Phylogeography from South-Western Atlantic Ocean: Challenges for the Southern Hemisphere

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1. Introduction

Since 20 years ago from its emergence in the Evolutionary Genetics area the Phylogeography has experienced explosive growth enhanced by developments in DNA technology, coalescent theory and statistical analysis**.** Phylogeography is an integrative field of science that uses genetic information to analize the geographic distribution of genealogical lineages, focused within species and/ or between closely related taxa (Avise, 2000). Major impacts have produced at the Biodiversity conservation programs and managements strategies as well as investigating species boundaries and species complex or accessing the patterns and processes of cladogenetic events supporting biological diversity. In a recent review of phylogeography, Beheregaray (2008) identify disparities in research productivity between different regions of the world. He report enormous differences in surface area of habitats, a smaller proportion of studies were conducted on marine organisms than in freshwater organisms. In particular in South America, despite the higher diversity of marine fishes, freshwater fishes were more intensively studied. He proposes that building up of regional comparative phylogeographic syntheses in the Southern Hemisphere is needed to access on the patterns of population history in understudied biotas.

The Southwest Atlantic Ocean region (SWA) generally encompasses the regional waters around Brazil, Uruguay, and Argentina excluding the Falklands/Malvinas Islands (Fig.1). This area, which includes the Patagonian Shelf (Croxall & Wood, 2002) and the convergence of the warm Brazil current from the north and the cold Malvinas current from the south, is characterized by high and consistent levels of primary productivity and supports robust national and international fisheries activities (Campos et al., 1995). Moreover, this region presents unique oceanographic (convergence zone) and physiographic (large continental shelf area) features which also result in high biodiversity of seabird and marine mammal species, as well as sea turtles, all of which use the region for reproduction and/or foraging. In the mid-latitude shelf of eastern South America the discharge of the Plata and the Patos/Mirim lagoons are the major sources of continental runoff. The along-shelf extent of the low salinity plume associated with these systems undergoes large seasonal changes (Piola et al., 2000).The Río de la Plata and its Maritime Front constitute part of the Southwestern Atlantic continental shelf, an ecosystem largely influenced by both Malvinas and Brazilian currents, which conform a confluence in this area. These two water masses

have distinct characteristics and constitute a sharp transition zone referred as the subtropical shelf front (Piola et al., 2000).

Fig. 1.1. Map of bathymetry from SWA Ocean. Arrows indicate the main currents as follows: A-warm Brazil current from the north, B- the cold Malvinas current from the south, C- Subtropical convergence. D- The subtropical shelf front in the border of the Río de la Plata and its Maritime Front as part of the Southwestern Atlantic continental shelf. (Adapted from http://en.wikipedia.org/wiki/ General_Bathymetric_Chart_of_the_Oceans).

In present work, I present a synthesis of key findings over the scarce phylogeographic research on marine and estuarine organisms mainly fish models from the Southwest Atlantic Ocean region (SWA), to identify research gaps, to drive insight into patterns and processes of taxa diversification associated with the Quaternary Period which have interest not only at regional but also at global marine research. A major goal of present article is to contrast patterns of differentiation among different SWA Ocean endemic fishes and mammals models in which the present distribution in their genetic lineages were strongly

influenced by Quaternary events. In fact Pleistocene and Post-Pleistocene marine transgression produced habitat modifications and fragmentations in particular in coastal and shelf regions from South America (Sprechman, 1978). As a principal consequence of these events, several rivers and coastal lagoons system were separated from the Atlantic Ocean by sand bars, generating associated estuarine environments along South America coast (Montaña & Bossi, 1995). In South America, the marine biogeographic history recorded three main glaciations events during the Pleistocene (Rabassa et al., 2005). During the last glacial period (LGM), cold marine water moved northwards, changing the Malvinas-Brazil convergence (38º to 20º).

Several studies have shown that the historical demography of some estuarine fish was profoundly affected by the Pleistocene glaciations in temperate areas. In fact, during Pleistocene glaciations the sea level had a deep impact on the ecosystems promoting population differentiation or bottleneck events. In a more limited timescale (a few centuries) estuarine conditions also appear to be extremely fluctuating, conforming an interface between marine and riverine influences (Durand et al., 2005). The comparative analysis of phylogeographic patterns would highlighted the relevance of this adapted local marine/estuarine environments to generate and to sustain endemic SWA biodiversity.

2. Assessing the genetic structure in marine populations using molecular data analysis

Species are not genetically homogeneous along its distribution, but they are structured into groups of individuals that are typically more or less isolated from each other through or without geographic barriers. The resulting pattern for distribution of genetic variation within and between populations is referred as the *genetic population structure* of the species (Laikre et al., 2005).The basic unit within each of these populations is considered to be a group of individuals characterized by approximate random mating (panmixia) and site tenacity to a particular geographic area (Carvalho & Hauser, 1994). This basic unit represents the "local population", where local refers to the geographic location of the spawning site. As Laikre et al. (2005) explains the genetic population structure of a species within a particular geographic area may take a large number of different forms. In fisheries biology the "stock", rather than the local population, is frequently referred as the basic unit for harvest and management. Biologically sustainable management based on knowledge of this structure may reduce the risk for depletion of genetic resources (Laikre et al., 2005). Up to date, most empirical population genetic studies have been based on genetic markers assumed to primarily reflect selectively neutral DNA variation (most allozymes, microsatellites, SNPs and mtDNA markers). Recent molecular developments provide now increased opportunities for studying known markers to be located within functional genes of potential importance for fitness (Cano et al., 2008). Among the most used mitochondrial genes and regions in phylogeographic studies the cytochrome b (*cyt-b*) gene has a great utility to resolve phylogenetic relationships in several taxonomic levels (Kocher et al., 1989; Cantatore et al., 1994). This selected molecular marker (*cyt b*) gene and the coalescent in the population genetic theory, allowed a retrospective reconstruction of phylogenetic relationships among closely related populations in a past recent time. Moreover, Irwin (2002) argued that mitochondrial DNA are more likely than nuclear markers to show evidence of real barriers to gene flow for two main reasons.: 1) maternally inherited markers have effective population sizes that are generally one fourth from those of nuclear genes, 2)

mitochondrial DNA do not undergo recombination, and hence clear genealogical patterns can be reconstructed.

