El lobo marino común, *Otaria flavescens*, en Chile:
distribución espacial, historia demográfica y estructuración genética

Tesis entregada a la Pontificia Universidad Católica de Chile en cumplimiento parcial de los requisitos para optar al Grado de Doctor en Ciencias con mención en Ecología

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a mi madre,

el amor por la naturaleza

se lo debo a ella

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4.- RESUMEN

O*taria flavescens* se encuentra ampliamente distribuida en America del Sur, donde ha sido objeto de explotación indiscriminada, llevando a la especie a drásticas fluctuaciones poblacionales durante el siglo pasado. Actualmente, la especie se encuentra protegida por ley. Sin embargo, debido a sus hábitos alimenticios, la especie interfiere con las actividades de pesca extractiva, existiendo una presión constante por parte de los pescadores por la apertura de la veda. A esta presión antropogénica se suma los efectos de fluctuaciones ambientales decadales, principalmente del ENSO. Debido a esto, se requiere establecer estrategias de manejo de largo plazo para la especie. El comportamiento reproductivo de *O. flavescens*, al igual que en otros otáridos, se encuentra determinado por la existencia de reproducción anual con agregación reproductiva, y un posible trade-off entre los costos y beneficios de la filopatría y la dispersión. Este patrón determina la estructuración espacial de la especie, dominada por el comportamiento metapoblacional. Así, para el manejo de *O. flavescens*, se debe considerar su estructura espacial así como su dinámica metapoblacional. Adicionalmente, el entendimiento de los efectos antropogénicos y ambientales en el pasado, permite predecir cambios demográficos futuros.

En esta tesis se pretendió responder a diversas preguntas sobre la estructura y dinámica metapoblacional de *O. flavescenes*, así como sobre su demografía histórica. Se evaluó la filogeografía de *O. flavescens*, así como la demografía histórica en Chile, mediante el análisis de secuencias de la región control del ADN mitocondrial. Igualmente, se determinaron patrones comunes de demografía histórica en otáridos. El segundo capítulo abarcó la estructuración genética de la especie en Chile, así como los efectos demográficos de la caza y de los eventos ENSO, mediante el uso de marcadores microsatellitales y de frecuencias alélicas de la región control de *mt*DNA. El tercer capítulo se basó en el análisis de la distribución espacial de la especie en Chile, con un enfoque en conservación y manejo. Para esto se evaluaron los resultados de los dos censos completos de la especie, analizando la distribución espacial de abundancias mediante el uso de teoría de grafos y tomando en cuenta las estimaciones de distancias de dispersión de la especie, determinadas mediante análisis de autocorrelación espacial de abundancias.

El análisis del *mt*DNA (n=72) muestra la existencia de dos clados filogenéticos para la especie, un clado en el océano Atlántico y otro en el océano Pacífico. Cada uno de estos clados presenta adaptación particulares, por lo que enfrentan el cambio global de forma

diferenciada. En el Estrecho de Magallanes se encontraron individuos pertenecientes a ambos clados, representando una zona de mezcla particularmente susceptible a efectos ambientales y antropogénicos debido al bajo tamaño poblacional. El tiempo estimado de divergencia entre ambos clados fue de 77.441-79.828 años antes del presente, consistente con las características ambientales durante el Último Período Glacial. La evidencia genética sugiere que *O. flavescens* experimientó una expansión demográfica aproximadamente hace 13.000 años antes del presente, acorde con el fin del Último Máximo Glacial. Este resultado concuerda con lo señalado por otro autores para la especie en el Atlántico, así como para la mayoría de las especies de otáridos, sugiriendo condiciones climáticas favorables para el taxa a nivel global. Por otro lado, los resultados de ocho loci microsatelitales (n=63) muestran la existencia de dos clusters genéticos separados aproximadamente a 41°S, representando dos Unidades de Manejo (MU), consistentes con el mayor quiebre oceanográfico y biogeográfico de la costa Pacífico Sur. No se obtuvo registros de un cuello de botella genético, con valores de N_e por encima del valor mínimo viable descrito para vertebrados (N_e norte = 12.320, N_e sur =7.475 individuos). A pesar de esto, los valores de la razón N_e/N encontrado para la MU sur (0,229) se encuentra por debajo del rango normal descrito para especies silvestres (0,25-0,75) y para la MU norte esta razón N_e/N (0,296) se encuentra en el límite inferior del rango, advirtiendo sobre la vulnerabilidad de sus poblaciones. Por otro lado, el análisis de autocorrelación espacial de abundancias mostró una disminución de la autocorrelación entre colonias ubicadas a distancias mayores a 100 km, consistente con la distancia de forrajeo registrada para la especie. A pesar de esto, el análisis de parentesco no mostró relación con la distancia geográfica, no pudiendo descartarse la existencia de dispersión tipo "*stepping stone*". La distribución espacial de abundancias, así como el efecto de la distancia entre colonias sobre la conectividad de la red espacial, corroboran la presencia de un quiebre en la distribución de la especie a ~40°S, confirmando la existencia de 2 metapoblaciones o Unidades de Manejo. Estos resultados muestran también un cambio en la distribución de abundancias y en la conectividad por distancia a ~30°S, acorde con cambios en los regimenes de surgencia. La distribución espacial de *O. flavescens* en Chile mostró depender de la presencia de varias colonias distribuidas a lo largo del país, y por lo tanto de importancia para la persistencia de sus metapoblaciones.

A pesar de que las condiciones genéticas y demográficas de *O. flavescens* no representan un problema poblacional actual en Chile, la explotación de la especie, con el fin de mitigar la interferencia de la misma con la pesquería, debe ser tomado con cautela. Esto debido a la dependencia de las poblaciones del lobo marino con la abundancia de recursos, en conjunto con el declive, durante las últimas décadas, de las poblaciones de algunas presas representativas de la dieta de *O. flavescens* por la industria pesquera, y por la dependencia de la dinámica poblacional de la especie a las condiciones climáticas.

5.- ABSTRACT

O*taria flavescens* is widely distributed in South America, and was historically exploited to almost extinction in much of its range. In Chile, this situation has led the species to constant population fluctuations in the last century. Currently, the species is protected by law, and thus sealing is prohibited. However, due to its trophic habits, this species is usually in conflict with fisheries, which has led to fishermen pushing for the opening of the exploitation ban. To this anthropogenic pressure, other environmental effect, mostly associated to decadal fluctuations such as ENSO, should be added. Because of that, long-term management are necessary for the species. The reproductive behaviour of *O. flavescens*, as in other otariids, is determined by annual reproduction, reproductive aggregation and a possible trade-off between the cost and benefits of philopatry and dispersal. This pattern determines the spatial structure of the species, dominated by a metapopulation-type behaviour. So, for management of *O. flavescens*, the spatial structure and its metapopulation dynamics must be considered, taking into account the pattern of connectivity between colonies, and they contribution for the persistence of the metapopulation. Additionally, the understanding of the anthropogenic and environmental past effects, will allows to predict future demographic and spatial changes.

This thesis aims to answer several questions about the structure and metapopulation dynamics of *O. flavescens* and on its demographic history. The first chapter assesses the phylogeography of *O. flavescens* on its distribution range and its demographic history in Chile, by means of population genetics analyses, using the mitochondrial DNA control region (*mt*DNA) as genetic marker. Also, it is pretended to investigate common historical demographic patterns for otariids. The second chapter covers the genetic structure of the species in Chile, and evaluates the effects of past indiscriminate hunting and ENSO events on the species demography, using microsatellitales markers and alelle frequencies of the *mt*DNA control region. The third chapter is based on the implications of the species spatial distribution in Chile, for conservation and management. In particular, we evaluated the two complete census of the species, analysing the spatial distribution of abundances and using graph theory

and taking into account the estimations of the species dispersal distance, based on the spatial abundance autocorrelation analysis.

The *mt*DNA analysis (n = 72) shows the existence of two phylogenetic clades for the species, one in the Atlantic Ocean and the other for the Pacific Ocean. In the Strait of Magellan there are individuals from both clades. The estimated divergence time between clades was 77.441 – 79.828 years ago, consistent with the climate conditions during the Last Glacial Period. Our analysis also suggest that *O. flavescens* experienced a demographic expansion approximately 13.000 years ago, associated with the end of the Last Glacial Maximum. This result is consistent with observations for the species in the Atlantic and also with results obtained for most otariids, suggesting the existent of worldwide favourable climatic conditions for the taxa. On the other hand, the results of eight microsatellite loci (n = 63) show the existence of two genetic clusters separated at approximately 41°S, representing two Management Units (MU). These results are consistent with the location of the largest oceanographic and biogeographic break found at this latitude in the South Pacific coast. No records of genetic bottleneck were found, with Ne for each MU well above the minimum viable value described for vertebrates (Ne north = 12320, Ne south= 7475 individuals). Despite this, the Ne/N ratio for the south MU (0229) is below the normal range described for wild species (0,25-0,75) and for the north MU, this ratio (0,296) is in the lower part of normal range, warning about the vulnerability of the species populations. By the other hand, spatial autocorrelation analysis of abundances showed a decrease of the autocorrelation between colonies located at distances bigger than 100 km, consistent with the foraging distance recorded for the species. Despite this, genetic parentage analysis showed no relation to geographical distance, not discarting "stepping stone" dispersion. The abundance distribution analysis and the distance connectivity network confirmed the existence of a discontinuity distribution of the species at approximately 40°S, supporting the existence of two metapopulations or Management Units. Those Results also showed a change in the abundance distribution of the species and in the distance connectivity around 30°S, where a biogeographic break has also been recorded due to changes in upwelling regimes. The spatial distribution of *O. flavescens* in Chile showed depend on the present of some particular colonies distributed along the Chilean coast and hence, of great importance for the persistence of the species metapopulations.

Although, genetic and demographic conditions of the Southern sea lion do not show a population problem in most the Chilean coast, exploitation of the species as a resource, to avoid competition with fisheries, should be taken with caution. This because the dependence of the sea lion populations with resource abundance, together with the decline of representative sea lion preys by fishery industry during last decades, and the dependence of the population dynamic of the species to climate conditions.

6.- INTRODUCCIÓN

En Chile habitan cuatro especies de lobos marinos (familia Otaridae, orden Carnivora): lobo marino común o lobo de un pelo, *Otaria flavescens* (Shaw 1800); lobo fino austral o lobo de dos pelos, *Arctocephalus australis* (Zimmermann 1783); lobo fino antártico, *A. gazella* (Peters 1875); y lobo fino de Juan Fernández, *A. phillippi* (Peters 1866). Además, en las tres últimas décadas se ha observado la presencia del lobo fino subantártico, *A. tropicalis* (Sielfeld 1999). *O. flavescens* es la especie más frecuente del litoral chileno, encontrándose distribuida actualmente a lo largo de toda la zona templada del cono sudamericano, desde el norte del Perú (~ 4°S) hasta Cabo de Hornos e isla Diego Ramírez, en el océano Pacífico; y desde Tierra de Fuego hasta el sur de Brasil (~29°S), por el océano Atlántico, incluyendo las Islas Malvinas-Falklands (Scheffer 1958, Bonner and Laws 1964, Vaz-Ferreira 1976, Tovar and Fuentes, 1984).

O. *flavescens* es una especie generalista en cuanto a sus hábitos alimenticios, incluyendo en su dieta peces, crustáceos y moluscos. Además, es una especie oportunista, cuya dieta se compone de las presas de mayor disponibilidad en la zona donde se encuentra (George-Nascimento et al. 1985, Sielfeld 1997, Alonso et al. 2000). De esta manera, en el litoral chileno, el consumo se centra en peces óseos y cefalópodos presentes en la plataforma continental (Sielfeld et al. 1997), sobreponiéndose en el uso de recursos con aquellos extraídos por la pesquería, que representa una actividad extractiva potencialmente competidora directa del lobo marino común. Tanto así que, en 1929-53 la Ley de caza la catalogaba como "especie perjudicial", permitiéndose su explotación legal (Sielfeld 1999) hasta el punto de llevar la especie casi a la extinción, desapareciendo la mayoría de las colonias de gran parte del litorial chileno, principalmente de la zona central de Chile. Debido a esta drástica disminución poblacional, la especie comenzó a ser protegida por ley; para luego, en 1976, volver a considerarse una especie "perjudicial" debido al incremento de sus poblaciones, y comenzar a explotarse nuevamente de forma indiscriminada hasta 1993, donde nuevamente la especie desapareció de gran parte del litoral y volvió a considerarse especie en peligro y a protegerse por ley contra la cacería. Actualmente la especie se encuentra protegida, presentándose conflictos entre el lobo común y la pesquería artesanal en todas las zonas donde existen colonias de la especie próximas a caletas pesqueras (Szteren y Páez 2002; Oliva et al. 2003, 2007; Sepúlveda et al. 2007a; Riet-Sapriza et al. 2012). También se han reportado para algunas zonas mar adentro (300 km de la costa), donde se lleva a cabo actividades de pesca industrial, principalmente de la pesquería del jurel (*Trachurus symmetricus*) (Huckstadt and Krautz 2004; Riet-Sapriza et al. 2012).

Existen dos tipos de interacción entre la actividad pesquera y la presencia del lobo marino común: una potencial interacción de competencia por explotación, donde pescadores y otáridos se afectan negativamente al consumir un recurso común; y una interacción de interferencia directa, en la cual los animales interfieren con la actividad de pesca extrayendo parte de la captura y dañando las redes de pesca. Esta interacción de interferencia, muchas veces conlleva a la muerte de los lobos marinos, ya sea por heridas irreparables con anzuelos, por quedar enredados en las redes de pesca o por ser cazados por los pescadores (Hückstädt and Antezana 2003, Sepúlveda et al. 2007^{A}, Reyes et al. 2013). Igualmente, la salmonicultura, que representa una actividad económica importante en el sur de Chile, se encuentra afectada por la presencia de lobos marinos, ya que extraen parte de los salmones (Oliva et al. 2003, 2007; Vilata et al. 2010). Pero, Oliva et al. 2007 determinaron que esto se debe al mal mantenimiento de las redes protectoras de los cultivos de salmones.

En la actualidad, la explotación de lobos marinos en Chile está prohibida, pero existe una presión constante por parte de la pesquería, salmonicultura y de la industria lobera por la apertura de la veda. Debido a esto, el Gobierno de Chile, por medio del Fondo de Investigación Pesquera y Acuicultura (FIP), financió la realización de dos censos de la especie a lo largo de la costa del país. El primer censo se realizó entre los años 1996 y 2000 (Sielfeld et al. 1997, Aguayo et al. 1998, Oporto et al. 1999, Venegas et al. 2001) y el segundo en 2006 (Bartheld et al. 2007, Oliva et al. 2007, Sepúlveda et al. 2007b). El análisis de estos censos no toma en cuenta la dinámica espacial de la especie, la cual es de gran importancia debido a que la mayoría de los otáridos parecen presentar un compromiso entre el comportamiento filopátrico y el de dispersión (Cassini 2000; Cassini and Fernández-Juricic 2003; Grandi *et al.* 2008), lo que hace necesario considerar la estructura poblacional de la especie en un contexto metapoblacional (York *et al.* 1996; Raum-Suryan *et al.* 2002). Estando definida una metapoblación como un ensamble de poblaciones interactuantes conectadas por la dispersión de individuos entre éstas (Levin 1974, Hanski and Simberloff 1997, Marquet 2002).

