number of Samples	Accession Numbers
Ringed Seal	<i>Phoca hispida</i>	2	NC 008433 AM181036
Harbor Seal	<i>Phoca vitulina</i>	2	FJ 472428 FJ 472426
Harp Seal	<i>Pagophilus groenlandicus</i>	2	NC 008429 AM181030
Bearded Seal	<i>Erignathus barbatus</i>	2	NC 008426 AM 181027
Ribbon seal	<i>Phoca fasciata</i>	2	NC 008428 AM 181029
Hawaiian Monk Seal	<i>Monachus schauinslandi</i>	1	NC 008421
Walrus	<i>Odobenus rosmarus</i>	1	NC 004029

Table 3- Pairwise differentiation (F_{ST} below diagonal) and combined probability test for allele frequency differences (P value above diagonal) show no differentiation between subpopulations.

	Wandering	West Ice	The Front	The Gulf	Davis Strait
Wandering		0.926 ±0.0014	0.532 ±0.0028	0.814 ±0.0021	0.637 ±0.0028
West Ice	-0.021		0.13	0.54	0.36
The Front	-0.005	0.0001		0.45	0.59
The Gulf	-0.024	0.0009	-0.0003		0.54
Davis Strait	-0.012	0.0003	-0.0005	-0.0022	

Results not in bold taken from Coltman et al. (2007).

Table 4- Number of individuals, number of haplotypes, haplotype diversity (h), number of polymorphic sites, nucleotide diversity and Tajima's D for each subpopulation.

Subpopulation	Number of individuals	Number of Haplotypes	$h \pm SE$	Number of polymorphic sites	$\Pi \pm SE$	Tajima's D	Tajima's D P-value
Wandering	11	11	1.00 ±0.0388	33	0.031 ±0.017	-0.591	0.292
West Ice	60	53	1.00 ±0.003	77	0.019 ±0.010	-0.822	0.223
The Front	21	19	0.991 ±0.018	48	0.021 ±0.011	0.378	0.693
The Gulf	21	21	1.00 ±0.015	54	0.021 ±0.011	-0.539	0.327
Davis Strait	21	21	1.00 ±0.015	53	0.022 ±0.012	-0.128	0.494

Results not in bold taken from Coltman et al. (2007)

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