2.1 Current knowledge in the phylogeography of different endemics marine-estuarine fish ecotypes from SWA Ocean

Estuaries and lagoons are discrete habitats separated by physical and/or ecophysiological barriers that prevent or limit gene flow of estuarine species (Durand et al., 2005). In temperate regions, nearshore marine waters and estuaries act like important nursery areas for several marine teleost species, before they mature and migrate out to deeper waters. In fact, several spawning and nurseries areas for different fish species were detected in rivers, in the Atlantic coastal lagoons system and in the Río de la Plata nearshore environments (García et al., 2008). We have focused present phylogeographic patterns analyses among different selected fish models.

2.1.1 Pelagic fish

In general, pelagic fishes present complex life cycle. According to Sinclair & Iles (1989) in complex life histories, eggs, larvae and juveniles exhibit geographic or spatial distributions that are usually different from those characteristics of the adult phase. Many pelagic fish swim in schools which generally are size-specific, exhibiting a strong preference for similar sized individuals. The school stability can not only have consequences for the population structure and the evolution of the species, but also can have implications for the management purposes of the fishery (Hauser et al., 1998). Despite of the lack of genetic differentiation on a large geographic scale, many studies on pelagic fish detected small but statistically significant genetic differentiation among samples collected from very proximate localities within a short interval of time (Grant, 1985).

Brevoortia aurea. Among migratory pelagic marine fish, the Southwestern Atlantic menhaden *B. aurea* (Clupeidae, Alosinae) represents an important species model to investigate the patterns of genetic differentiation. It is abundant in the Río de la Plata, in the Maritime Front and in the coastal Atlantic lagoons system from southern Brazil, Uruguay and Argentina (García et al., 2008). This taxon is the target of commercial fishery and plays a critical role in the ecology because the individuals are fillter feeders that primarily ingest phytoplankton, providing a direct link between primary productivity and the availability of the forage fish for larger piscivorous predators. In present work, phylogeographic approach based on mitochondrial *cyt*-b gene (Fig. 2.1.1.1) recovered an unexpected high genetic variation in this pelagic marine fish. Bayesian Inference phylogenetic reconstruction using BEAST v.1.5.4 software package (Drummond & Rambaut, 2007) showed a major clade (Fig. 2.1.1.1) including several minor ones with high probability posterior of occurrence.

These minor clades were integrated by structured mixing samples from Rio de la Plata, Atlantic coast and the associated estuarine environments (Mar Chiquita, José Ignacio, Rocha and Castillos coastal lagoons). Present AMOVA analysis revealed a high level of intrapopulation diversity consistent with an extensive and low regional structured population in *B. aurea*. Following Grant & Bowen (1998) for *cyt-b* divergence a rate of 2% per million years can be used to date the nodes in the phylogeny. In present work, *B.aurea* clades from SWA Ocean differentiate since the Plio-Pleistocene, whereas the split from this taxon
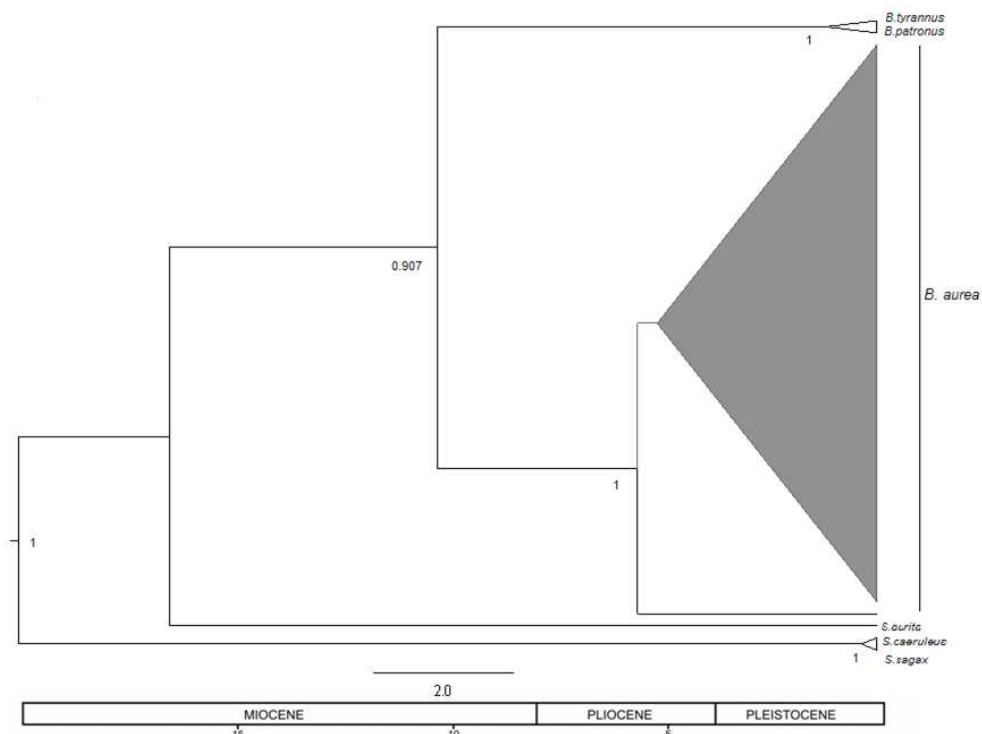
Fig. 2.1.1.1. Bayesian phylogeographic inference framework based on 48 *cyt-b* haplotypes of *Brevoortia aurea* implemented BEAST v.1.5.4 software package (Drummond & Rambaut, 2007). Values below branch nodes refer to highest posterior probability of occurrence for clades. Other Clupeiformes were included as outgoup taxa: *Sardinops sagax*, *S. caeruleus*, *Sardinella aurita*, *Brevoortia patronus* and *B. tyrannus.*The bar below summarize the time-scale divergence dates.

and the northern species of the genus could have occurred during the Miocene. The high values of haplotype and nucleotide diversity (Table 2.1.1.) detected in *B. aurea* were concordant with those reported by Anderson (2007) in four species of the Northern Atlantic menhaden. The present results were also congruent with previous population genetic analyses which suggested the existence of a long-term stability of the *B. aurea* schools, leading to a microgeographical genetic differentiation after the mixture of different stocks in the Río de la Plata and in the Atlantic Ocean from the associated estuarine environments (García et al., 2008). The data revealed that the recruitment of unrelated mtDNA haplotypes carried out by individuals within schools could be occurring in the same nursery areas, revealing the existence of many different maternal lineages. Remarkably, high degree of geographic differentiation was found in the related clupeid *Ethmalosa fimbriata*. In this case, the AMOVA analysis revealed three major geographic units (North, Center and South) for the West African coast populations (Durand et al., 2005). In contrast to the isolation by distance model of population differentiation found in *E. fimbriata* from Western African estuaries (Durand et al. 2005) *B. aurea* shows significant negative values in the Mantel test

corroborating a non-association between genetic and geographic distances and excluding the aforementioned possible scenarios (García et al., 2008).