A la amenaza que representa la actividad pesquera, se suma el hecho de que el cambio climático se considera la mayor amenaza para los mamíferos marinos en un futuro cercano (Kovacs et al. 2012). Los pinnípedos, mamíferos marinos que poseen aletas delanteras y traseras (focas y lobos marinos), son generalmente animales de ambientes de agua fría que no se encuentran adaptados a las condiciones climáticas del trópico. El calentamiento global, a grandes rasgos, trae como consecuencia la expansión de zonas de clima tropical, reduciéndose los ambientes aptos para soportar grandes poblaciones de pinnípedos. Además, el cambio climático tiene fuerte efectos sobre los procesos oceanográficos y biológicos que dan lugar a la alta productividad capaz de soportar grandes poblaciones de pinnípedos y otros depredadores superiores (Kovacs et al. 2012). En este sentido, en la costa sureste del océano Pacífico, los pinnípedos han sufrido por lo menos dos reducciones drásticas de su tamaño poblacional durante los últimos veinte años, debido al ENSO (El Niño *Southern Oscillation*) (1982-83 y 1997–98) (e.g.. Trillmich *et al*. 1991; Guinet *et al*. 1994; Sielfeld and Guzman 1999; Bradshaw *et al*. 2000; Soto *et al.* 2004, 2006; Le Boeuf and Crocker 2005; Oliveira *et al*. 2006). El actual sistema de surgencia del Pacífico sur-oeste se ve afectado por los eventos ENSO, produciendo un incremento en la temperatura superficial del mar (SST) y una reducción de la productividad primaria durante períodos El Niño, lo cual influye directamente en la distribución y abundancia de presas de otáridos (Trillmich et al 1991, Thiel et al., 2009).

No solo las condiciones climáticas que afectan la abundancia de presas producirían reducciones drásticas del tamaño poblacional de *O. flavescens* (Sielfeld and Guzmán 2002, Soto et al. 2004, 2006), sino también los efectos antropogénicos que afectan la abundancia de presas. A este respecto, durante las últimas décadas, la industria pesquera parece estar produciendo una reducción considerable de las poblaciones de algunas de las especies más representativas de la dieta de *O. flavescens*. La merluza común, *Merluccius gay*, presa importante de la dieta del lobo marino suramericano en toda la costa de Chile (Aguayo and Maturana 1973, Nacimento et al. 1985), ha mostrado una reducción drástica en las toneladas de desembarque de la pesquería desde el 2003, ligado al declive de las poblaciones de estas especies (Moreno and Fedele 2008). Este mismo patrón se observa para la Anchoveta, *Eugraulis ringes*, desde el 2005 (Moreno and Fedele 2008) , especie representativa de la dieta del lobo marino suramericano en el norte de Chile (Sielfeld et al. 1997). Es de esperarse que el declive de las poblaciones de estos recursos por la industria pesquera, conlleve a un incremento de la competencia de esta última y el lobo marino suramericano, intensificando la interferencia entre ambos competidores.

Por otro lado, la amplia distribución latitudinal y la estructura metapoblacional de la mayoría de las especies de otáridos, podría ayudar a amortiguar los efectos de las perturbaciones antropogénicas y ambientales, en la medida que existan a “efectos de rescate” entre las poblaciones locales de estas especies (Hanski 1982). Lo cual a su vez es posible en la medida en que aquellas subpoblaciones con alta probabilidad de extinción, debido a su reducido número, puedan ser rescatadas por inmigrantes provenientes de subpoblaciones de alta densidad y con baja probabilidad de extinción (Gotelli 1991; Raum-Suryan et al., 2002; Lancaster et al., 2010; Pinsky et al., 2010), la existencia de efectos como éste, hace patente la importancia de considerar la dinámica espacial en la persistencia de estas especies.

Tomando en cuenta la actual presión pesquera sobre *O. flavescens*, su historia reciente de cacería y explotación (Sielfeld 1999) (que ha llevado a la especie a fluctuaciones drásticas del tamaño poblacional), en conjunto con los potenciales efectos del cambio climático sobre los pinípedos (Kovacs et al. 2012) y la disminución en las últimas décadas de la abundancia de presas representativas de la dieta de *O. flavescens* por la industria pesquera, es de gran importancia desarrollar un plan de manejo y conservación para la especie que tome en cuenta su dinámica espacial, así como los efectos históricos de las perturbaciones antropogénicas y ambientales.

Las perturbaciones demográficas, ya sean de origen antropogénico o ambiental, pueden resultar en un cuello de botella genético, cuando conllevan a una disminución drástica del tamaño poblacional (e.g. Oliveira *et al*. 2006). Ésto es debido a que la pérdida masiva de individuos generalmente lleva a la extinción de varios linages genéticos de la población (Nei et al. 1997) trayendo como consecuencia la pérdida de la variabilidad genética y la disminución del tamaño poblacional efectivo (e.g. Weber *et al.* 2004; Oliveira *et al.* 2009), reduciendo el potencial evolutivo de las poblaciones para responder a cambios ambientales (Hartl 2000; O'Corry-Crowe 2008). Debido a esto, es importante determinar los efectos genéticos de la cacería y del cambio climático sobre la demografía de *O. flavescens*, y de esta manera, generar estrategias de manejo y conservación que apunten a mitigar el impacto de cambios futuros y a asegurar la persistencia de sus poblaciones.

En el contexto de diseñar estrategias de manejo y conservación de una especie, es fundamental determinar los clados filogenéticos de la especie o Unidades Evolutivamente Significativas (ESU, *por sus siglas en inglés*) (Ryder, 1986) y las Unidades de Manejo (MU, *por sus siglas en inglés*) (Moritz 1994) de la especie. Una ESU se define como una unidad por debajo del nivel de especie con una historia evolutiva monofilética, con diversidad adaptativa y potencial evolutivo propios (Oyler-McCance and Leberg 2005). Mientras que una MU se define como poblaciones con divergencia significativa en las frecuencias alélicas del ADN nuclear o mitocondrial, independientemente de la diferenciación filogenética de alelos (Moritz 1994). La identificación de estas unidades nos permite ir más allá de la aproximación clásica de conservación, inspirada en las aproximaciones demográficas cuyo foco esta en maximizar persitencia o evitar extinción, a un enfoque más genético, que se focaliza en el potencial adaptativo de las especies, siendo este la capacidad de responder ante un ambiente variable. Esto último es particularmente importante en el contexto del cambio global.

A este respecto, Artico et al. (2010) y Feijoo et al. (2011) analizaron fragmentos cortos (287 bp) de la región control del ADN mitocondrial de *O. flavescens*, usando muestras de la costa Atlántica y cinco haplotipos adicionales de Perú, encontrando dos clados filogenéticos distintos entre ambos océanos. Esta conclusión es bastante apresurada en función del tamaño de los fragmentos de ADN y del número de muestras analizadas, principalmente para la costa del Pacífico, donde no se incluyó la costa de Chile. De esta manera, la costa del Pacífico pudiera estar representada por un único clado filogenético, por varios clados distintos o existir un clado sur compuesto por haplotipos tanto del Atlántico como del Pacífico. Por otro lado, en la costa del Pacífico, es de esperarse la presencia de varias Unidades de Manejo para la especie, en relación a la existencia de una pronunciada discontinuidad en los procesos y regímenes oceanográficos y en la distribución de diferentes tipos de organismos en la zona (Camus 2001, Escribano et al. 2003, Valdovinos et al. 2003, Navarrete et al. 2005), así como al aislamiento y las condiciones marinas particulares del Estrecho de Magallanes (Diraison et al. 1997). A este respecto, Camus (2001) propone una clasificación biogeográfica que identifica 3 unidades espaciales mayores: un área sur, conformada por la provincia Magallánica (aproximadamente desde los 42°S a los 56°S); un área norte, Provincia Peruana (que incluye la costa de Perú y el norte de Chile hasta aproximadamente 30°S); y un área intermedia extensa (entre 30 y 42°S).

Otro aspecto importante de considerar para comprender la dinámica espacial del lobo marino común, así como su importancia en el manejo y conservación de la especie, tiene que ver con su ciclo de vida y su comportamiento reproductivo, así como la influencia de éstos en la formación de una estructura metapoblacional.

6.1.- Ciclo de vida y comportamiento reproductivo de *O. flavescens*

Las poblaciones de pinnípedos se encuentran distribuidas en parches, siendo éstos roqueríos, playas arenosas y/o islotes que son utilizados por la especie como paraderos de descanso o como colonias reproductivas. Las poblaciones del lobo común en Chile presentan estas características en su comportamiento de distribución y reproducción, siendo los parches en su mayoría roqueríos costeros que se encuentran distribuidos a lo largo de todo el país (Sielfeld 1999).

O. *flavescens* es una especie poliginia; durante la época de apareamiento, verano austral, los machos arriban a los roqueríos reproductivos a comienzos de la temporada, compitiendo con otros machos por la posesión de territorios, los que son celosamente defendidos. Las hembras arriban luego a estos territorios protegidos por uno o pocos machos, donde paren una sola cría, para luego aparearse, generalmente con el macho dominante. Así, durante la época de reproducción, las hembras de la especie se agregan formando colonias de unos pocos machos (Campagna and Le Boeuf 1988, Cassini and Vila 1990, Acevedo et al. 2003). El apareamiento ocurre desde enero hasta los primeros días de marzo (días después del parto) (Acevedo et al. 2003), presentando variaciones de días entre las poblaciones en función de la latitud y entre las poblaciones de la costa Pacífica y Atlántica, pero manteniéndose la sincronización dentro de cada localidad de manera interanual (Acevedo et al. 2003, Paves et al. 2005).

El ciclo reproductivo de la especie, al igual que de todos los otáridos, se caracteriza por el apareamiento post-parto, durando el estro de las hembras entre 6 y 8 días; y por la capacidad de retrasar este período del ciclo, por medio del retardo de la implantación del embrión. El tiempo de gestación permanece invariable en estas especies, con duración de 8 meses (Boyd et al. 1999). Durante el período de lactancia, las hembras de *O. flavescens*, al igual que de todos los otáridos, alternan entre estar en el paridero alimentando a la cría o forrajeando mientras la cría permanece en el roquerío. Estas últimas permanecen con su madre hasta el año de edad, siendo amamantadas hasta poco más de los 3 meses, edad en la cual aprenden a nadar y comienzan a buscar su alimento (Campagna and Le Boeuf 1988).

En cuanto a la edad de reproducción sexual, se ha estimado en 3 años para las hembras, estando todas sexualmente maduras a los 4 años, y los machos a partir de los 2 años, aunque estos son recién capaces de defender un territorio a los 8 años de edad (Sielfeld 1999, Acevedo et al. 2003). La longevidad máxima de la especie para animales de la costa Pacífica ha sido estimada en 18 años para los machos y en 16 años para las hembras (Grau and Acuña 1998).

6.1.1.- *Agregación reproductiva*

La agregación en colonias durante la época reproductiva es un comportamiento social que ocurre en muchas especies de vertebrados, incluyendo a las especies de mamíferos marinos de la familia Otariidae y tres especies de la familia Phocidae: dos especies de elefantes marinos (*Mirounga* spp.) y el león marino (*Halichoerus grypus*). A pesar de lo común de este comportamiento gregario, el mismo no ha podido ser explicado hasta la actualidad, aunque muchas hipótesis han sido planteadas (Danchin and Warger 1997, Cassini 1999).

Las hipótesis más recientes para explicar este comportamiento de agregación reproductiva, están basadas en observaciones que muestran que la distribución de los individuos es el resultado de la elección de los mismos por un territorio para la reproducción, estando la selección de hábitat a la base de estas reflexiones. Éstas se centran en tres factores que influyen en la decisión por parte del animal para asentarse o dispersar durante la época reproductiva: 1.- la presencia de coespecíficos, 2.- el éxito reproductivo de los mismos y 3.- las características de las parejas potenciales (Danchin and Warger 1997, Clobert et al. 2004).

Estos tres factores pudieran estar siendo mediados por las características del ambiente. En este caso, el rango de densidad óptimo de agregación se esperaría presente una relación directa con la ‘calidad’ del hábitat, idea referida como *The Ideal Free Distribution* (IFD) por (Fretwell and Lucas 1970); entendiéndose por ‘calidad’ del hábitat las condiciones físicas de un determinado sitio que influyen en la subsistencia de los individuos que conforman la agregación. Dentro de este contexto, para las hembras de especies de pinnípedos que presentan comportamiento gregario durante la reproducción, Cassini (1999) expone la idea de que, al estar los sitios 'aptos' distribuidos en parches, la distribución de las hembras se espera se asocie con la distribución heterogénea de los recursos. Pero, por otro lado, este autor también plantea la idea de que la distribución de los recursos no lograría explicar la extrema agregación que se observa entre estos individuos, ya que para varias especies se ha observado la existencia de parches 'aptos' pero vacíos y una densidad mucho mayor a la esperada en algunos parches reproductivos (Cassini 2000). De esta manera, la hipótesis actualmente más aceptada para explicar esta extrema agregación en estas especies es la de "evasión del acoso agresivo por parte de los machos" (Cassini 2000).

Durante la época de apareamiento, los machos de la especie que no lograron defender territorio son extremadamente agresivos, intentando durante toda la época reproductiva aparearse con alguna hembra que, generalmente, no están receptivas a machos satélites. Por lo que, en el caso de que el macho satélite logre aparearse, muchas veces lo hace hiriendo a la hembra y en algunos casos produciéndole la muerte. La agresividad de estos machos satélites también conlleva a la muerte de crías, las cuales son agredidas de forma intencional o separadas de la madre hasta morir por falta de alimento (Campagna and Le Boeuf 1988, Cassini and Vila 1990). Cassini y Fernández- Juricic (2003) exponen que la alta densidad de hembras en un mismo paridero produce un efecto de dilución de este tipo de agresión, debido a la disminución de las interacciones agresivas hembra-macho per cápita. Igualmente, al haber más hembras aumenta la cantidad de machos en la agregación, por lo que aumentan las interacciones entre machos, lo que ocasiona una disminución de la interacción agresiva macho-hembra. Pero, por otro lado, un número muy grande de hembras disminuye la proporción hembra/área y aumenta las interacciones hembra-hembra, al mismo tiempo que aumenta el grado de agresividad de los machos, por la competencia entre éstos por defensa de territorio donde hay más hembras.

De esta forma, el reproducirse en grupos de coespecíficos parece indicar la existencia de un trade-offs entre los costos y beneficios denso-dependientes (Danchin and Warger 1997, Cassini and Fernandez-Juricic 2003)

6.1.2.- ***Filopatría***

La filopatría se refiere a la estabilidad temporal de la composición de las colonias reproductivas, así como de la estructura social de las mismas, formándose agregaciones entre individuos emparentados (Greenwood 1980). En pinnípedos, por ejemplo, esto es debido a que se reconoce fidelidad por parte de las hembras hacia los parches donde nacieron, para parir y reproducirse (ej. *Halichoerus grypus* (Pomeroy et al. 1994, Pomeroy et al. 2000b); *Zalophus wollebaeki* (Wolf and Trillmich 2007); *Phoca vitulina* (Harkonen and Harding 2001). Este comportamiento filopátrico también ha sido reconocido en las hembras de *O. flavescens*, presentándose una tendencia a regresar todos los años a reproducirse al roquerío de origen (Cassini 1999, 2000). La existencia de fidelidad territorial por parte de los machos de la especie es desconocida, aunque se ha visto para otras especies de pinnípedos que algunos machos también presentan filopatría (ej. Twiss et al. (1994), Pomeroy et al. (2000b) para *H. grypus*; Wolf and Trillmich (2007) para *Z. wollebaeki*; y Hoffman et al. (2006b) para *Arctocephalus Gazella*).

El comportamiento filopátrico es un interrogante dentro del área de la ecología, presentándose como hipótesis para explicar este comportamiento los beneficios de agregación entre individuos conocidos y emparentados. Estos beneficios se basan en las ideas de *kin selection*, donde la cooperación entre individuos emparentados incrementa el fitness inclusivo de los mismos (Hamilton 1964, Maynard Smith 1964). En el caso de pinnípedos coloniales, la defensa ante agresores, generalmente machos satélites y en algunas especies, la lactancia compartida, representarían los beneficios de la agregación familiar. Sumado a esto, la agregación de individuos conocidos supone la disminución de agresión entre éstos y la posible formación de una estructura jerárquica respetada (Danchin and Warger 1997; Cassini 1999). Esta explicación del comportamiento filopátrico por medio de beneficios de agregación familiar o entre individuos conocidos, sugiere la existencia de mecanismos de *kin recognition*, lo cual ha sido demostrado para algunas especies de pinnípedos (Insley et al. 2003).