Species	Variable Sites	Parsimony informative Sites	Number of Haplotypes	Haplotype Diversity (SD)	π (SD)	Kimura 2P Distance (Tv+Ts) (SD)	D
B.aurea	209	91	48	1.000 (0.004)	0.037 (0.008)	0.035 (0.008)	-1.883 (P<0.05)
E.anchoita	108	58	10	0.978 (0.003)	0.060 (0.030)	0.086 (0.014)	-1.121 (P>0.10)
L.grossidens	41	18	15	0.838 (0.070)	0.060 (0.013)	0.102 (0.020)	-0.508 (P>0.10)
P. platana	123	20	11	0.908 (0.051)	0.060 (0.037)	0.149 (0.025)	-2.345 (P<0.01)
Ramnogaster sp.	23	4	4	1.000 (0.177)	0.027 (0.006)	0.037 (0.011)	0.373 (P>0.10)

Table 2.1.1. Estimates of population DNA polymorphism in SWA Ocean Clupeiformes. Variables and phylogenetic informative sites among 720 bp in the total data set; Haplotype diversity (h = gene) (Nei, 1987); π = Nucleotide diversity (Nei, 1987); Corrected Kimura 2P distances (Kimura, 1980). D = Neutrality test (Tajima, 1989).

Engraulis anchoita. Fishes of the Engraulidae family, known as anchovies, are widely distributed in tropical and sub-tropical waters. *Engraulis anchoita* is the cold-temperate anchovy in the SWA Ocean. Most anchovies spawn in open coastal areas in the inner continental shelf. Recruitment occurs in protected, shallow areas that offer food and shelter against predators. Adults move during seasons between open coastal areas and bays, where they form large aggregations that are targeted by important fisheries (Araújo et al., 2008). Present phylogeographic analysis based on mitochondrial *cyt-b* sequences in *E. anchoita* from three different collecting regions in the Río de la Plata and the border of continental shelf revealed unexpected large values for haplotype and nucleotide diversity in this taxon. Bayesian Inference phylogenetic reconstruction showed three deepest differentiate clades with high probability posterior of occurrence (Fig. 2.1.1.2). One major clade (Fig. 2.1.1.2b) included most diverse haplotypes belonging to the inner continental shelf (at 35ºS-53ºW). A sister clade (Fig. 2.1.1.2c) was integrated by haplotypes from the Río de la Plata mouth and outer shelf and the last basal one (Fig. 2.1.1.2a) was represented by haplotypes from inner Shelf (at 36ºS-54ºW) and Río de la Plata mouth. These results were concordant with the presence of at less three different long-term genetic stocks of *E. anchoita* in the Río de la Plata and its Maritime Front. Therefore the mix of different stocks in the border of the Río de la Plata estuary and SWA Ocean continental shelf at these latitudes may explain the high level of genetic diversity detected in *E. anchoita* according to the present results (Table 2.1.1). Assuming a *cyt-b* rate of 2% of nucleotide divergence these clades could have differentiated since the Plio-Pleistocene. This scenario was consistent with previous data based on *cyt-b* in this taxon (García et al., 2011). Moreover, a haplotype with high probability of occurrence from Rio de la Plata mouth collapse basal in the aforementioned clades representing perhaps a possible ancestral estuarine stock from which populations colonize the Atlantic
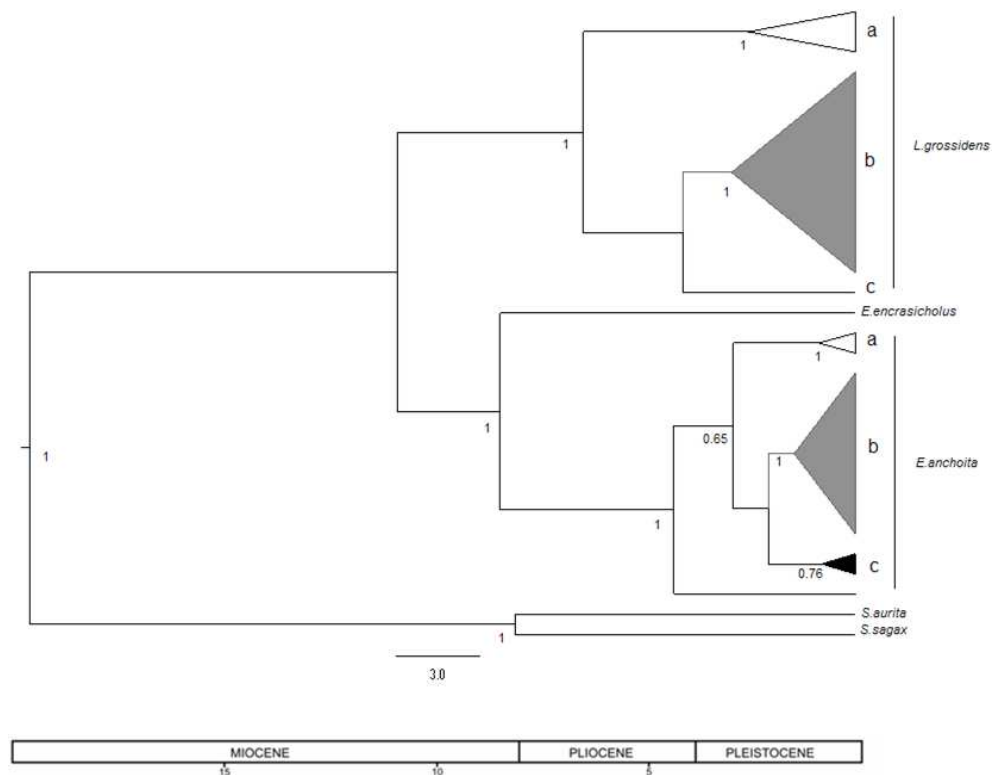
Fig. 2.1.1.2. Bayesian phylogeographic inference framework based on 10 *cyt-b* haplotypes (subclades a,b,c) of *Engraulis anchoita* and 15 *cyt-b* haplotypes (subclades a,b,c) belonging to *Lycengraulis grossidens*. The analysis was implemented in BEAST v.1.5.4 software package (Drummond & Rambaut, 2007). Values below branch nodes refer to highest posterior probability of occurrence for clades. Other Clupeiformes were included as outgoup taxa: *Engraulis encrasicolus*, *Sardinops sagax*, *S. caeruleus*.The bar below summarize the time-scale divergence dates.

Ocean shelf environments since the Plio-Pleistocene. In concordance with present data, Late Pleistocene glaciations associated with temperatures, salinity and global shifts in ocean circulation could have had great effect on the historical demography in the Japanese (*Engraulis japonicus*) and Australian (*Engraulis australi*) anchovies, in the northern anchovy *Engraulis mordax* and in the Pacific sardine *Sardinops sagax* (Liu et al., 2006; Lecomte et al., 2004).

Interestingly, present data showed the split of *E. anchoita* and the northern Atlantic-Mediterranean anchovy *Engraulis encrasicolus* since the Miocene, which is consistent with previous hypotheses of differentiation in the genus *Engraulis* (Grant et al., 2005). Although only two species were included in present analysis the genus *Engraulis* appeared as a monophyletic entity whereas *Lycengraulis grossidens* from associated estuarine environments of the SWA Ocean represented a sister clade of *Engraulis*. However, a non overlapping in their respective environments and niches was reported.

Lycengraulis grossidens. The Atlantic sabretooth anchovy occurs in brackish estuaries and adjacent marine areas, penetrating freshwater environments. They form moderate schools usually migrating from estuaries or the sea and spawns in freshwater (Cervigón et al., 1992). The level of population polymorphisms are shown in Table 2.1.1. Present Bayesian Inference based on mitochondrial *cyt-b* sequences in *L. grossidens* from different collecting sites in the Río de la Plata estuary and the associate coastal lagoons between 34ºS- 59ºW and 36ºS-54ºW (Fig. 2.1.1.2) revealed the existence of deep differentiate clades. A major clade (Fig. 2.1.1.2b) grouping most haplotypes form all Rio de la Plata and coastal lagoons sites and a single sister haplotype (Fig. 2.1.1.2c) whereas the other minor clade collapse basal (Fig. 2.1.1.2a) to them. The last taxon and minor clade were integrated by samples from a single estuarine site in the border of the Río de la Plata and Atlantic Ocean. Under a *cyt-b* rate of 2% of divergence these clades could have differentiate since the Plio-Pleistocene. Interestingly, the most basal clade could represent perhaps the ancestral estuarine stock from which populations colonize the associate coastal Atlantic lagoons and freshwater environments since the Plio-Pleistocene encompassing major geological and climatic changes in this region.

Platanichthys platana. The Rio Plata sprat is a very small species of fish belonging to the family Clupeidae from SWA Ocean and constitute an endemic monotypic genus. The species inhabit fresh- brackish waters of coastal lagoons, estuaries and the lower reaches of rivers associate to marine areas (Whitehead, 1985). The level of population polymorphisms are shown in Table 2.1.1. Present Bayesian Inference based on mitochondrial *cyt-b* sequences in *P. platana* from different collecting sites in the Río de la Plata estuary and the associate coastal lagoons between 34ºS- 59ºW and 36ºS-54ºW (Fig. 2.1.1.3) revealed the existence of two deepest differentiate clades. Assuming a *cyt-b* rate of 2% of divergence, the differentiation of these phylogroups could have occurred since the Plio-Pleistocene. A major clade included all haplotypes from different coastal lagoons (Fig. 2.1.1.3b) and the minor one grouped samples from a single site, Rocha coastal lagoon (Fig. 2.1.1.3a). *Platanychtys platana* clade collapsed in an unresolved basal polytomy with other clupeid genera. These basal split events were dated since the Miocene.

Ramnogaster sp. These small clupeid fish inhabiting littoral areas, estuaries and rivers from Uruguay to Patagonia, constitute endemics taxa from SWA Ocean. They are coastal, pelagic, schooling inshore but not entering freshwaters (Whitehead, 1985). The level of population polymorphisms are shown in Table 2.1.1. Present Bayesian Inference based on mitochondrial *cyt-b* sequences including samples of this genus from different collecting sites in the Río de la Plata estuary and the associate coastal lagoons between 34ºS- 59ºW and 36ºS-54ºW (Fig. 2.1.1.3) revealed the existence of two clades with highest posterior probability of occurrence. Both clades (Fig. 2.1.1.3a,b) of *Ramnogaster* sp. could have differentiated since the late Plesitocene. Remarkably, present molecular data does not support the existence of the two described *Ramnogaster* species: *R. arcuata* and *R. melanostoma*. This taxonomic incongruence with previous morphological analysis (Cione et al., 1998) will be clarified in further studies including additional number of samples from both taxa.