Por otro lado y de modo contrario, se reconocen ciertos costos del comportamiento filopátrico, siendo éstos los asociados al comportamiento gregario en sí y determinados por factores denso-dependientes, como lo son la competencia por recursos y el incremento de transmisión de enfermedades (Cassini and Fernandez-Juricic 2003), así como el incremento de la probabilidad de extinción por estocasticidad ambiental (Hanski 1991). Además, el entrecruzamiento o *inbreeding*, también podría representar un costo de agregación filopátrica.

6.2.- Estructuración metapoblacional

Las evidencias de colonización de nuevos parches y de extinción de otros en estas especies (e.g. Rodriguez and Bastida 1998 y Thompson et al. 2005, para *O. flavescens* en Argentina y las Islas Malvinas-Falkland, respectivamente), y de dispersión tanto de machos como de hembras (e.g. Raum-Suryan et al. 2002, Hoffman et al. 2006a para *E. jubatus* entre Oregon, Alaska y Rusia), avalan la existencia de una estructuración metapoblacional en estas especies. Igualmente, existen evidencias genéticas que confirman la existencia de una estructura metapoblacional en especies de pinnípedos (Wynen et al. 2000, para *A. gazella*; Gaggiotti et al. 2002 para *H. grypus*; y Robertson y Gemmell 2005, para *A. fosteri*).

A pesar del reconocimiento de una estructura metapoblacional en varias especie de pinnípedos coloniales (e.g. Harwood and Stanley (1996) para *Monachus monachus*, Merrick and Loughlin (1997), Geber and VanBlaricom (2001) y Fay (2004) para *E. jubatus y* Thomas et al. (2005) y Harrison et al. (2006) para *Halichoerus grypus*), solo los trabajos de Thomas et al. (2005), Harrison et al. (2006) y Fay (2004) analizaron la dinámica metapoblacional en este grupo taxonómico. Thomas et al. (2005) y Harrison et al. (2006) evaluaron el comportamiento demográfico metapoblacional entre algunas subpoblaciones locales de *H. grypus* en la costa británica del Mar del Norte, ajustando un modelo metapoblacional espacialmente explícito (state-space model; SSM) entre grupos (regiones) (Thomas et al. 2005) o para cuatro colonias reproductivas de la región norte de Inglaterra (Harrison et al. 2006). En este último trabajo también se determinó la tasa de movimiento de estos individuos entre colonias, determinada por métodos de marcaje y recaptura durante 20 años, período para el cual también se registró la abundancia de individuos, principalmente de crías. De esta forma, estos autores encontraron que la dispersión entre colonias representaba un factor determinante para la dinámica global de la especie en esta zona, a pesar de la alta tasa de fidelidad territorial que se detectó en estos organismos. Como argumento se expone que el modelo de dinámica poblacional que no toma en cuenta el movimiento de individuos entre parches presentó el menor ajuste a la serie de tiempo. De manera similar, estos autores encontraron que la probabilidad de dispersión se redujo al incrementar la distancia entre las colonias y que estas focas eran atraídas hacia las colonias más grandes. Por su lado, Fay (2004) ajustó un modelo metapoblacional espacialmente explícito a la distribución de abundancias del *stock* oeste de Alaska de *E. jubatus*, tomando como subpoblaciones las distintas regiones cuyas colonias presentaban tendencias poblaciones distintas. En este trabajo se encontró que la aproximación metapoblacional, que permitió evaluar distintos efectos ambientales en el espacio sobre la dinámica poblacional, presentó un mejor ajuste a la distribución de abundancias, que el enfoque que considera al *stock* como una población única.

6.2.1.- *Factores influyentes en la dispersión y dinámica metapoblacional*

A este respecto, Cote et al. (2007) exponen que la dispersión, por lo menos para algunos vertebrados, corresponde a una necesidad, reflejando un proceso activo, más que a un proceso pasivo en el cual los individuos alcanzan un hábitat apto por simple azar. Dado que la dispersión activa implica necesariamente la decisión de no permanecer en un parche o agregación determinada, se espera que ésta esté asociada a los factores que determinan la selección del hábitat por parte de los individuos (Danchin and Warger 1997; Clobert et al. 2004; Fretwell and Lucas 1970). De esta manera, el patrón de dispersión estaría siendo moldeado por factores demográficos y ambientales que determinan la selección del hábitat.

6.2.1.1.- *Factores demográficos denso-dependientes*

La abundancia y distribución de las especies suelen estar correlacionadas de manera positiva (Hanski 1982, Brown 1984). A este respecto, varias especies de pinnípedos coloniales evidencian colonización en relación al incremento del tamaño poblacional (e.g. *O. flavescens* en el norte de la patagonia argentina (Dans et al. 2004), *A. gazella* en South Georgia (Boyd 1993) y *A. fosteri* en Nueva Zelanda (Bradshaw et al. 2000). En estos trabajos se detectó un incremento paulatino del área habitada por estas especies, asociado al incremento en la abundancia total de individuos; mostrándose que esta última conlleva a la expansión de estas poblaciones.

Esta relación observada entre abundancia de individuos y expansión paulatina, sugieren una posible relación entre la dispersión asociada a la densidad de individuos y la distancia física, sugiriéndose una relación inversa entre estas variables. A este respecto, como se mencionó anteriormente, el comportamiento gregario y filopátrico conlleva al incremento de la densidad de individuos el cual acarrea un aumento en la tasa de mortalidad de crías debido a efectos denso-dependientes (Cassini and Fernandez-Juricic 2003), existiendo evidencias sustanciales que corroboran este hecho (e.g. Harcourt (1992) para *A. australis,* Doidge et al. (1984) para *A. gazella,* Le Boeuf and Briggs (1977) para *M. leonina*). En este sentido, Baldi et al. (1996) encontraron que en el elefante marino, *M. leonina*, en la costa Argentina, la tasa de dispersión de las hembras disminuía la probabilidad de interacciones agresivas hembra-hembra, incrementando la probabilidad de sobrevivencia de las crías. Igualmente, Harrison et al. (2006) encontraron que para *H. grypus* el modelo de probabilidad de dispersión de mejor ajuste siguió una tendencia lineal negativa con la distancia física entre sitios, aunque la importancia de incorporar la abundancia de individuos el modelo de dispersión mostró ser significativa. Además, utilizando información de genética de poblaciones, Gaggiotti et al. (2002) y Gaggiotti et al. (2004) estimaron la contribución de la densidad y de la distancia geográfica en la colonización de nuevos parches para esta especie, encontrando que la interacción entre ambos factores eran los responsables de la colonización de nuevos parches.

6.2.1.2.- *Inbreeding avoidance*

Altos niveles de filopatría en ambos sexos durante generaciones sucesivas, conlleva a la formación de agregaciones altamente emparentadas, lo cual puede traer como consecuencia el entrecruzamiento entre estos individuos emparentados (*inbreeding*) y esto a su vez, la disminución de la heterocigocidad en la población (Hartl 2000, Gillespie 2004, Freeland 2005). Este efecto ha mostrado ser perjudicial para especies de pinnípedos, afectando la sobrevivencia y resistencia a enfermedades por parásitos de los individuos juveniles y en el éxito reproductivo de los machos adultos (e.g. Amos et al. 2001b y Bean et al. 2004 para *H. grypus* y Hoffman et al. 2004 para *A. gazella*).

El *inbreeding* parece no ocurrir en algunas poblaciones de pinnípedos coloniales (e.g. Wilmer et al. 1999, Wilmer et al. 2000, Amos et al. 2001a y Gemmell et al. 2001 para *H. grypus*), evidencia que sugiere la posible existencia de algún mecanismo de elección por parte de las hembras por parejas poco o nada emparentadas. Por lo que, una posible razón para la dispersión por parte de las hembras pinnípedas es la selección de machos no emparentados, siendo ésta una medida de evasión de *inbreeding* en agregaciones altamente emparentadas (Greenwood 1980); selección mediada por mecanismos de *kin recognition*. En este contexto, Hoffman et al. (2007) encontraron para *A. gazella* en South Georgia, un alto porcentaje de crías (>50%) provenientes de padres alejado de la hembra a más de 35 m, a pesar de que la distancia máxima de separación entre hembra-macho era de 6 m, estando 70% de las hembras a una distancia de 2 m del macho más cercano. Estos autores estudiaron la relación entre el parentesco genético de hembras y machos, buscando determinar una posible implicancia sobre la elección del macho por parte de la hembra, ya que éstas no se aparean con el macho más cercano a pesar de mantener la misma ubicación durante todo el período reproductivo. Así, estos autores encontraron una elección activa de la pareja por parte de las hembras, moviéndose éstas temporalmente de su ubicación en la colonia; presentándose una relación lineal entre la distancia de movimiento de las hembras y la interacción de parentesco hembra-macho e IR, *internal relatedness*, una medida de la heterocigocidad genética de un individuos (Amos et al. 2001b) del macho. De esta manera, se manifiesta un balance en la elección de la hembra por machos poco emparentados y altamente heterocigotos, ambos influyentes en la heterocigocidad de las crías. Resultados similares se han obtenido para otras especies de mamíferos (e.g. para la rata canguro, Winters and Waser 2003).

6.2.1.3.- *Factores ambientales*

Como se ha mencionado anteriormente, para muchas especies de pinnípedos se ha observado que la proporción de parches que son ocupados por los individuos es menor a la disponibilidad total de playas o roqueríos, según sea el caso. Además, se presentan densidades muy altas en algunos parches y densidades muy bajas en otros, y solo algunos de los parches en los que se encuentran los individuos son utilizados como sitios de reproducción (Cassini 1999).

En la sección anterior se expusieron las posibles causas demográficas que pudieran estar influyendo en la elección por parte de los individuos para permanecer en un determinado parche o dispersar a otros sitios; jugando la dispersión un papel crucial en la estructura y dinámica metapoblacional. Se mencionó también que algunos de los factores que determinan la selección del hábitat son de carácter ambiental. En pinnípedos, tanto la topográfica de los sitios como la disponibilidad de alimento en la zona, parecen representar los factores ambientales más determinantes.

6.2.1.3.1.- *Topografía*

En cuanto a las características topográficas relacionadas a la selección de sitios como propicios para la utilización de los mismos por parte de especies de pinnípedos, Pomeroy et al. (2000a, b) y Twiss et al. (2000, 2001) estudiaron las colonias de *H. grypus* en Escocia, comparando entre parches utilizados como zonas reproductivas con parches apostaderos, así como con demás parches disponibles. Igualmente, Wolf et al. (2005) estudiaron las características topográficas de los territorios utilizados por el lobo marino de Galápagos, *Zalophus californianus*. Estos autores encontraron que para ambas especies los factores más trascendentales para el uso de un hábitat eran los costos de locomoción, además de la termorregulación para *Z. californianus*. De esta forma, los parches de mayor calidad se caracterizaban por ser los de fácil acceso al mar (poca elevación, zona plana, amplia superficie de contacto con el agua) y, para *Z. californianus*, por la presencia de 'piscinas' y de extensa área de sombra; siendo estos los utilizados por los individuos tanto como parideros como apostaderos. Comparativamente hablando, los parideros presentaron siempre mayor calidad topográfica que los apostaderos para ambas especies. Para *Z. californianus*, los parches únicamente apostaderos, el único prerrequisito que cumplían era la presencia de sombra. Dentro de este contexto, la dispersión entre colonias también podría estar influenciada por la capacidad topográfica de las colonias, tanto emisora como receptora, de permitir la existencia de un número determinado de individuos bajo condiciones favorables para la reproducción y crianza.

6.2.1.3.2.- *Disponibilidad de alimento*

Otra de las características que hace favorable a una colonia para permanecer en ella o dispersar, es la disponibilidad de alimento en la cercanía. A este respecto, Boyd et al. (1998) exponen que la explotación de los recursos locales durante la lactancia temprana de otáridos se explica por las restricciones del tiempo de forrajeo asociado a los requerimiento energéticos de las crías. Este hecho ha sido corroborado por estudios de comportamiento de forrajeo en hembras lactantes de la especie (e.g. Thompson et al. (1998) en las Islas Falkland y Campagna et al. (2001) y Werner and Campagna (1995) en la Patagonia Argentina). Además, Campagna et al. (2001) encontraron que la distancia y duración de los viajes migratorios de las hembras patagónicas eran mucho mayores que los valores reportados por Thompson et al. (1998) para las hembras de las Islas Falkland, asociándose estas diferencias a variaciones en la disponibilidad de alimento en la zona.

Dentro de esta misma idea, se ha observado que cuando el alimento es escaso, como durante eventos El Niño, los individuos de especies de pinnípedos coloniales tienen que forrajear por más tiempo y a mayores distancias de la colonia (e.g. Soto et al. 2006 para *O. flavescens,* Boyd et al. 1994 para *A. gazella*, y Le Boeuf and Crocker 2005 para *Mironga angustirostris*). Esto representa un alto costo energético que, para las hembras, se ve reflejado en una disminución en la energía disponible para el período reproductivo, teniendo que comprometer la lactancia y el cuidado maternal por tener que salir a forrajear durante los primeros meses de crianza. De esta forma, se incrementa el tiempo de separación madre-cría lo cual puede producir la muerte de esta última, obteniéndose una disminución en la tasa de sobrevivencia de las crías durante períodos reproductivos de baja productividad (e.g. Sielfeld and Guzmán (1999) y Soto et al. (2004, 2006) para *O. flavescens*, Lunn et al. (1993) y Forcada et al. (2005) para *A. gazella*, Guinet et al. (1994) para *A. gazella* y *A. tropicalis* y Le Boeuf and Crocker (2005) para *Mironga angustirostris,* McMahon and Burton (2005) *para Mironga leonina*).

En general, la variabilidad climática produce fuertes efectos en los ecosistemas marinos, con repercusiones que pueden alterar toda la red trófica. Los cambios inducidos por el clima en la abundancia de especies de bajos niveles tróficos pueden producir un efecto en cascada hasta los depredadores topes afectando la tasa de crecimiento de sus poblaciones (Lea et al. (2006), Trathan et al. 2007, Siniff et al. 2008 y Forcada 2008).

A este respecto, Schmelzer (2000) correlacionó la heterogeneidad espacial en la disponibilidad de los recursos alimenticios, estimada mediante la determinación de la productividad primaria, con las variaciones en la abundancia de individuos de las colonias reproductivas de *Monachus schauinslandi* (Phocidae) en Hawai, encontrando una correlación positiva entre ambas variables. De esta manera, este autor concluye sobre la posible influencia de la calidad del hábitat, determinada por la abundancia de los recursos, sobre los patrones de distribución de abundancia de la especie.

Distintos factores demográficos y ambientales, parecen estar determinando los patrones de agregación y dispersión en otáridos, produciendo una estructuración espacial dominada por el comportamiento metapoblacional. Así, para la conservación y manejo de *Otaria flavescens*, se debe considerar esta estructura y dinámica metapoblacional, tomando en cuenta los patrones de conectividad entre parches, así como la importancia de los mismos para la persistencia de la metapoblación. De este modo se podrá establecer estrategias de conservación y manejo a largo plazo para la especie. Adicionalmente, el entendimiento de la estructura y dinámica poblacional y metapoblacional de la especie en el pasado, afectadas por factores tanto antropogénicos como ambientales, permitirá predecir cambios demográficos y espaciales futuros.

Esta tesis pretende responder a diversas preguntas sobre la estructura y dinámica metapoblacional de *O. flavescenes*, así como sobre su demografía histórica. Para esto, la tesis se dividió en tres capítulos. Los dos primeros capítulos responden a estas preguntas desde un punto de vista de genética de poblaciones, utilizando herramientas moleculares, para lo cual se debió obtener muestras de individuos de lobo marino común a lo largo de Chile. Mientras que el tercer capítulo se basa en el análisis de la distribución espacial de la especie en Chile, con un enfoque directo en la conservación y manejo de la especie.

En el primer capítulo se responde a preguntas evolutivas de la especie: ¿Cómo es la filogeografía de la especie?, ¿Presenta la especie distintos clados filogenéticos relacionados con la disyunción Antlantico/Pacifico?, ¿Cuál ha sido la historia demográfica de la especie en Chile? y ¿cómo han influenciado en la misma la cacería histórica y los efectos del cambio climático?. Estas preguntas serán respondidas por medio del análisis del marcador región control del ADN mitocondrial, comparando los resultados con el conocimiento que se tiene en las demás especies de otáridos, pretendiendo establecer patrones comunes del taxa.

El segundo capítulo de la tesis responde a: en Chile, ¿cómo se estructura espacialmente las poblaciones de *O. flavescenes*?, ¿cuántas unidades de manejo se presentan en el país?, ¿se encuentra esta estructuración determinada por los procesos oceanográficos y biogeogŕafico descritos para la costa de Chile?, ¿se presenta un cuello de botella en las poblaciones chilenas de la especie debido a la reciente cacería indiscriminada que sufrió la especie?. Para responder a estas preguntas, se utilizarán marcadores microsatellitales y frecuencias alélicas de la región control del ADN mitocondrial.

El tercer capítulo busca responder si la distribución espacial de *O. flavescens* en Chile es coherente con los procesos oceanográficos y biogeográficos descritos para la zona costera, ¿cuáles son las zonas de mayor preocupación para la conservación de la especie en Chile? y ¿cuáles son las colonias más influyentes en el mantenimiento de la conectividad de la especie a lo largo de su distribución en país?. Estas preguntas serán respondidas por medio de la evaluación de los resultados de los censos FIP (Sielfeld et al. 1997; Aguayo et al. 1998;

Oporto et al. 1999; Venegas et al. 2001; Bartheld et al. 2007; Oliva et al. 2007; Sepúlveda et al. 2007b) y del uso de teoría de grafos (Watts 2004; Rayfield 2011). Adicionalmente, en este capítulo, se busca responder si existe un patrón claro de dispersión en *O. flavescens* determinado por el comportamiento filopátrico de la especie. Para esto, por un lado se evaluará la distribución espacial de abundancias de individuos y por otro lado se revisará la distribución espacial del parentesco entre individuos, mediante el uso de marcadores microsatelitales.

6.3.- BIBLIOGRAFÍA

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7.- CAPÍTULO I

Filogeografía del lobo marino común, *Otaria flavescens*, asociada al Último Período Glacial

Phylography of the South American sea lion, *Otaria flavescens*, related to the Last Glacial Period

7.1.- INTRODUCTION

Populations of most species of seals (family Phocidae) and sea lions (family Otariidae) were substantially reduced by commercial sealers in the 18th and 19th centuries (Bonner and Laws, 1964; Lotze and Worm, 2009). Their colonial terrestrial breeding, at traditional locations, made them highly vulnerable to over-exploitation and hence virtually all pinnipeds survived historical sealing only in dramatically reduced numbers in few locations (Kovacs et al. 2012). Currently, most otariids had been managed to increase its population size after the reduction of hunting pressure (Lotze and Worm, 2009; Wickens and York, 1997). Recovery have been impressive in some species, especially among pinnipeds (seals and sea lions) once protection or hunting controls were set, although lag times occurred at sites that were reduced to very small numbers or at sites that had to be recolonized. In spite of this, fisheries interactions continue to be considered as the dominant recognized threat over pinnipeds. For the 85% threatened taxa, direct or indirect fisheries interactions are identified as the primary or secondary threat. The indirect fisheries interactions include intentional shooting by fishermen, which happens even among critically endangered (CR) taxa, as well as competition for fish resources and fisheries induced changes to ecosystems that cause nutritional stress among pinnipeds (Kovacs et al. 2012).

Global climate change is another likely threat to pinnipeds worldwide. The predicted changes in the physical environment are likely to have impacts ranging from extinction of taxa currently listed as threatened, to endangerment of taxa currently considered as least concern (LC). Pinnipeds are generally cold water animals that are poorly adapted to tropical conditions. Accordingly, climate change will alter the suitable areas for supporting large pinniped populations. Some ice associated pinnipeds in the Arctic are already being challenged by reductions in the geographic extent, seasonal duration and stability of sea ice. Additionally, the presence of sea ice has strong effects on oceanographic and biological processes that result in regions of high productivity capable of supporting large populations of pinnipeds and other top predators (Kovacs et al. 2012).

In the southeastern Pacific, pinnipeds have suffered at least two drastic reductions in numbers in the last 20 years due to El Niño Southern Oscillation (ENSO) effects (1982-83 and 1997–98) (e.g. Trillmich et al., 1991; Guinet et al., 1994; Sielfeld and Guzman, 1999; Bradshaw et al., 2000; Soto et al., 2004, 2006; Le Boeuf et al., 2005; Oliveira et al., 2006). In the southeast Pacific, the Humboldt Current upwelling system, is affected by ENSO events with increased SST and reduced primary productivity directly influencing the distribution and abundance of fish preys (Trillmich et al 1991, Thiel et al., 2009). On other side, it seems that the large and fragmented distribution of most species of otariids may help to buffer the past anthropogenic and climatic disturbances such that, local populations can be rebuilt from repeated migration events from other populations within the range (Raum-Suryan et al., 2002; Lancaster et al., 2010; Pinsky et al., 2010). At present, however, little is known regarding the connectivity and genetic diversity of most otariids populations, which renders the issue of identifying the population network that best samples the functional diversity within the species (Crandall el al., 2000).

In addition, climate and anthropogenic factors act on the genetic variation patterns of a species, leading to evolutionary processes (Oyler-McCance and Leberg, 2005; Hartl and Clark, 2007; O'Corry-Crowe, 2008; Curtis, 2009). Anthropogenic disturbances often result in substantial reductions in population size (demographic bottlenecks) (e.g. Oliveira et al., 2006) and consequent loss of genetic variability (genetic bottlenecks) (e.g. Weber et al., 2004; Oliveira et al., 2009), that may reduce the evolutionary potential of a population to respond to a changing environment and may produce inbreeding depression (Amos et al., 2001; Hoffman et al., 2004; Hartl and Clark, 2007; O'Corry-Crowe, 2008).

Of the seven otarrids species of South America, five of them are present in Chile: the South American sea lion, *Otaria flavescens* (Shaw 1800), the South American fur seal, *Arctocephalus australis* (Zimmermann 1783), the Juan Fernández fur seal, *A. phillippi* (Peters 1866), the Antarctic fur seal, *A. gazella* (Peters 1875) and the subantarctic fur seal, *A. tropicalis* (Sielfeld 1999). *O. flavescens* is the most common species of otariids in the Chilean coast, and with *A. australis*, the otariid with highest geographic distribution and the most abundant of South America (Oliveira et al., 2012). Its global distribution include from Torres, Brazil (29°200S, 49°430W), in the Southwestern Atlantic Ocean (Scheffer, 1958; Bonner and Laws, 1964; Vaz-Ferreira, 1976) to Cape Horn in the extreme south of South America and to Zorritos-Peru (34°00S, 80°340W) in the Southeastern Pacific Ocean (Tovar and Fuentes, 1984).

As for many pinnipeds species (Kovacs et al., 2012), *O. flavescens* is usually in conflict with fisheries, because they compete for the same resources (Häckstädt and Antezana, 2003; Hückstädt and Krautz, 2004; Hückstädt et al. 2007; Sepúlveda et al., 2007; Vilata et al. 2010; Riet-Saprizaa et al. 2012). In Chile, due to the interference with fisheries, by the last century, during 1929 - 1953, the species was cataloged as "damager" and was indiscriminately exploited until it became almost extinct and began to be protected. This situation was repeated later again in 1976 – 1993 (Sielfeld, 1999). At present, the sea lion exploitation in Chile is prohibited, but the fishery pressures and seal oil industry are mounting. Given these conservation concerns and the recent history of decline, it is very important to know the genetic state of this species and the distribution of the genetic variation that influences on the adaptation of the species, and to understand the effects of past sealing and climate change on its historical population demography, with emphasis on predicting and avoiding future negative effects of population disturbances.

Respect to past climate conditions, the effects of the historical climate change on the South American sea lion as on the others southern pinnipeds, is unknown. It is likely that the geographic distribution of the South American sea lion has been under the influence of glaciations events, that include drastic oceanographic changes (Lamy et al., 1998; Romero et al., 2006; Jouzel et al., 2007; Marchant et al., 2007). In particular, it is expected that the southernmost populations of South-America went extinct during the Last Glacial Maximum because of extensive ice cover. This is supported by preliminary studies on samples from the Atlantic coast and five individuals from Peru that showed a clear divergence between western and eastern continental distributions based on short fragments (287 bp) of the *mt*DNA control region (Artico et al. 2010; Feijoo et al. 2011). Nevertheless, these studies did not take into account the most extensive Pacific distribution of the species. In that sense, Túnez et al. (2007) and Feijoo et al. (2011) using the cytochrome B, D-loop *mt*DNA and microsatellite loci as genetic markers, describe the individuals from Uruguayan and Argentinean distribution of the species as members of the same phylogenetic clade but representing different genetic groups. On the other hand, acknowledging the genetic history of *O. flavescens*, Freilich (2004) and Túnez et al. (2010) evaluated the control region and flanking *t*RNA sequences from *mt*DNA. Freilich (2004) analyzed the north Peninsula Valdés (42°-47°S) and the Falklands Islands (Malvinas) colonies, whereas Túnez et al. (2010) analyzed northern and central Patagonia (where the largest colonies of the *O. flavescens* within Argentina are located). Both works found signals of population expansion related to late Pleistocene glaciations. Latter, Feijoo et al. (2011) confirmed the demographic history by two molecular markers, the *mt*DNA control region and thirteen polymorphic microsatellite loci covering most of the Atlantic Ocean distribution of the species. They found that most of the Atlantic sea lion colonies are in mutation-drift equilibrium, with not signals of recent genetic bottleneck and with signs of demographic expansion for the north Patagonian region.

Phylogeographic studies are lacking in marine species of the Southern Hemisphere and in particular in the southeastern Pacific. For marine mammals only information for the marine otter *Lontra felina* (Vianna et al. 2010) is available for the south Pacific. Determining the phylogeography may also has important implications for conservation and management, by the identification of different clades with unique genetic variation, that may have particular adaptive diversity and evolutionary potential, that may influence on the susceptibility of the populations to the effects of rapid climate changes.

This research aims to evaluate the phylogeography of *Otaria flavescens*, emphasizing whether Atlantic and Pacific populations of the species belong to two different clades, and inferring connectivity and divergence time between populations located at both sides of the continent. We hypothesize that possible divergence of the specie in both coast of America are associated to past climate conditions during the Last Glacial Period, were ice sheet extended and covered the southern part of the continent (Jouzel et al. 2007).

We also determinate the past demographic history of the species in the Chilean coast, hypothesizing that the retract of the ice sheet during the transition between the Last Glacial Maximum and the Interglacial Period (Jouzel et al. 2007, Marchant et al. 2007), allow the recolonization of southern Chile by *O. flavescens*, either by the northern populations or by population present in glacial refuges. In that sense, in Chile, the marine otter *L. felina* seems to experienced a recent colonization toward the south but, if the southward colonization process is post-glacial, following ice sheet retreat, is unknown (Vianna et al. 2010). There are also registers of past demographic expansion for some species of otariids (e.g. Weber et al. 2004 for the Guadalupe fur seal, *A. townsendi*; Matthee et al. 2206 for the Australian fur seal, *A. pussilus*; Freilich 2004, Túnez et al. 2007, Feijoo et al. 2011 for *O. flavescens* in the Atlantic).

Finally we compile the demographic history information of all otariids species for comparison, looking for common patterns associated with climate and anthropogenic causes. We used the mitochondrial DNA control region as the genetic marker because it is an hypervariable and rapidly evolving non-coding genetic region that have been extensively used in otariids in the last decade for the study of these topics (e.g. Goldsworthy et al. (2000) for the Juan Fernández fur seal; Wynen et al. (2000) for the Antarctic and Subantarctic fur seal; Weber et al. (2004) for the Guadalupe fur seal; Matthee et al. (2006) for the South African fur seal; Hoffman et al. (2006) and Harlin-Cognato et al. (2006) for the steller sea lion; Pinski et al. (2010) and Dickerson et al. (2010) for Northern fur seal; Schramm et al. (2009) for the California and Galápagos sea lions; Lancaster et al. (2010) for the Australian fur seal; and Freilich (2004), Túnez et al. (2010) and Feijoo et al. (2011) for the Atlantic distribution of the South American sea lion).

7.2.- METHODS

7.2.1.- Study area and samples collection

Tissues samples from 72 individuals of Southern sea lion were collected from 21 colonies distributed along the entire Chilean coast (Figure 1). Sampling was performed by a remote biopsy system, between January and February 2008 and December and February 2009 (breeding season).

A biopsy dart was thrown by a crossbow from either land or boat (Figures 2, 3a, 3b), from a distance of 8 – 15 m (Figures 3c, 3d). Both the bow and the biopsy dart have a modified design for sampling sea lions, based on Hoberecht (2006) and Cuadron et al (2007). As can be seen at the pictures, the retractile system consists of a fishing reel attached to the crossbow (with minimum friction) and a strong and thin fiber wire strapped to the upper edge of the dart. The dart has a removable stainless steel tip, specially designed to penetrate the dense skin of these animals (Figure 2). This tip extracts a tissue sample (5 mm diameter and 1 cm deep) and rooted hair. The skin and hair gets trapped on the penetration stop, which has tanglefoot glue used in mouse traps (Figure 3e). With the remote biopsy system we obtained samples from adult males and females. We also collected tissue samples from dead individuals found on shore and dead pups found floating on water. The samples were preserved in 96% alcohol for subsequent genetic analysis. The dart tips were then washed, disinfected with chlorine and boiled for reused.

7.2.2.- DNA extraction, PCR analysis and sequencing

DNA from tissue samples was extracted using the DNeasy Blood and Tissue Kit (QIAGEN) according to manufacturer's protocol. A ~550-bp fragment of the *mt*DNA control region (D-loop) was amplified by the polymerase chain reaction (PCR) using the primers L15926 (5'-TCAAAGCTTACACCAGTCTTGTAAACC-3') (Kocher et al. 1989) and CCR-DR1 (5'- CTGTGACCATTGACTGAATAGC-3')(Tchaicka et al. 2007). PCRs were carried out in a 50 ml volume containing 4 ml of DNA (~60 ng), 1x reaction buffer, 1.5 mM of $MgCl_2$, 200 mM of each dNTP, 0.4 mM of each primer, and 1 unit of Taq DNA polymerase Platinum (Invitrogen). The PCR protocol was as follows: 10 min at 95°C, a touchdown of 95°C for 15 s, 60–50°C for 30 s, 72°C for 45 s, with 2 cycles at each annealing temperature, and 35 amplification cycles of 95°C for 15 s, 50°C for 30 s, 72°C for 45 s, followed by a final extension period of 30 min at 72°C. PCR product was checked with a 0.8% agarose gel electrophoresis, visualized with ethidium bromide, purified using QIAquick PCR purification Kit (QIAGEN), and sequenced by Macrogen Inc. (Seoul, South Korea). All samples were sequenced at least once in both directions. All *O. flavescens* D-loop haplotype sequences have been deposited in the GenBank database under accession numbers JQ434428 to JQ434457.

7.2.3.- Data Analysis

The *mt*DNA D-loop sequences were aligned, and mutations were confirmed by eye, according to the chromatogram using Proseq v3.0 (Filatov 2002). All sequences were realigned using ClustalX v2.012 (Thompson et al. 1997). The Chilean sequence were aligned with 10 D-loop haplotypes (from 49 individual samples) available on Genebank (GI:299033272-299033281) from Túnez el al (2010), for a total of 121 sequences of 453 bp for genealogy and divergence analysis.

We used Bayesian Inference (BI) methods implemented in the software MrBayes v3.1.2 (Huelsenbeck and Ronquist, 2001) to reconstruct the genealogy of the *O. flavescens* linages, using *C. ursinus* as outgroup. BI was performed using the general type of the best-fit model parameters defined for the data set, in which 4 independent analyses were run with 4 chains each, for 6 million generations and then sampled at intervals of 1000 generations. The first 25% of sampled trees were discarded to ensure stabilization and the remaining used to compute a consensus tree. For this coalescent based genealogy reconstruction, we used the model of DNA evolution estimated with MODELTEST v3.06 (Posada and Crandall, 1998), via the Akaike information criterion (AIC). The most appropriate model of DNA evolution for the sequences was GTR+G+I .