Odontesthes perugiae complex. Beheregaray et al. (2002) have investigated patterns of evolutionary divergence and the vicariant history of a group of silverside genus *Odontesthes* distributed in a coastal region of southern Brazil formed during the Pleistocene and Holocene using microsatellite markers and mitochondrial (*D-loop*) DNA sequences. *Odontesthes* is a diverse and widespread genus, with a minimum of 13 species groups
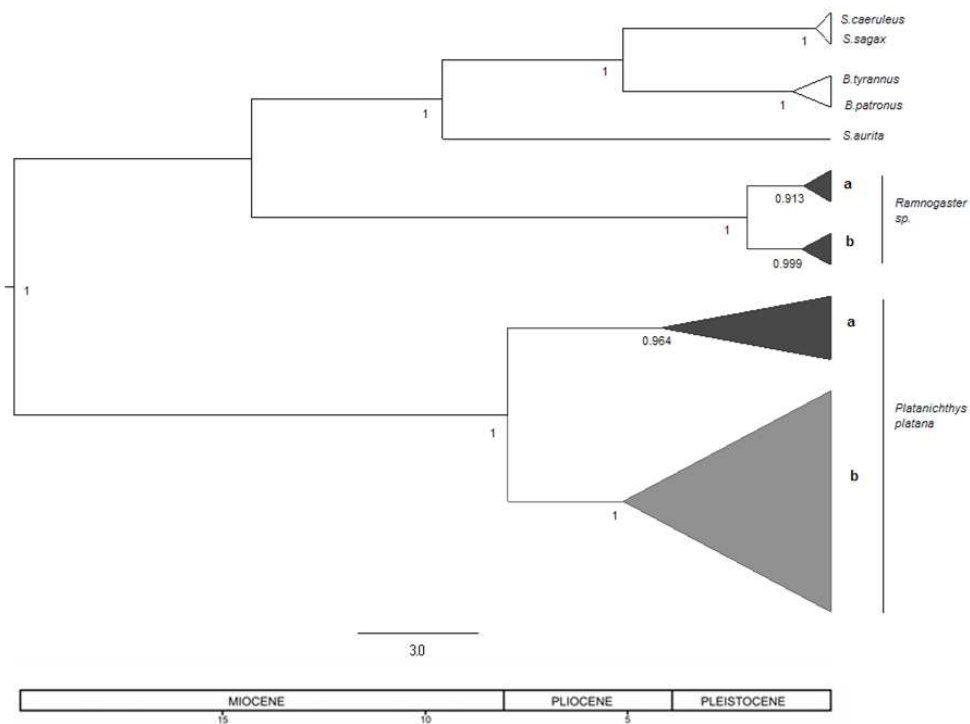
Fig. 2.1.1.3. Bayesian phylogeographic inference framework based on 11 *cyt-b* haplotypes (subclades a,b) of *Platanichthys platana* and 4 *cyt-b* haplotypes (subclades a,b) belonging to *Ramnogaster* sp. The analysis was implemented in BEAST v.1.5.4 software package (Drummond & Rambaut, 2007). Values below branch nodes refer to highest posterior probability of occurrence for clades. Other Clupeiformes were included as outgoup taxa: *Sardinops sagax*, *S. caeruleus*, *Sardinella aurita*, *Brevoortia patronus* and *B. tyrannus.*The bar below summarize the time-scale divergence dates.

distributed in marine, estuarine and freshwater environments of temperate South America (Dyer 1998). The results support the proposal of a silverside radiation chronologically shaped by the sea-level changes of the Pleistocene and Holocene. The radiating lineage comprises a minimum of three allopatric and two sympatric lacustrine species. Four species displayed extremely high levels of genetic variation and some of the most rapid speciation rates reported in fishes. These features were related to a marine- estuarine origin of the radiation. The other interesting feature of *perugiae* is their exceptionally fast rates of speciation. The maximum divergence time based on geology for two of the northern *perugiae* is no more than 5000 years. Based on the model of speciation of silverside fishes of Bamber & Henderson (1988) the aforementioned authors proposed that the rapid divergence of *perugiae* could also be related to its marine- estuarine origin. This model, supported by the reproductive biology and presumed evolutionary patterns of silversides, predicts that physically variable environments, such as estuaries and coastal brackish lagoons, pre-adapt silverside populations to invade, colonize and rapidly speciate into vacant niches in freshwater (Bamber & Henderson, 1988).

2.1.2 Demersal fish

Micropogonias furnieri. The whitemouth croaker *M. furnieri* (Perciformes: Sciaenidae) is a demersal sciaenid with a wide distribution in the central and south-western Atlantic Ocean. Populations of this fish are distributed from the southern Caribbean to the Gulf of San Matías in Argentina. The species occurs along the coast, in the mouth of rivers and lagoons, and also in coastal waters to 50 m (Pereira et al., 2009), being an important commercial fishing resource and at present considered as 'fully exploited'. Recently Pereira et al. (2009), in population genetic analysis based on mitochondrial *D-loop* region detected the presence of two stocks of the *M. furnieri* among three different areas (Bahía Blanca, Río de la Plata and Atlantic Ocean). Remarkably, Río de la Plata locality have the lower values of haplotype and nucleotide diversity as well as demographic signatures of population declination whereas Atlantic Ocean collecting sites showed the highest values of genetic diversity and signatures of a past recent population expansion. More recently, D´Anatro et al. (in press) using seven microsatellite loci, characterized genetic variation of *M. furnieri* in the Río de La Plata estuary and its Maritime Front and in two coastal lagoons. They found three major groups formed by Río de la Plata, Atlantic Ocean and Rocha coastal lagoon populations.

Macrodon ancylodon. The king weakfish *Macrodon ancylodon* (Perciformes: Sciaenidae) is a demersal (bottom-feeding) marine species found in South American Atlantic coastal waters from the Gulf of Paria in Venezuela to Bahia Blanca in Argentina and is economically important because of its abundance and wide consumer species found in South America Atlantic coastal waters from the Gulf of Paria in Venezuela to Bahia Blanca in Argentina (Haimovici *et al.*, 1996). Santos et al. (2006) investigated the phylogeographic patterns in *Macrodon ancylodon* sampled from 12 locations across all its distribution using mitochondrial DNA *cyt-b* sequences together with patterns of morphometric differentiation. Populations of the North Brazil and the Brazil currents, with warmer waters, form a clade (tropical clade) separated by 23 fixed mutations from the populations that inhabit regions of colder waters influenced by the Brazil and Malvinas currents (subtropical clade). No gene flow exists between the tropical and subtropical clades, and most likely also between the two groups of the tropical clade. Distribution of these clades and groups is correlated with flow of currents and their temperatures, and is facilitated by larval retention and low adult migration. Despite the differentiation at the molecular level, fishes analysed from all these current-influenced regions are morphometrically homogeneous. Throughout its range *M. ancylodon* inhabits the same or very similar niche; thus, stabilizing selection probably promotes the retention of highly conserved morphology despite deep genetic divergence at the mitochondrial DNA *cyt-b.*

Cynoscion guatucupa. The striped weakfish (Perciformes: Sciaenidae) widespread pelagic-demersal fish predominantly found on the coast of South America, ranging from Rio de Janeiro, Brazil (22°S), to Chubut province, Argentina (43°S) (Cousseau & Perrotta, 2004). *Cynoscion guatucupa* is considered the second species in commercial importance after the whitemouth croaker *M. furnieri* (Ruarte & Aubone, 2004).

Fernández Iriarte et al. (2011) conducted an analysis based on 365 bp sequence of the mitochondrial control region in four coastal sites located in the SWA Ocean to assess in the pattern of molecular diversity and historical demography of this taxon. Haplotype diversity was high, whereas nucleotide diversity was low and similar at each sample site. AMOVA failed to detect population structure. This lack of differentiation was subsequently observed in the distribution of samples sites in the haplotype network. Fu's Fs was negative and

highly significant while the mismatch analysis yielded a unimodal distribution, indicating a global population expansion. This study clearly provides evidence of an older demographic expansion and no evidence of population phylogeographic structure of *C. guatucupa* from the southwestern Atlantic coast.

2.1.3 Endemics benthic and pelagic coastal sharks

Squatina guggenheim. Angel sharks (Squatiniformes) are benthic elasmobranchs that inhabit shelf and upper slope environments in temperate and tropical regions of the world (Compagno, 1984). Among four angel sharks species in the South Atlantic Ocean the angular angel shark *S. guggenheim* which represent one of the principal coastal fishing resources has a wide geographic distribution from Espíritu Santo (Brazil) to central Patagonia, Argentina (Vooren & da Silva, 1991), in waters 10–80 m deep (Cousseau & Figueroa, 2001). Like other benthic elasmobranchs, they tend to have low dispersal capability, which usually result in specimens from nearby areas which have almost no mixing. As this restricted mixing may produce different life history parameters, it is important to study possible life history differences within angel shark species, even at small geographic scales (Colonello et al., 2007). Present phylogeographic approach based on *cyt-b* sequences in *S. guggenheim* from three different collecting sites from the Río de la Plata mouth and its Maritime Front as a part of the Southwestern Atlantic continental shelf and the Atlantic coast (Fig. 1D) revealed very low values of haplotype diversity (h=0.382, SD=0.078) and nucleotide diversity (π= 0.011, SD=0.003). Tajima test (1989) was significative (D=-2.591, p<0.001) indicating a departure from neutrality in the data set. Despite of the low genetic diversity detected, Bayesian Inference reconstruction grouped the fifteen haplotypes (Fig.2.1.3.1) in two major deepest differentiate clades. One minor clade integrated by haplotypes from Río de la Plata mouth outer shelf (Fig.2.1.3.1a), a second major one formed by samples from Atlantic Ocean coast, Río de la Plata mouth and outer shelf (Fig.2.1.3.1c-d). Remarkably the most frequent and basal haplotype 1 (Fig.2.1.3.1b) was shared by samples from the three aforementioned regions. The split between these deepest clades could have occurred since the Miocene, but subclade differentiation events were dated since Plio-Pleistocene.

Different grouping hypotheses performed in the AMOVA analysis failed to detect significant values in the geographic partition of the molecular variance (García et al., 2009). Therefore all present data about genetic stock structure support the hypothesis that S. guggenheim constitute a single panmictic unit in the Río de la Plata and its Maritime Front. Low genetic diversity and neutrality departure in angel shark populations would indicate long term population declination since the Pleistocene.

Mustelus schmitti. The narrownose smooth-hound shark, *Mustelus schmitti* is a coastal species endemic to the Southwestern Atlantic Ocean. This species is distributed from Río de Janeiro (Brazil) to Patagonia in Argentina (Chiaramonte & Pettovello, 2000). Pereyra et al. (2010) have used mitochondrial *cyt-b* gene sequences to examine the genetic structure of the narrownose smooth-hound populations within the Río de la Plata and its Maritime Front in the SW Atlantic Ocean. They found no evidence for genetic structure in the analyzed samples. Low levels of pairwise FST values indicated high connectivity and suggested genetic homogeneity at this geographic range. Additionally, notably low nucleotide and haplotype diversities found in this species could indicate that *M. schmitti* experienced a population bottleneck, recent expansion or selection associated with Pleistocene events. The
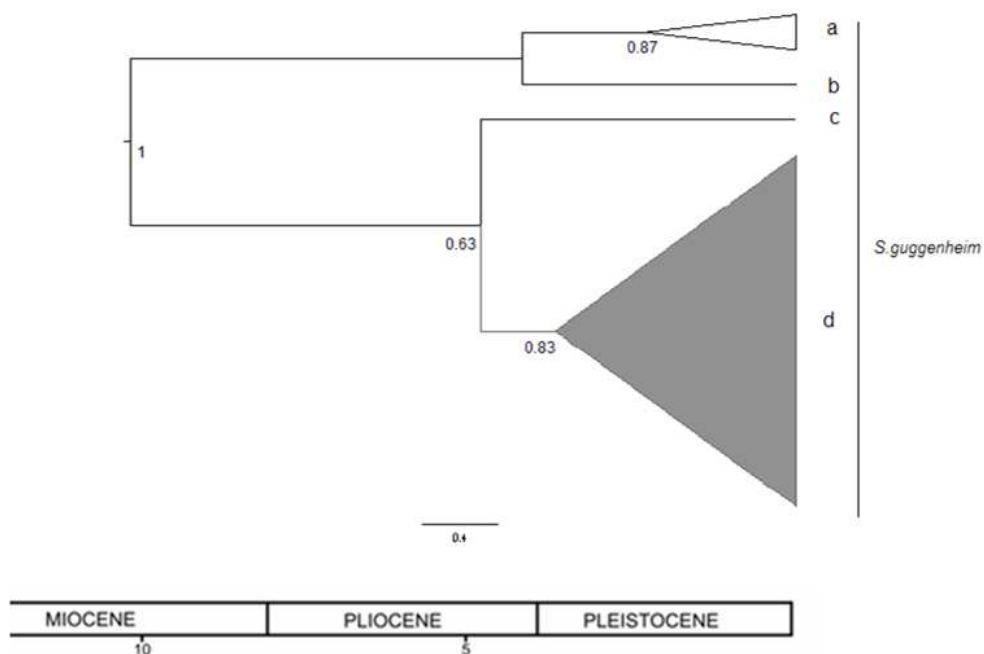
Fig. 2.1.3.1. Bayesian phylogeographic inference framework based on 15 *cyt-b* haplotypes of *Squatina guggenheim* implemented BEAST v.1.5.4 software package (Drummond & Rambaut, 2007). Values below branch nodes refer to highest posterior probability of occurrence for clades. The bar below summarize the time-scale divergence dates assuming a synonymous, per-site divergence rate of 0.0414/million years according to Pereyra et al. (2010).

results presented here indicate that *M. schmitti* exists as a single demographic unit in the Río de la Plata and its Maritime Front.