The Genealogy was visualized in TreeView (Page, 1996) and edited using the software Dendroscope (Huson et al. 2007). We also examined the relationships between Chilean and Argentinean haplotypes by constructing a median-joining network (MJN) using the software Network v4 (Bandelt et al. 1999).

Bayesian estimation of divergence times was performed using BEAST v1.5.4

(Drummond & Rambaut, 2007) for the 121 D-loop sequences from Chile and Argentina. We assumed the GTR+G+I mutational model and a strict clock. Following Ho et al. (2005, 2007) for the time dependency of molecular mutation rate and an increase of the mutation rate for calibrating times of less than 1 million years, we used a mutational rate of 0.2745 $*10^{-6}$ substitutions per site per year, estimated for the *mt*DNA control region of the Steller sea lion, *Eumetopias jubatus* (Phillips et al., 2009). Markov chains were run for 10.000.000 generations and sampled every 1000 generations with the first 1.000.000 generations discarded as burn-in. Three independent runs were performed and combined parameters estimated were visualized using Tracer v1.4 (Rambaut and Drummond 2007).

Nucleotide diversity (Nei, 1987) and haplotype diversity were estimated for Chilean samples using ARLEQUIN V3.1 (Excoffier et al., 2005). Tajima's *D* neutrality statistic (Tajima,1989) and Fu's *Fs* value (Fu, 1997) were calculated to detect deviations from a neutral Wright–Fisher model of mutation-drift equilibrium. Nucleotide mismatch frequency distributions (Rogers and Harpending, 1992; Rogers, 1995) were used to investigate historical demography in ARLEQUIN V3.1 (Excoffier et al., 2005). For this analysis, we employed the parametric bootstrapping to test the goodness of fit of the observed mismatch distribution to that expected under the sudden expansion model using the sum of squared deviations (SSD) statistic. A demographic expansion event in the recent past may result in a unimodal mismatch distribution (an excess of low pairwise nucleotide differences between sequences), while a multimodal distribution is encountered in populations at equilibrium.

Also, we used Bayesian skyline plots in BEAST v1.5.4 (Drummond et al., 2005) to estimate changes in Chilean common sea lion over time by providing highly parametric estimates of effective population size (N_e). With mtDNA sequence, this approach produces serial estimates of female effective population size (N_{ef}) from the time intervals between coalescent events, using a Markov chain Monte Carlo simulation approach to integrate over all credible genealogies, allowing to determine demographic changes between coalescent intervals. We assumed a generation time of 10 years (based in the average reproductive age, life time and evidence of senescence in otariids (Grau and Acuña, 1998; Beauplet et al., 2006; Boyd et al., 1999; Wickens and York, 1997). Skyline plots were generated for the 72 sequences of *mt*DNA control region using the program BEAST v1.5.4 (Drummond et al., 2005). We assumed the GTR+G+I mutational model and a strict clock with mutation rate of $2.745e^{-7}$ substitutions per year. Markov chains were run for 10.000.000 generations and sampled every 1000 generations with the first 1.000.000 generations discarded as burn-in. Three independent runs were performed for the Bayesian skyline plot analyses. Markov chain samples from the three independent analysis were combined and analyzed using Tracer v1.4 (Rambaut and Drummond, 2007) to produce the final Bayesian skyline plots.

7.3.- RESULTS

A total of 72 tissue samples from 21 colonies were successfully amplified for *mtDNA* control region (Figure 1). For the consensus region of 453 bases from the *mt*DNA control region, we found 28 different haplotypes for the 72 *O. flavescens* samples from Chile (Table 1) versus 10 haplotypes for the 49 sequences from Argentina. The genetic diversity for the Chilean clade is high (h = 0.98 ± 0.01) in relation to the postsealing genetic diversity of others species of sea lion (Wynen et al., 2000), but nucleotide diversity is low (π= 0.01 +/- 0.01). The *O. flavescens* phylogeny of 456 bp from the 38 *mt*DNA D-loop haplotypes shows two main different clades with 99% of posterior support (Figure 4). However, one Chilean haplotype belong to the Argentinean clade (Ot-28). This haplotype comes from a female from Punta Arenas, in the Strait of Magellan in contact to both the Pacific and the Atlantic oceans (Figure 1: the Southernmost sampled location in Chile).

For the constant population size coalescent model, the divergence time between the Chilean and the Argentinean clades was 79.828 ($CI_{95\%}$: 48.437 – 116.110) years before present; and with the expansion population model, the mean was 77.441 ($CI_{95\%}$: 46.456 – 111.930) yr. B.P.

The median-joining network (Figure 5) also shows the same two main clades, with distance between them higher than between haplotypes inside clades. Gene diversity within the Chilean clade was the highest, but with many haplotypes being in low frequencies. Tajima's *D* and Fu's *Fs* neutrality test confirm this pattern: Tajima's *D* = -1.40 (p= 0.07) and *Fs* = -7.20 (p = 0.01), demonstrating an excess of low frequency polymorphisms for the Chilean clade.

The mismatch distribution of the Chilean haplotypes follows a unimodal distribution, with $\tau = 3.28$ (Figure 6). The parameters values of the mismatch distribution show a good fit to the sudden expansion model, as shown by the Sum of squared deviation SSD= 0.00137 (p= 0.73, meaning that the null hypothesis of population expansion could not be rejected) and the Harpending's raggedness index of 0.01605, that shows non-significant deviation of the mismatch distribution from this demographic expansion model (p= 0.70). These results, together with the haplotype network and those of the neutrality tests, suggest that the Chilean clade experienced an expansion in relative recent evolutionary history. Assuming a mutation rate of $2.745*10^{-7}$ substitutions per site per year, and $\tau = 2\mu * t$, were μ=mutation rate* sequence length (Rogers and Harpending 1992; Rogers 1995; Excoffier 2004), we estimate the time of expansion at 13.189 yr. B.P.

This historic expansion is further confirmed by the Skyline plot for the Chilean clade (Figure 7), showing that 10.000 yr. B.P. there was already an expansion process that continued until today, without signature of recent bottleneck. With the mutational rate of $2.745*10^{-7}$ substitutions per site per year, the present female effective population size (N_{ef}) for the Chilean clade is estimated at 63.400 ($CI_{95\%}$: 10.000– 550.000) females.

7.4.- DISCUSION

7.4.1.- Pacific and Atlantic ESU

This work represents the first evidence that both phylogeographic clades of *O. flavescens* are divergent, not sharing haplotypes between the Atlantic and the Pacific distribution of the species, but revealing the presence of mixed populations in the contact zone (Magellan Strait, in southern Chile). Although we only analyzed two sequences from Magellan Strait, due to the extreme climatic conditions at the period we sampled, one of those samples was from the Argentinean clade and the other from the Chilean clade. Therefore, the Magellan Strait, that connects both oceans, seems to represent a mixing zone of both genetic clades.

This result is relevant for conservation and management propose for the species, because each clade has unique genetic diversity that influence in the future adaptations of the species to a changing environment (Oyler-McCance and Leberg 2005). Those unique genetic variation must be preserved to avoid possible future population collapse, because of the effect of rapid climate change (Oyler-McCance and Leberg 2005, Oliveira et al. 2012).

The differentiation in an Atlantic clade and a Pacific clade is also hypothesized for *Arctocephalus australis*, that also present a phylogeographic divergence between the Argentinean and Uruguayan populations with the Peruvian populations (Túnez et al., 2007; Oliveira et a., 2008). This species is completely absent in central Chile between latitudes 40° and 20° South (Sielfeld, 1999), suggesting that it could also be divided in two different genetic clades in the Pacific Coast. This scenario is also observed for the marine otter, *Lontra felina* (Vianna et al. 2010), explained by the progress of the colonization process.

We estimated the divergence time between the Pacific and Atlantic clades of *O. flavescens* in 80.000 yr. B.P. The relatively rapid mutation rate of the *mt*DNA control region may produce homoplasy, and therefore underestimate the divergence time (Hartl and Clark, 2007). Also, the small sample size may affect the estimation. However, this estimated divergence time is consistent with particular climate conditions between 60.000 – 100.000 years ago, during the Last Glacial Period (Jouzel et al., 2007). At that time, Patagonia was covered by ice (Jouzel et al. 2007) and possible the Magellan Strait not exist or was to small for connecting population of both oceans. Also, at that time, paleoceanographic records show a latitudinal shift of the dominant atmospheric and oceanographic currents along the Chilean coast, with periods of an equator-ward shift of the northern margin of the Antarctic Circumpolar Current (ACC) off Chile. The ACC originate from Antarctica and the surrounding Southern Ocean, and divided in the Humboldt Current and Cape Horn Current (which go through the Strait of Magellan, connecting the Pacific and Atlantic Oceans (Lamy et al., 1998 and 2000). The northward shift of the ACC may influence the circulation pattern of the Cape Horn Current. The shift in ocean circulations had recorded changes in the distribution of primary productivity (Marchant et al., 2007) and hence in the distribution of marine predators (Le Boeuf and Crocker, 2005). In that regard, it is expected first, that the northward shift of the ACC may affect the Southern sea lion's prey distribution and hence, the species distribution and foraging behavior. This because Southern sea lion seems to present fidelity to a movement area around the colony (Thompson et al. 1998, Riet-Sapriza et al. 2012, Rodríguez et al. 2012), associated with prey abundance distribution (Thompson et al. 1998). Secondly, ice covered of Patagonia prevents colonies formation in this area, separating populations of both sites of South America.

7.4.2.- Chilean demographic history

The Southern sea lion in Chile present an haplotype diversity of 0.98, that could be underestimated by the small sample size. But, compared to the others otariids species (see Table 2) and with the marine mammals in general (see Oliveira et al. 2012), this value is high and consistent with most otariids, particularly with the Atlantic populations of the species. The high genetic diversity in the Pacific distribution of the species, is probably due to the presence of many low frequency alleles, because of the probable demographic expansion since glaciations. The high genetic diversity was possibly maintained, despite high sealing pressure, by the existence of colonies of difficult access for sealing together with high dispersion rate between colonies.

High genetic diversity allows population effective size (N_e) to be relative high. But, on the other hand and as seen in the haplotype network (Fig. 6), the Southern sea lion has not haplotypes of high frequency, indicating that the species is susceptible to climate and anthropogenic impacts, because negative effects would decrease haplotype diversity, affecting the N_e in a negative manner. This two contrasting scenarios that affect the N_e in opposite directions, could produce fluctuations in the historical N_e of the species. Although, the skyline plot shows no fluctuations and instead it shows a continue but smooth demographic grow. It is possible that climate and anthropogenic effects produced intermittent value between N_e in bad moments and N_e in recovery moments, but negative events may be not long enough to reduce effective population size and thus increase genetic drift to a point where the period of recovery could not balance.

On the whole, results show that the South American sea lion experienced demographic expansion in Chile (~12.000 yr. B.P.) without signs of a glacial genetic bottleneck. The small sample size makes this results imprecise, due to the underestimation of haplotype frequency and haplotype diversity. Despite that, interestingly, similar results were found for the Atlantic clade (Túnez et al., 2010; Feijoo et al., 2011) and many others otariids species. The demographic expansion and the date of expansion is also consistent with evidences for other aquatic species in Southern Chile, such as the marine gastropod (Cárdenas et al. 2009), the jumbo squid (Ibáñez et al. 2011), and also for some fresh water fish species (e.g. *Galaxias platei*, Ruzzante et al., 2008).

This general pattern evidences the relationship between population expansion and the occurrence of certain climatic conditions and is consistent with the events associated with the end of the Last Glacial Maximum (LGM) and the beginning of the present interglacial period. Throughout the Last Glacial Maximum (LGM, 23 000–17 000 yr. B.P.) an ice sheet covered southern Chile from 56 to 35°S in the Andes Mountains and to 41°S in the lowlands and at sea level (McCulloch et al. 2000). After that, at the Late Glacial Maximun (13.000 – 10.000 years before present), the Patagonian Ice sheet began to retract and several changes in oceanographic conditions also began. The major large-scale control of palaeocenographic changes off Chile is related to latitudinal shifts of the northern margin of the ACC (Marchant et al., 2007). Between T1 (19.000-12.000 yr. B.P.) and Early Holocene (12.000-7.000 yr. B.P.), with the poleward shift of the ACC northern margin, the subtropical high-pressure system became the dominant atmospheric component off Chile and caused surface water productivity to increase through an enhanced upwelling system (Romero et al., 2006), allowing higher trophic level to increase (Le Boeuf and Crocker, 2005). In that sense, it is possible that recent demographic disturbances, like severe sealing and ENSO events, had not been serious problems in the species history in relation to major post-glaciation events.

The time of expansion for *O. flavescens* in Chile is consistent with the results obtained for the species in the South Argentina and the Malvinas Islands, when the time of expansion is estimated by the same mutation rate (μ=2.745^{-7}). The other Southwest American marine mammal for which there are registers, the marine otter *Lontra felina* seems not to experienced any recent population expansion (Vianna et al. 2010). Despite this, those authors found that this marine otter conform two genetic clades in its Pacific distribution, one from Peru and the other from Chile, and that this species had experienced a recent southward colonization from the north. For *L. felina*, the high divergence observed in the northern lineages fits the hypothesis of an ancient distribution in this region, and the low diversity and divergence, together with the high isolation pattern in the South strongly supports the hypothesis of the recent colonization toward the south. Glacial cycles generally result in species range contractions into lower latitudes followed by range expansions during interglacial periods (Hewitt 1996, 2000, 2004). But, for the marine otter, if the southward colonization process is post-glacial, following ice sheet retreat, is unknown. This because the southernmost haplotypes diverged from the central-south ones approximately 35000 years ago (predated the LGM at 23-17000 years ago). In contrast to *L. felina* and despite the evidence of demographic expansion for the Southern sea lion, the phylogeny and the geographic distributions of the Chilean haplotypes did not show any pattern of geographic colonization, suggesting high gene flow.

For *O. flavescens*, the expansion process is best explained by the existence of multiple refuges instead of a southward recolonization process. This because, as seen in Figure 1,4 and 5, haplotypes from southern Chile not derived from any haplotype or group of haplotypes from the north, and instead, populations from both Chilean zones shared only few haplotypes.

7.4.3.- General pattern in otariids

The demographic genetic status of otariids, including all information currently available, is summarized in Table 2. The only two species (The Guadalupe fur seal, *Arctocephalus townsendi* and the northern fur seal, *Callorhinus ursinus*) for which the pre-sealing molecular diversity is determined show different patterns. The Guadalupe fur seal shows decrease in haplotype and nucleotide diversities, meaning that the species experienced loss of haplotypes with sealing, thus corroborating a population bottleneck effect (Weber et al., 2004). In the case of the northern fur seal, despite the evidence of a genetic bottleneck due to sealing, the species did not lose molecular diversity (Pinsky et al., 2010). Both species are constituted by only one genetic clade within their geographic distributions (Weber et al., 2004; Dickerson et al., 2010) and show high gene flow between colonies (Weber et al., 2004; Pinsky et al., 2010), permitting to assume that for both species gene flow mitigates the loss of molecular diversity. Those two species differentiate each other in their geographic distribution. The Northern fur seal is distributed along the northernmost area of the North Pacific Ocean, where the extreme climatic conditions prevent the easy access to hunters (Pinsky et al., 2010). Instead of that, the distribution of the Guadalupe fur seal is restricted to the Guadalupe Island and the Pacific coast of Mexico, where the sealing activity was very intense and the species was almost extinct (Townsend, 1916, 1931; Bartholomew, 1950; Hubbs 1956). The Guadalupe fur seal increased its size in the last decades, but it is the otariid with the smallest population size today (Weber et al., 2004). In general, the otariids for which the actual molecular diversity was estimated, show similar high haplotype diversity and relatively low nucleotide diversity. Also most of them did not show a genetic bottleneck due to sealing. Of the 23 otariids species, 14 did not present a recent genetic bottleneck, 5 species showed genetic bottleneck due to sealing, and in four species genetic bottleneck have not yet been investigate. The 5 bottlenecked species are: the Guadalupe, the Northern, the South American and the Antarctic fur seals and the New Zealand sea lion. In the case of the South American fur seal, *A. autralis*, the genetic bottleneck seems to have been not very strong in its Peruvian population (Oliveira et al., 2009), however, there is an absence of information for the remaining species distribution. The Antarctic fur seal (*A. gazella*) was also almost extinct, with an estimated bottleneck population size of 30 females for the largest population (Hoffman et al., 2011). Contrary to the Guadalupe fur seal, the Antarctic fur seal, have been recovery with an extremely rapid increase since 1950, with an estimation population size of 3 million for 1999 (Hoffman et al., 2011).