2.2 Population genetic structure in marine mammal species models from SWA Ocean

Otaria flavescens. The Southern sea lion distribute in breeding colonies along the entire Atlantic coast. The north-central Patagonian coast is the sea lions most abundant area in Argentina. Túnez et al. (2010) studied the genetic structure and historical population dynamics of the species in five colonies in this area, using the mitochondrial *D-loop* control region. The distribution of breeding colonies at this smaller geographical scale is also patchy, showing at least three areas with breeding activity. The genealogical relationship between haplotypes revealed a shallow pattern of phylogeographic structure. The analysis of molecular variance showed significant differences between colonies, however, pairwise comparisons only indicate significant differences between a pair of colonies belonging to different breeding areas. The pattern of haplotype differentiation and the mismatch distribution analysis suggest a possible bottleneck that would have occurred 64,000 years ago, followed by a demographic expansion of the three southernmost colonies. Thus, the historical population dynamics of *O. flavescens* in north-central Patagonia appears to be closely related with the dynamics of the Late Pleistocene glaciations.

Pontoporia blainville. The "franciscana" is endemic of South Atlantic coast of South America. The species is under conservation concern because it suffers elevated mortality rates due to incidental captures in fishing nets, and perhaps it is one of the most threatened small cetaceans in this region. Previous morphological and genetic studies have suggested the existence of at least two distinct stocks to the north and south of Santa Catarina Island in Brazil. Secchi et al. (2003) based on mtDNA, morphometrics and population parameters showed that all together provide evidence for splitting the species into four management stocks: two inhabiting coastal waters in Brazil; the third occurring in Rio Grande do Sul State (southern Brazil) and Uruguay, and the fourth inhabiting Argentine coastal waters. However, Lázaro et al. (2004) found fixed differences between a sample from Rio de Janeiro and one from Rio Grande do Sul, in southern Brazil. Using control region of mitochondrial DNA, the authors examined the genetic structure of the species and found no shared haplotypes between Rio de Janeiro and samples from the southern range of the species distribution. However, a phylogenetic analysis suggests that the former population is diphyletic with respect to the southern samples. This suggests that the populations have not been isolated long enough to reach reciprocal monophyly. Furthermore, genetic differentiation is broadly consistent with a simple model of isolation by distance, therefore that appears as an alternative to a model of strict isolation of two stocks. The estimated levels of gene flow are higher among neighboring populations, and decrease when more distant localities are compared. Finally, the molecular data suggest that the "franciscanas" have expanded in Rio de Janeiro.

3. Contrasting phylogeographic patterns in marine-estuarine taxa from SWA Ocean

Like several authors have suggested present analyses reinforce the role of Pleistocene glaciations events to shape the phylogeographic mitochondrial DNA patterns and population structure in marine fish species (Beheregaray et al., 2002; García et al., 2008, 2011). During Pleistocene glaciations the sea level had a deep impact on the ecosystems promoting population differentiation or bottleneck events. In this sense, Fernández-Iriarte et al. (2011) mentioned that the pattern is not necessarily reflected in all coastal fish species, as they could differ in their adaptive response to climate changes (mainly temperature, salinity, marine currents and loss/gain of coastal habitats). Therefore we could expect a different pattern for organism inhabiting pelagic and benthic coastal habitats.

Nevertheless, independently of their adscription to different ecotypes, several major facts not mutually exclusives emerged from present comparative phylogeographic patterns in SWA Ocean among cases analyzed here: 1) population signatures of expansion/declining encompassing environmental changes during the Quaternary, 2) successive colonization-recolonization of marine from estuarine environments in the Quaternary, 3) unexpected and complex population structuring patterns in pelagic fish ecotype, 4) radiation of genetic lineages shaped by the sea-level changes of the Pleistocene and Holocene, 5) Phylogeographic breaks without any specific geographic barriers to gene flow, meanly influenced by Quaternary events and/or of currents and their temperatures , 6) The origin of marine-estuarine endemisms at local and regional level in the SWA Ocean.

1. Genetic footprints of demographic expansion were evident among several studied taxa. In *B. aurea* coastal lagoons have acted like a source of new genetic variants from which

expansion have occurred; *M. furnieri* population stock from Atlantic Ocean showed the highest values of genetic diversity and signatures of a past recent population expansion whereas *C. guatupuca* demographic parameters indicated a global past population expansion. Similar patterns were detected in franciscanas expanding in Rio de Janeiro and in *O. flavescens* showing signature of possible bottleneck, followed by a demographic expansion. It is more difficult to explain the low level of genetic variation and population structure in the benthic angular angel shark *S. guggenheim* and in the narrownose smooth-hound shark, *Mustelus schmitti*. The lowest genetic diversity values detected in these taxa will be indicating the existence of long-term population declination or a past recent population bottleneck associate with major environments and biota changes since the Plio-Pleistocene.

2. Successive colonization-recolonization of marine from estuarine environments promoting dramatic changes in the level of intrapopulation genetic diversity. Several of such environments in the Rio de la Plata and the associate rivers and costal lagoons would acted as glacial refugia from which the recolonization could have occurred. This fact was evident in most Clupeiformes analyzed here. In the other hand, following Avise (1994) the demographic signatures of population declination in *M. furnieri* from the Rio de la Plata stock could be explained if repeated widespread disturbances and founder-flush cycles caused by multiple glacial expansion and retreats, could increase the possibility that the majority of intraspecific mitochondrial diversity originally present would be randomly lost.

3. The unexpected and complex population structuring patterns were evident in pelagic fish ecotypes. In broadly distributed marine fish species that exhibit high vagility, higher dispersal potential during planktonic egg, larval or adult life-history stages low levels of population differentiation are expected. However, in *B. aurea* the analyses suggested the existence of a long-term stability of schools, leading to a microgeographical genetic differentiation after the mixture of different stocks in the Río de la Plata and in the Atlantic Ocean from the associate estuarine environments.