The low genetic bottleneck detection in otariids, despite the known demographic bottleneck for those species, could be due the present of an excess of rare haplotypes closely related to one another (high haplotype diversity and low nucleotide diversity) that characterize a demographic expansion (Tajima, 1989; Rogers and Harpending, 1992), together with the absent of pre-sealing genetic diversity estimations. As can be seen in Table 2, demographic expansions seem to dominate the historical dynamics of many otariids species, despite this process occurred at different geologic times between otariid species and is estimated by different mutation rates (Table 2).

In summary, comparing the genetic patterns of species in pre and post-sealing conditions suggest that species with high gene flow experienced different genetics effects due to the indiscriminate sealing. Colonies of difficult access may have acted as possible refuges for recolonization. Also, the high levels of gene flow that seem to have experienced most otariids species (except for *Neophoca cinerea* that has extreme philopatric behavior (Campbell et al., 2008)), together with the existence of historical demographic expansions in most of them, may have reduced the genetic effects that could have been produced by the severe sealing. In the particular case of *O. flavescens* in Chile, those factors acting together may have contributed to the maintenance of the effective populations size (N_{ef} ~ 10.000 – 1.000.000 individuals) well above the minimum viable levels of N_e (~ 1.800 individuals) for vertebrates, as estimated by Reed et al. (2003) for 102 vertebrate species including some pinnipeds species. Despite that, confidence intervals of the N_e estimation are very high, affecting the accuracy of the parameter estimations.

The geographical distribution of otariids is associate with the cold Wind-Driven Surface Currents of the South hemisphere and of the North Pacific Ocean (Thurman and Burton, 2001). These currents are associated with the subtropical high-pressure system, that in the Early Holocene became the dominant atmospheric component and cause surface water productivity to increase through enhanced upwelling (Mohtadi et al., 2004; Romero et al., 2006; Marchant et al., 2007; Koutavas, 2006). The evident dependence on climatic conditions of otariids demography, largely related to marine productivity, anticipate possible future demographic declines for *O. flavescens*, if El Niño events, which have negative effects on otariid population sizes (Trillmich et al, 1991; Sielfeld and Guzmán, 1999; Oliveira et al. 2009; Le Boeuf and Crocker, 2005) become more frequent and intense as has been the tendency in the 80s and 90s compared with the previous three decades (Koutavas, 2006; Garreaud et al., 2009). This tendency is very important for management purposes of those species, moreover considering that ENSO plays the mayor role determining the interannual climate variability in most regions of South America (Garreaud et al., 2008). Garreaud et al. (2009) also exposed that the prominent “climate shift” is also caused by the change in polarity of the Pacific Decadal Oscillation (PDO), a long-lived pattern of Pacific climate variability, around the mid-70s (from cold to warm). The PDO is described as ENSO-like, because its warm and cold phase has strong resemblance with those of El Niño and La Niña, respectively. Andreoli and Kayano (2005) considered as a low-frequency modulator of the ENSO-related variability, been a “constructive interference”, incrementing the intense of ENSO.

7.5.- BIBLIOGRAPHY

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7.6.- TABLES AND FIGURES

Table 1: Frequency and relative position of variable nucleotides of the 28 *mt*DNA control region haplotypes found in the 72 *O. flavescens* sequences from Chile and in 10 haplotypes from Argentina used for the genealogy analysis.

Table 2: Phylogeographic, demographic and genetic information available for the species in the Family Otariidae. a, Oliveira et al (2008); b, Oliveira et al. (2009); c, Túnez et al. (2007); d, Feijoo et al. (2011); e, Freilich (2004); f, Artico et al. (2010); g, Túnez et al. (2010); h, this work; I, unpublished data; j, Dickerson et al. (2010); k, Pinsky et al. (2010); L, Wynen et al. (2000); m, Harlin-Cognato et al. (2006); n, Hoffman et al. (2009); o, Hoffman et al. (2006); p, Phillips et al. (2009); q, Campbell et al. (2008); r, Campbell (2006); s, Gonzáles-Suárez et al. (2009); t, Schramm et al. (2009); u, Matthee et al. (2006); v, Lancaster et al. (2010); w, Lento et al. (1997); x, Goldsworthy et al. (2000); y, Wolf et al. (2007); z, Weber et al. (2004); A, Osborne (2011); B, Hoffman et al. (2011).

Figure 1: Map of Chile showing the location of samples and sample size.

Figure 2: Biopsy dart design.

Figure 3 (a): Nicolás Zalaquett in a boat shooting a biopsy dart to a swimming sea lion. The crossbow design is shown, with the fishing reel set. Arica, northern Chile. Photo by Leonardo de la Barra.

Figure 3 (b): Nicolás Zalaquett in a boat shooting a biopsy dart to a sea lion resting in the breeding colony of Punta Lobos - Arica, northern Chile. Photo by Leonardo de la Barra.

Figure 3 (c): Shoot of a biopsy dart to a female sea lion in the breeding colony of Punta Lobos - Arica, northern Chile. Photos by Leonardo de la Barra.

Figure 3 (d): Male sea lion with a biopsy dart. Resting colony Pan de Azúcar, northern Chile. Photo by Tomás Rock.

Figure 3 (e): Sea lion tissue and hair sample obtained with the biopsy system.

Figure 4: Phylogeny of *Otaria flavescens* from Chile and Patagonia Argentina. Bayesian phylogenetic analysis of 453 length sequences of *mt*DNA control region from 121 individuals. *Callorhinus ursinus* is the outgroup. Labeled haplotypes are from Argentina (Ot-A to Ot-J) and haplotypes and numbered ones are from Chile (Ot-01 to Ot-28). Numbers on the genealogy are posterior support values.

Figure 5: Median-joining network of *Otaria flavescens* haplotypes observed in Chile and Argentina. Analysis of 453 length sequences of *mt*DNA control region from 121 individuals. The node size represent the relative haplotype frequency and the length of the edges the number of mutations between haplotypes. Chilean haplotypes are in black and Argentinean haplotypes are in gray. Unfilled nodes are intermediate non-sampled haplotypes..

Figure 6: Mismatch distribution for the Chilean haplotypes of *Otaria flavescens* (bars in black) compared with the distribution expected by the sudden expansion model (line in red). Analysis of 453 length sequences of *mt*DNA control region from 71 individuals from the clade of Chile (the haplotype Ot28 is not included).

Figure 7 Bayesian skyline plot for the *mt*DNA control region sequences from the Chilean clade (27 haplotypes, 453 bp). Thick lines corresponds to the median N_{ef} with its 95% CI indicated by the light gray lines. The calculated N_{ef} assumes a generation time of 10 years.

Table 1

control region haplotypes	Relative position of variable nucleotides 10 20 30 40 * * * *	N
Ot01	TTCTTTT-CCGGTAAAACACAATCGTGTCGCCCGCGGTAGTTTG	14
Ot02	.......-..........G...................G.....	10
Ot03	.......-......G.......................G.....	6
Ot04	.......-............G.......TA..............	6
Ot05	.......--...................................	4
Ot06	.......-................A.A.T....A..........	3
Ot07	......--..........G...................G.....	3
Ot08	.......-.......G................T.TA........	2
Ot09	.......-..A.........G.......TA..............	2
Ot10	.....C.-..A.................................	1
Ot11	.......-..............................G.....	1
Ot12	.......T..A...........................G.....	1
Ot13	.......-..........G.G.................G.....	1
Ot14	.......-................A...................	1
Ot15	.......-............G.......................	1
Ot16	.....C.-..A.........................A.......	1
Ot17	.......-.......G...............T...A.....C..	1
Ot18	.......-............G.................G.....	1
Ot19	C......-.TA.................................	1
Ot20	.......-................................C...	1
Ot21	.......-.................................C..	1
Ot22	.......-...A................................	1
Ot23	....C..-........G.......A.A.T..........A....	1
Ot24	.C.....-............G.......T............C..	1
Ot25	.C.....-............G.......T...............	2
Ot26	.......-............G.......T...............	2
Ot27	.......-.........................A..........	2
Ot28	..TC..---........T....CTACA..............CCA	1
Ot_J	..TC..---...G.G.......CTACA..............CC.	
Ot_I	..TC..---.....G......GCTACA...TT.A.......CC.	
Ot_H	..TC..---...G.G....T.GCTACA...TT.A.......CC.	
Ot_G	..TC..---.....G.......CTACA......A.......CC.	
Ot_F	..TC..---....GG....A..CTACAC.....A....G..CC.	
Ot_E	..TC..---.....G.......CTACA..........AG..CC.	
Ot_D	..TC..---...........G.CTACA...........G..CC.	
Ot_C	..TC..---.....G.......CTACA...........G..CC.	
Ot_B	..TC..---.....G....T.GCTACA...TT.A.......CC.	
Ot_A	..TC..---.....G.......CTACA..............CC.	

Table 2

Scientific name	Common name	Genetic markers (N,bp or # loci)	ESU	Distribution	Historical Demographic Dynamic	Pre-sealing (D-loop)		Post-sealing (D-loop)		Recent genetic bottleneck
						Haplotype Diversity	Nucleotide Diversity	Haplotype Diversity	Nucleotide Diversity	
A. tropicalis	Subantarctic fur seal	D-loop(103,316)[L]	1[L]	Islands at the south of Antarctic Polar Front	-	-	-	-	0.048[L]	-
A. gazella	Antarctic fur seal	D-loop(145-246,316-263)[L,B], microsatellite(246,21)[B]	1[L]	Islands at the north of the Antarctic Polar Front	No historial expansion[B]	-	-	-	0.032[L]	Yes [B]
A. pusillus	Cape fur seal and Australian fur seal	D-loop(118-106,344-361)[v,u], cytB(42,)[w], microsatellite (183,5)[v]	2[w,u]	South-West Africa	Expansion:~18.000–37.000 ybp($\mu=5.8^{-7}$)[u]; expansion:~26.000 ybp($\mu=2.745^{-7}$), estimated from mismatch in u	-	-	0.975[u]	0.011[u]	No[u]
				South-East Australia	Expansion[v]	-	-	0.820[v]	0.007[v]	No[v]
A. australis	South American fur seal	CytB (15,445)[c], microsatellite (226,7)[a,b]	2[a,c]	South East Atlantic (Argentina –Uruguay, Falkland Is.)	-	-	-	-	-	No[b]
				South West Pacific(South Chile and North Chile-Perú)	-	-	-	-	-	Yes(not strong)[b]
A. phillippii	Juan Fernandez fur seal	D-loop(28,315)[x]	1[x]	Juan Fernández Island in Chile (pacific coast)[x]	Stationary, not sings historical population expansion[x]	-	-	0.905[x]	0.030[x]	No[x]
A. fosteri	New Zealand fur seal	CytB(56,)[w]	2[w]	South Island of New Zealand	-	-	-	-	-	-
				South-West Australia	-	-	-	-	-	-
A. galapagoensis	Galápagos fur seal	-	-	West coast of the Archipelago Galápagos	-	-	-	-	-	-
Zalophus wollebaeki	Galápagos sea lion	D-loop+cytB(336,1123), microsatellite(1323,25)[y]	1[y]	Archipelago Galápagos	-	-	-	-	-	No[y]
A. townsendi	Guadalupe fur seal	D-loop(33,181)[z]	1[z]	Isla Guadalupe, Mexico (east pacific ocean)[z]	Historical expansion in the pre-bottleneck population, that changed to a bottleneck demographic state after harvest[z]	0.997[z]	0.055[z]	0.798[z]	0.025[z]	Yes[z]
Callorhinus ursinus	Northern fur seal	D-loop(414-619,157-375)[j,k], microsatellite (619,7)[j]	1[j]	Sea of Okhotsk,Bering Sea,North Pacific Ocean (north of 34°N)	Expansion:~11.000ybp and Bottleneck: ~2.000ybp until now ($\mu=5.8^{-8}$)[j]; expansion:~23.000 ybp($\mu=2.745^{-7}$), estimated from mismatch in j	0.989[k]	0.048[k]	0.989[k] – 0.994[j]	0.024[j] - 0.048[k]	Yes[j], 50% population reduction[k]
Zalophus californianus	California sea lion	D-loop(299-355,355-550)[s,t]	1[s,t]	North-East Pacific Ocean	Stationary, not signs of expansion or retract[t]	-	-	0.880[t]	0.009[t]	No[t]
Phocarctos hookeri	New Zealand sea lion	Microsatellite(1351,21)[A]	1[A]	New Zealand coast	-	-	-	-	-	Possible yes[A]
Otaria flavescens	South American sea lion	D-loop(49-115,266-750)[d,e,f,g,h], cytB(49,445)[c], microsatellite (60-63,8-13)[d,i]	2[c,d,e,f,g,h]	South East Atlantic(Argentina–Uruguay,Falkland Is.)	Expansion only in 42-47°S (Argentina):~27.000 ybp[c,d] and for the Falkland Is.: ~12.000 ($\mu=2.745^{-7}$)	-	-	0.841 – 0.987[d,e]	0.008 – 0.210[d,e]	No[d]
				South West Pacific(Chile–Perú)	Expansion ~11.500ybp ($\mu=2.745^{-7}$)[h]	-	-	0.980[h]	0.010[h]	No[h,i]
Neophoca cinerea	Australian Sea lion	D-loop(149,360)[q], microsatellite(149,5)[r]	3[q,r]	West coast Australia	South and West ESU divergence ~130.000 - 190.000 ybp ($m=7.5^{-8}$)[r]	-	-	0.900[r]	0.016[r]	No[r]
				South-West Australia						No[r]
				South Australia						No[r]
Eumetopias jubatus	Steller sea lion	AFLP(285,238)[n],D-loop+cytB(336,1378)[m], D-loop(1131-1559,238)[n,p], microsatelitte(700,13)[o,n], CytB(1131,1140)[p]	2[o,p]	Sea of Okhotsk,Kuril Islands	Several retract and spatial expansion: ~60.000 -180.000 ybp ($m=1.7^{-7}$)[p]	-	-	0.890[m]	0.180[m]	No[n]
				Mixed zone:Berin Sea,Eleutian Islands,Alaska		-	-			No[n]
				North-East Pacific Ocean (north of 30°N)		-	-			No[n]