4. Radiation of genetic lineages shaped by sea-level changes of the Pleistocene and Holocene was reported in the pelagic coastal silverside *Odontesthes* (Beheregaray et al., 2002). In this case, estuarine associate environment from coastal lagoon system allowed the divergence of allopatric and lacustrine sympatric populations into different genetic lineages, enhancing cladogenetic events in this genus.

5. Phylogeographic breaks without any specific geographic barriers to gene flow influenced by Quaternary events and/or of currents and their temperatures emerge in different patterns of population genetic structuring analyzed here. Among SWA Ocean taxa, *Platanichthys platana*, *Ramnogaster* sp., *Lycengraulis grossiden*s, *Engraulis anchoita* as well as in *Squatina guggenheim* deepest population breaks in the phylogeny were evident. As several author have previously mentioned (Lessa et al., 2010) we have detected in these taxa phylogeographic breaks consisting of more than one well-differentiated phylogeographic unit within a region, that differed by more than 3% of sequence divergence from each others. Moreover, *Platanichthys platana*, *Ramnogaster* sp., *Lycengraulis grossiden*s inhabiting the same estuarine environments in coastal lagoons and associate rivers represent a concentration of phylogeographic breaks suggesting a shared history that have occurred at least in part within this region and in the same

scenarios of environment changes during the Quaternary. A remarkably case, is the phylogeographic break in *Macrodon ancylodon* in which the distribution of clades and groups is correlated with flow of currents and their temperatures, and is facilitated by larval retention and low adult migration. Despite of differentiation at the molecular level, fishes analyzed from all these current-influenced regions are morphometrically homogeneous. Nevertheless, only when multiple independent genetic markers show genealogical breaks in the same geographic location it will be possible to conclude that there is a specific geographic cause for the breaks (Avise 2000).

6. The origin of marine-estuarine regional endemisms. In the genera *Brevoortia* and *Engraulis* deepest split in the phylogeny between taxa from the Northern and the Southern Atlantic Ocean were evident since the Miocene. On the other hand, other monotypic and endemic genus *Platanichthys* split from a basal polytomy as phylogenetically separated taxon from the remaining SWA Ocean clupeids since earlier Miocene.

4. General conclusions and future directions

Present comparative analyses reinforce the role of two main factors in the phylogeographic patterns of marine-estuarine fishes and mammals from SWA Ocean: the existence of coastal estuarine associate environments (rivers and lagoon systems) and the ocean currents related with subtropical Convergence, both highly linked to Quaternary dynamics. The shared differentiation patterns detected in present comparative phylogeographic approach would be tested in further analyses including different molecular markers and other taxa from this region. In this sense, more effort is needed to generate not only multi-species, but also multi-locus genetic data-sets to compare and contrast the emerging phylogeographic patterns. Because of the high mutation rate microsatellites will allow researchers to study genetic patterns driven by e.g. fishing pressure and climate change, as well as to obtain more reliable information on gene flow. Migration rates estimated using coalescent-based methods as implemented in different software package often interpreted as reflecting contemporary gene flow may in fact be strongly influenced by historical events, this last emerging from mtDNA phylogeographic patterns. Recent advances in whole and partial sequencing technology (e.g. through 454 pyrosequencing) will allow the development of microsatellite and single nucleotide polymorphism markers more accessible to the world researchers. New and more strong genotype data can be used to identify candidate genes for local ecophysiological adaptations in wild populations reflecting different selection pressure associate to environmental gradients of salinity and temperature. A relatively poor understanding hydrodynamic complex nearshore and offshore patterns in the Rio de la Plata region and in other maritime fronts in the SW Atlantic Ocean represent major challenges to interpret genetic data from taxa that live in shallow waters and disperse within the nearshore environments. The incorporation of both experimental and modeling approaches becomes important for future investigations to interpret the evolutionary response of marine-estuarine species to climatic change.

For most studied species, present analyses support that the metapopulation represents the Management Unit, as well as the inclusion of the associated rivers and coastal lagoons, responsible for the origin of the major genetic diversity, in high priority conservation

programs in further Marine Protected Area Systems, which must be integrated at regional level in SWA Ocean. In the other hand, the existence of a long-term population declination or a past recent population bottleneck, alert about the degree of vulnerability to overexploitation in endemics SWA Ocean sharks, as well as, in other important species of Sciaenidae in commercial fisheries. The emerging results in population genetic structure in taxa from the SWA Ocean, Río de la Plata and its Maritime Front will allow to optimize and to develop technical guidelines for the best fishery management stocks as different fishing units in commercial and artisanal fisheries in the region. This knowledge may be increase in next years for most of the fish resources along SWA Ocean area. The molecular genetic markers constitute robust tools, allowing the management of species and stocks and to supervise the long term fishery sustainability.

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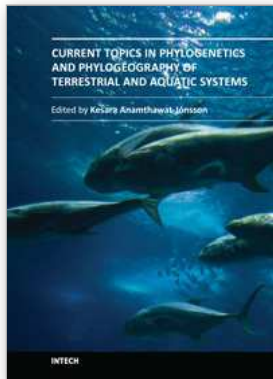
Current Topics in Phylogenetics and Phylogeography of Terrestrial and Aquatic Systems

Edited by Prof. Kesara Anamthawat-Jónsson

Mapping phylogenetics on geographical scales is one of the most important scientific aspects of bioscience research. Changes in the environment have evidently shaped the geographical distribution of organisms on land and in the oceans seen today. Overexploitation of key species has caused not only changes in the distribution and diversity of organisms and composition of the ecosystems, but is also leading to species extinction at accelerating rates. It is our duty as scientists to find ways of protecting the species endangered with extinction and preventing other species from entering the endangered stage. To manage this effectively, we need to map species distribution, understand life-history traits, define genetic variation within species and populations, identify lineages - especially at the molecular level - and correlate the historical, phylogenetic components with the spatial distributions of gene lineages. In this book, phylogenetics and phylogeography of a diverse range of organisms are reviewed: from microorganisms causing gastroenteritis in humans, fishes in the Southwest Atlantic Ocean and spiders of the western Indian Ocean, to mountain tapirs in South America and birch tree species of the Arctic tundra.

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