Figure 1

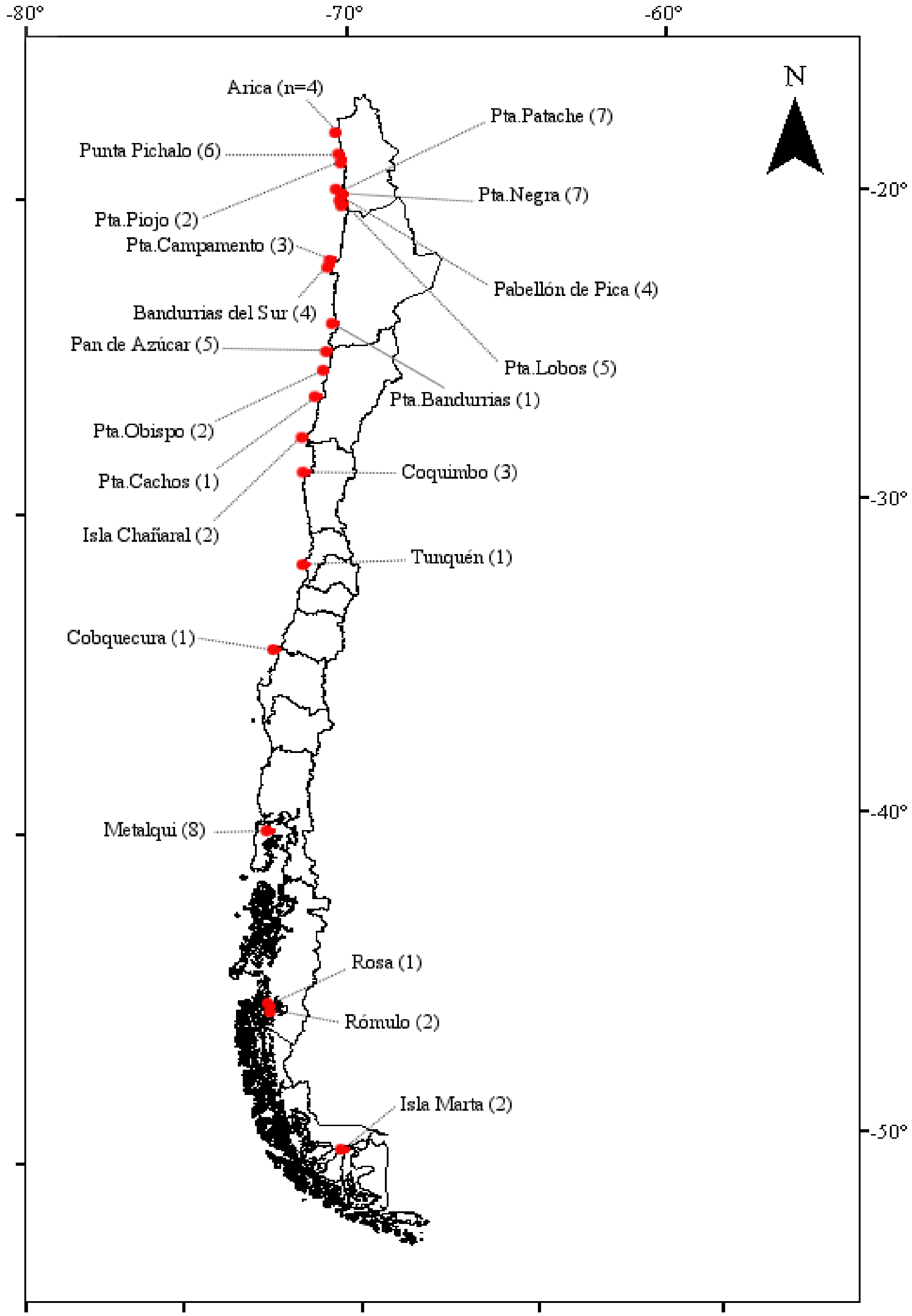
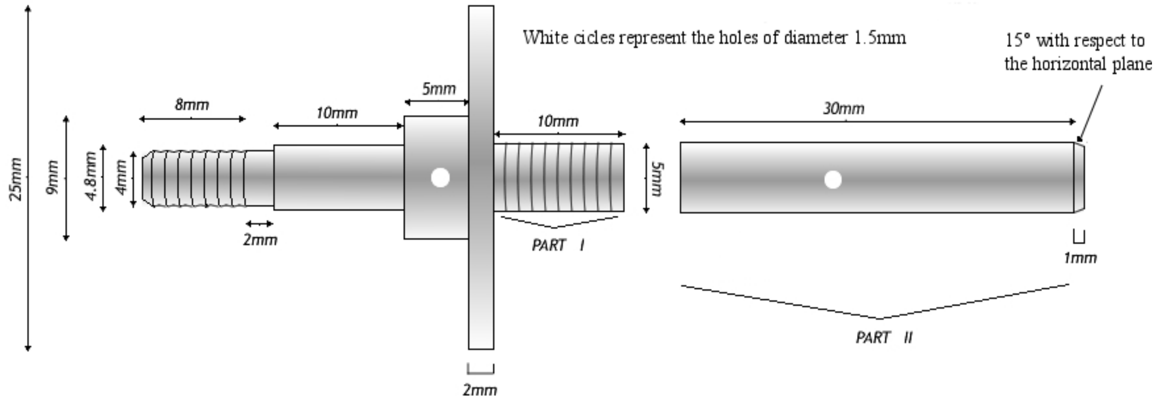

-80°
-70°
-60°
N
-20°
-30°
-40°
-50°
Arica (n=4)
Punta Pichalo (6)
Pta.Patache (7)
Pta.Negra (7)
Pta.Piojo (2)
Pta.Campamento (3)
Pabellón de Pica (4)
Bandurrias del Sur (4)
Pan de Azúcar (5)
Pta.Lobos (5)
Pta.Bandurrias (1)
Pta.Obispo (2)
Pta.Cachos (1)
Coquimbo (3)
Isla Chañaral (2)
Tunquén (1)
Cobquecura (1)
Metalqui (8)
Rosa (1)
Rómulo (2)
Isla Marta (2)

Figure 2


White cicles represent the holes of diameter 1.5mm

15° with respect to the horizontal plane

FRONTAL VIEW PART I

Small hole of diameter 2.5mm and depth 5mm

FRONTAL VIEW PART II

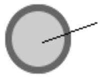

The tube is hollow with a thick of 1mm

Figure 3

(a)

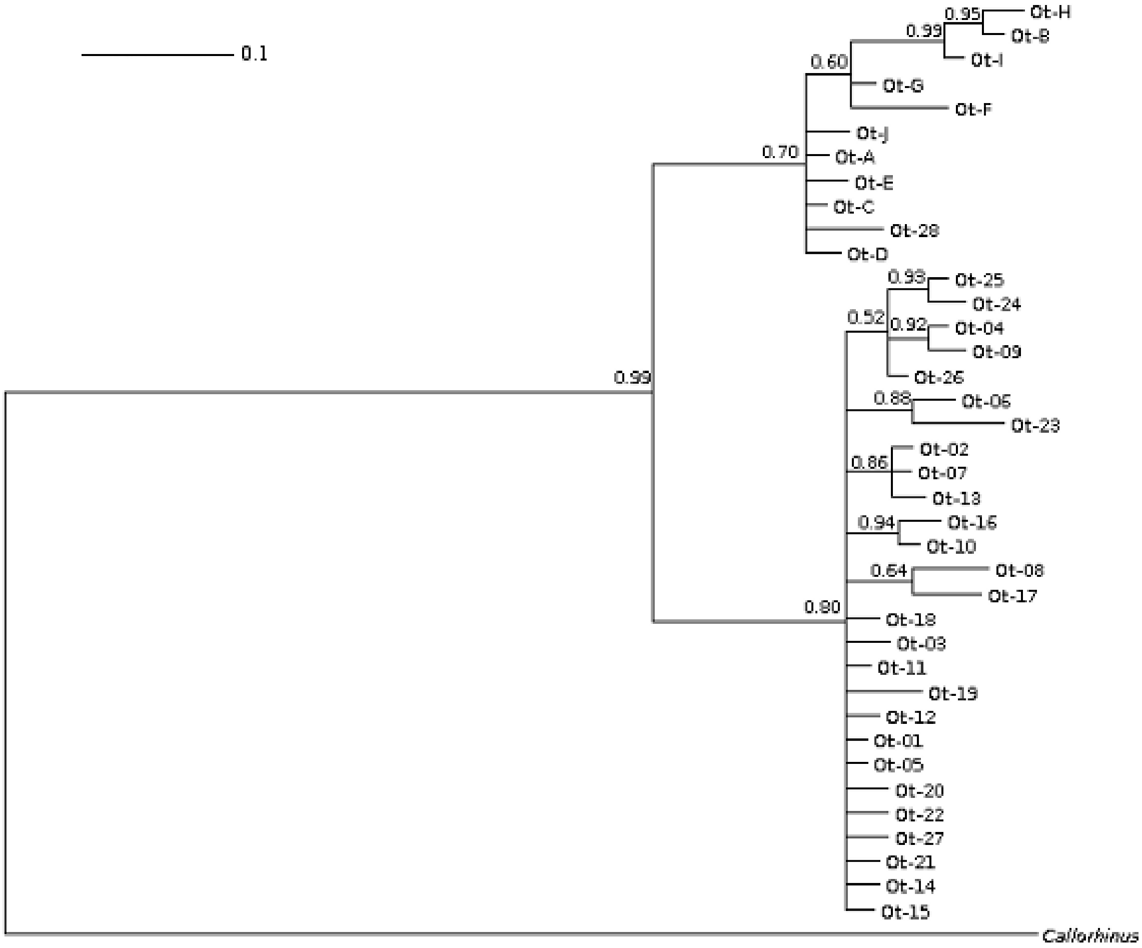
(b)

(c)

(d)

(e)

Figure 4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0.95
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0.60
0.70
0.99
0.93
0.52
0.92
0.88
0.86
0.94
0.64
0.80
Ot-H
Ot-B
Ot-I
Ot-G
Ot-F
Ot-J
Ot-A
Ot-E
Ot-C
Ot-28
Ot-D
Ot-25
Ot-24
Ot-04
Ot-09
Ot-26
Ot-06
Ot-23
Ot-02
Ot-07
Ot-13
Ot-16
Ot-10
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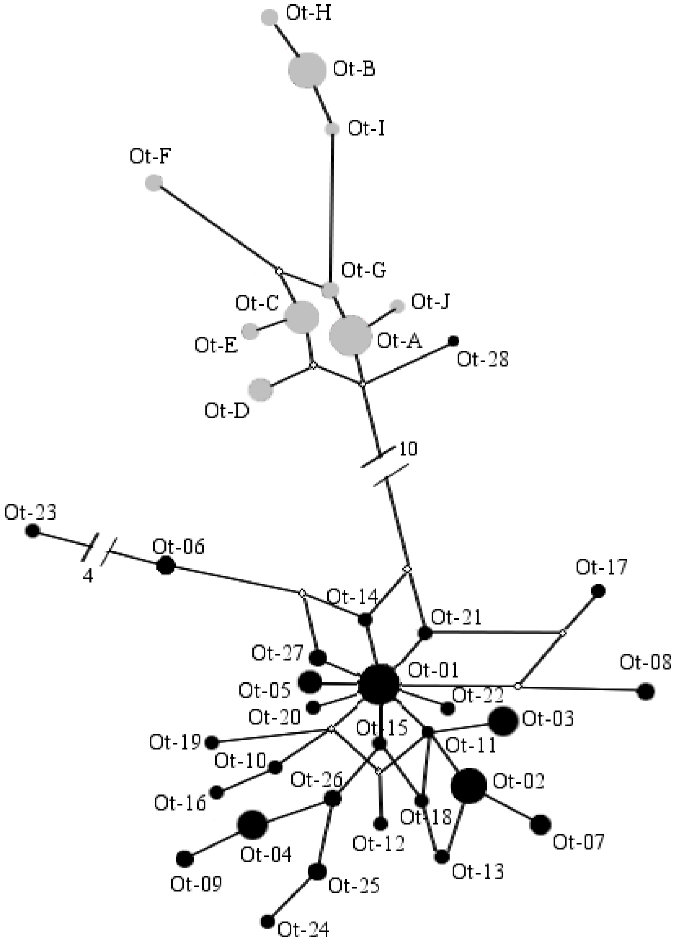
Ot-18
Ot-03
Ot-11
Ot-19
Ot-12
Ot-01
Ot-05
Ot-20
Ot-22
Ot-27
Ot-21
Ot-14
Ot-15
Callorhinus

Figure 5


Ot-H
Ot-B
Ot-I
Ot-F
Ot-G
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Ot-E
Ot-A
Ot-28
Ot-D
10
Ot-23
Ot-06
4
Ot-17
Ot-14
Ot-21
Ot-08
Ot-27
Ot-01
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Ot-20
Ot-03
Ot-15
Ot-19
Ot-11
Ot-10
Ot-26
Ot-02
Ot-16
Ot-18
Ot-04
Ot-12
Ot-07
Ot-13
Ot-09
Ot-25
Ot-24

Figure 6

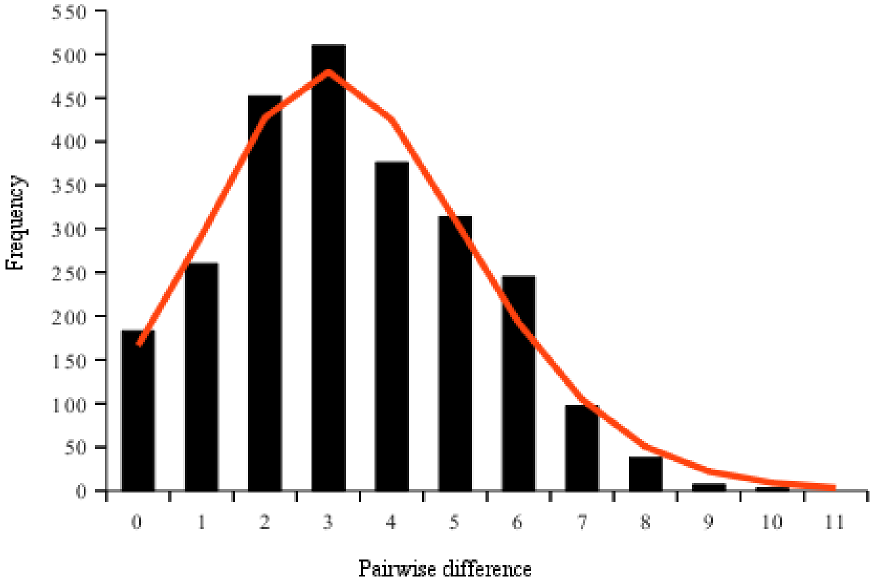
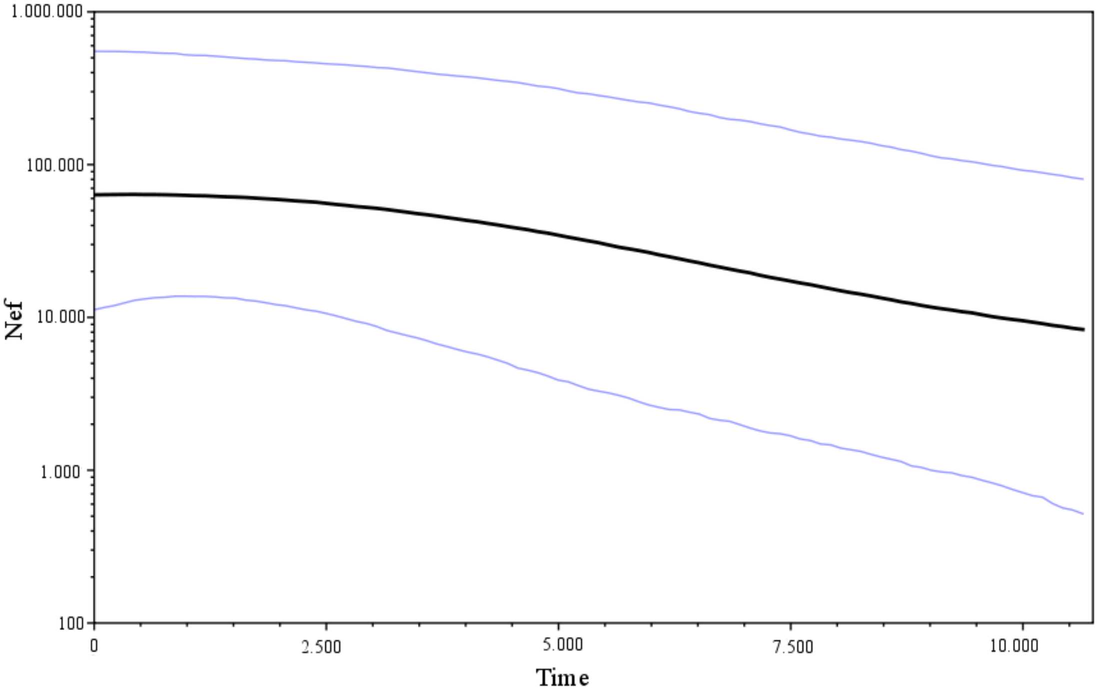

550
500
450
400
350
300
250
200
150
100
50
0
Frequency
0
1
2
3
4
5
6
7
8
9
10
11
Pairwise difference

Figure 7


1.000.000
100.000
10.000
1.000
100
Nef
0
2.500
5.000
7.500
10.000
Time

8.- CAPÍTULO II

Estructuración poblacional y efectos genéticos de la cacería y eventos ENSO en el lobo marino Suramericano, *Otaria flavescens*, en Chile

Population structure and genetic effects of sealing and ENSO events in the South American sea lion, *Otaria flavescens*, in Chile

8.1.- INTRODUCTION

Pinnipeds (seals and sea lions) were considerably reduced by sealers during the 18th and 19th centuries (Bonner and Laws 1964; Lotze and Worm 2009). Most species that suffered from severe historical population declines and local extinctions, however, have recovered after protection (Lotze and Worm 2009; Wickens and York 1997). And although at present many species of otariids reach high abundances, threats associated with accidental mortality and pollution are still a concern, and for at least half of the marine mammal species in the world (IUCN, 2008) harvesting is a major concern. It has been suggested that direct and indirect fisheries interactions are the dominant recognized threat for pinnipeds. The indirect fisheries interactions include intentional shooting by fishermen, as well as competition for fish resources (DeMaster *et al*. 2001; Szteren and Páez 2002; Hamer and Goldsworthy 2006; Goldsworthy 2007; Atkinson *et al*. 2008; Robertson and Chilvers 2011, Kovacs *et al*. 2012) and fisheries-induced changes to ecosystems that cause nutritional stress among pinnipeds (Kovacs *et al*. 2012).

The South American sea lion, *Otaria flavescens*, is affected by the threats mentioned above along its distribution. The species interferes with local small-scale artisanal fishery

(Szteren and Paéz 2002; Oliva et al. 2003; 2007; Sepúlveda *et al*. 2007*b*; Goetz *et al.* 2008; Riet-Sapriza et al. 2012), damaging their fishing gear and removing part of the catch. This species also interfere with the activities of industrial fisheries (Huckstadt and Antezana 2003; Huckstadt and Krautz 2004; Riet-Sapriza et al. 2012) and with salmon farms (Sepúlveda and Oliva 2005; Oliva et al. 2003; 2007; Vilata et al. 2010). In Chile, due to the interference with fisheries, by the beginning of the last century the South American sea lion was cataloged as a "damaging species" and was indiscriminately exploited until the species was driven to almost to the brink of extinction and began to be protected. This situation was repeated later again in 1972 (Sielfeld 1999). At present, the sea lion exploitation in Chile is prohibited, but the pressures exerted by the fishery and seal oil industry are mounting. Because of that, the Chilean government, through *the Fondo de Investigación Pesquera y Acuicultura* (FIP), financed the execution of two complete census of the species along the country (between 1996 and 2000 and in 2006) in order to estimate its population size and distribution and to define culling quotas (Sielfeld et al. 1997, Aguayo et al. 1998, Oporto et al. 1999, Venegas et al. 2001, Sepúlveda et al. 2007a; Bartheld et al. 2007; Oliva et al. 2007). However, this information should be complemented with a detailed assessment of the spatial structure and connectivity among local populations along the coast resulting from spatial variability in philopatry and dispersal behavior (Cassini 2000, Cassini and Fernández-Juricic 2003, Grandi *et al*. 2008). In fact, most pinniped species can be characterized as forming metapopulations (York *et al*. 1996, Raum-Suryan *et al*. 2002), that is an assemblage of populations connected by dispersal of individuals between them (e.g. Levin 1974, Hanski and Simberloff 1997, Marquet 2002). Management and exploitation of populations that do not take into account the existence of a metapopulation structure could be misleading (Harrison *et al*. 2006, Akcakaya et al 2007, Hoffman *et al.* 2009) with possible tragic consequences, as it happened with the management strategies applied the 19th century for *O. flavescens* in Chile (Sielfeld 1999).

For species structured as metapopulations the quantitative tools of population genetics can be useful in assessing connectivity and delimiting spatial structuring (Goodnight 2004, Hoffman *et al*. 2006*a,* Hoffman *et al*. 2009, Amaral et al 2012). For example, in conservation genetics, Moritz (1994) introduced the concept of Management Unit (MU).

Particularly for *Otaria flavescens,* it is known that the Pacific and the Atlantic distribution of the species represent two different genetic clades (Artico *et al*. 2010, Feijoo *et al*. 2011, Chapter I *of this Thesis*), that may have different adaptive diversity and evolutionary potential. However, only the Atlantic clade has been studied with relation to its population structure (Túnez *et al*. 2007; Feijoo *et al*. 2011). These authors show the existence of different genetic groups for the Uruguayan and Argentinean part of the distribution of the species thus suggesting the existence of two different metapopulations or management units in the Atlantic coast. We hypothesize that a similar structuring is likely along the Pacific coast given the existence of sharp discontinuities in the distribution of different types of organisms, processes and oceanographic regimes along this area (Camus 2001, Escribano et al. 2003, Valdovinos et al. 2003, Navarrete et al. 2005), delimiting different biogeographic zones (Camus 2001). According to Camus (2001), three major biogeographic provinces can be distinguished along this area: the Peruvian province (from Peru to ~30°S), the Intermediate Province (from ~30°S to ~ 41°S) and the Magellan Province (from ~41°S to ~56°S). In addition, the census recently made for the South American sea lion in Chile during the reproductive period of 2007

(Sepúlveda et al. 2007a; Bartheld et al. 2007; Oliva et al. 2007), shows different population trends associated to the biogeographic zones and the Magellan Strait and Cape Horn (Chapter III, this Thesis). North of 24°S and south of ~40°S in the Pacific coast, the southern sea lion reaches its highest abundance. Instead, between 24°S and ~40° and in the Magellan Strait and Cape Horn, the abundance is much lower.

Because of the biogeographic structuring of the Chilean coast, together with the spatial distribution and demographic trends in sea lions abundance, we hypothesized the existence of four management units for the South American sea lion: north of 30°S, from 30°S to ~41°S, south of ~41°S along the Pacific coast and the Magellan Strait and Cape Horn predicting different haplotypes frequencies between MU's for both *mt*DNA control region and microsatellite markers.

Together with the estimation of the genetic structure of a species, it is also very important to understand the impacts of past anthropogenic and climate disturbances upon its populations as these can be recurrent, an even intensify, in the near future. These effects often result in substantial reductions in population size (e.g. Oliveira *et al*. 2006), and therefore loss of genetic variability or genetic bottlenecks (e.g. Weber *et al.* 2004, Oliveira *et al.* 2009) associated to a decrease in the genetic effective population size (Frankham 1995*a,* Oliveira *et al*. 2009, Hoffman *et al*. 2011). Genetic bottlenecks may produce inbreeding depression and hence reduce the evolutionary potential of a population to respond to a changing environment (Amos *et al*. 2001, Hoffman *et al*. 2004, Hartl and Clark 2007, O'Corry-Crowe 2008). In that sense, as in most pinnipeds species, the abundance of the South American sea lion in Chile has been negatively affected by indiscriminate sealing until middle of past century (Sielfeld 1999).

Additionally, in Southeastern Pacific Ocean, pinnipeds have suffered at least two drastic reductions in numbers in the last 20 years due to El Niño Southern Oscillation (ENSO) effects (1982-83 and 1997–98) (e.g. Trillmich *et al*. 1991, Guinet *et al*. 1994, Sielfeld and Guzman 2002, Bradshaw *et al*. 2000, Soto *et al.* 2004, 2006, Le Boeuf *et al*. 2005, Oliveira *et al*. 2006). Consequently, we hypothesize that *Otaria flavescens* in Chile shows evidence of a genetic bottleneck, due to the drastic decline in population size during the past century. A genetic bottleneck was evaluated before by the analysis of *mt*DNA control region (Chapther I *of this Thesis*), but the loss of genetic diversity was not detected in that analysis, instead high genetic diversity and evidence of past demographic expansion was found. The mutation rate for *mt*DNA markers are too low to detect recent demographic changes (Ho *et al*. 2005; Ho *et al*. 2007), alike those produced by the effects of ENSO during the last twenty years and sealing during the past century. We expect the genetic bottleneck leave a signature on microsatellite markers not only in the genetic diversity, but also in the effective population size (Ne) compared to census population size (N). Ne and N will play key roles in determining the degree to which populations can avoid extinction from demographically, environmentally, or genetically stochastic events (Frankham et al. 2003, Palstra and Faser 2012).

Effective population size may also determine whether populations can maintain enough genetic variance for adaptive evolution, and hence response to environmental change (Newman and Pilson 1997, Lynch and Lande 1997, Frankham et al. 2003).

Several recent studies suggest that no simple relationship between Ne and N exist, either because population expansion and contraction or because of habitat factors (Vucetich *et al*. 1997, Waples et al 2010, Belmar-Lucero et al. 2012, Palstra and Faser 2012).

Despite that, analysis of ecological data suggests N_e/N ratio should range near 0,5 for wild populations of species with overlapping generations (Nunney and Elam 1994), meaning that Ne reaches half the value of N. Nunney (1995) theoretically states that if N_e/N is markedly below 0.11, then random drift can be strong although the population is large. As a result, a population that is highly resistant to random extinction from demographic causes can run into problems from a loss of genetic variation. Fluctuations in population size and unequal sex-ratios in the population, make the average N_e/N substantially smaller than 0,11(Frankham 1995*b*; Vucetich *et al*. 1997). Because of the changes in population size due to past sealing and the effect of ENSO events, we predict N_e/N ratio smaller than the normal range near the value of 0,5.

This study aims at determining the genetic population structure of the South American sea lion in Chile, in order to assess their spatial structure and particularly the existence of different metapopulations or management units, and its possible relation with the biogeographic zones. Also, we investigate, by the analysis of microsatellite, if the species in Chile has experienced any recent genetic bottleneck due to indiscriminate hunting or climate conditions like El Niño Southern Oscillation.

8.2.- METHODS

8.2.1.- Study area and sample collection

Data collection was made by sampling 145 sea lions from 22 colonies distributed along the entire Chilean coast (Figure 1). These samples were obtained between January through February 2008 and December through February 2009 (breeding period). Sampling was performed by a remote biopsy system or from dead individuals on beaches or treading water (described in Weinberger *et al. manuscript*). Sample locations and the presence or absence of reproductive activity are shown in Table 1.

8.2.2.- Laboratory

DNA from tissue was extracted using the DNeasy Tissue Kit (QIAGEN) according to manufacturer's protocol. DNA from hair was extracted following Caudron et al. (2007), as follows: follicles (1 to 8) were cut and put in 1 ml of water for 30 min, then centrifuged at 20,800 x g for 15 min and after discarding water, we added 80 µl Chelex 100 resin (5% Chelex in 10 mM Tris, 0,1 mM EDTA), the endolytic protease (proteinase K, 4 µl 20 mg/ml) and the reducing agent (dithiothreitol, 4 µl 1M DTT). The sample was then incubated at 58 °C for two hours with occasional shaking. Next, the solution was vortexed and boiled for 10 min, vortexed again and then centrifuged at 20.800 x g for five minutes. The resulting supernatant was used for DNA amplification. PCR was carried out in 10 µl reaction, with varying reagent concentrations for each of the 8 microsatellite loci: Aa_4, Hg3.7, Pv_11, Hg6.1, Pv_9, M11, Pv_17, Hg4.2 (Gemmell *et al*. 1997). The amplification reaction contained from 30 to 40 ng of template DNA, 1 µl of 10x Platinum® Taq Buffer (Invitrogen), 0,1 to 0,2 pmol of primer forward with M13 tail, 0,2 to 0,4 pmol of primer reverse and M13 tail with fluorescences, 2,5 nmol of each dNTP's, 1,5 to 3 mM MgCl2 and 0,25 unit of Platinum® Taq DNA Polymerase (Invitrogen). A Touchdown PCR was undertaken in which the annealing temperature was reduced every two cycles by 2°C for 10 cycles until the optimal annealing temperature of each primer (x: 51°C for Aa_4, Hg3.7, Pv_9, 54°C for Pv_11, Hg6.1, Pv_17°C, 46°C for M11 and 52°C for Hg4.2), and then 20 cycles at 53°C (optimal annealing temperature for the M13 fluorescence primer). The general thermocycling profile for all loci was: 95°C/30s, (x+10) to x°C/45s and 72°C/45s. All PCR products were checked with a 0.8% agarose gel electrophoresis and visualized with ethidium bromide. *mt*DNA samples were purified using QIAquick PCR purification Kit (QIAGEN) and sequenced by Macrogen Inc. (Seoul, South Korea). Also microsatellite fragments size were check by Macrogen Inc. (Seoul, South Korea). When a microsatellite fragment size was not clearly determined, the DNA sample was amplified again.

8.2.3.- Data analysis

The microsatellite allele size determination was made in Peak Scanner v1.0 (Applied

Biosystems). We also used the 28 sequences (Genbank sequence accession number JQ434428 to JQ434457) from 72 individuals of the 550-bp fragment of the *mt*DNA control region (D-loop) (obtained in Chapter I of this Thesis). For both markers (microsatellite and D-loop) the genetic diversity index was estimated in ARLEQUIN v3.1 (Excoffier *et al*. 2005) and the correlation between the diversity index and sample size was made in R v2.12.1.

8.2.3.1.- ***Population genetic structure***

Sequences of *mt*DNA D-loop and the microsatellite markers, allowed us to assess the population genetic structure of the South American sea lion in Chile using the spatial statistical model implemented in GENELAND package for R (Guillot *et al.* 2005*a*; Guillot *et al.* 2005*b*; Guillot *et al.* 2008; Guillot 2008; Guillot and Santos 2010; Guedj and Guillot 2011). In this model, the geo-referenced individuals are assumed to belong to one of several populations at Hardy-Weinberg equilibrium, to be randomly located inside the population and linkage equilibrium is assumed between loci. Populations are assumed to be spatially organized through a Poisson-Voronoi tessellation, and allele frequencies are drawn from a Dirichlet distribution (Guillot *et al*. 2005*a*). Bayesian inference is performed by Markov Chain Monte-Carlo algorithm (MCMC), obtaining a map of posterior probabilities of population membership. For the analysis of both genetic markers, the correlated model of allele frequency was used (Falush *et al*. 2003) and 100.000 iterations were ran, saving only one each 100 and eliminating the first 100.

To see if between colonies population differentiation is associated with geographical distance, we carried out a Mantel Test between individuals in R v2.12.1, using the packages ape v2.7-2 (Paradis *et al*. 2011) and bioDist v1.24.1 (Ding *et al*. 2010). For the *mt*DNA sequence data, genetic distance was estimated using the JC69 mutation model, that assumes equal base frequencies and equal mutation rate (Jukes and Cantor 1996), with g = 0,137, estimated with MODELTEST v3.06 (Posada and Crandall 1998). For the correlation analysis with microsatellite markers, the number of loci with allelic difference between individuals was used as the genetic distance. The geographic distance for all the correlation analysis was measured as Euclidean distance. The Mantel Test was run for 10.000 iterations.

Because the number of distinct alleles and the number of private alleles depend heavily on sample size, and they can be difficult to interpret when sample sizes differ across populations, we performed a rarefaction analysis in ADZE v1.0 (Szpiech *et al*. 2008), for a standardized estimation of allelic richness and private allelic richness.

8.2.3.2.- ***Populations genetic conditions***

The analysis of microsatellite data, with the MCMC coalescent genealogy sampler LAMARC 2.1 (Kuhner 2006), was used to estimated the parameter Theta (θ) for each populations, where $\theta = 4N_e\mu$, N_e is the effective population size and μ is the mutation rate per site per generation (Kuhner 2006; Hartl and Clark 2007), and the immigration rate (M) between them. We assumed a mutation rate $\mu = 5x10^{-4}$ per locus per generation (Garza and Williamson 2001) and a generation time of 10 years, based in the average reproductive age, life time and evidence of senescence in otariids (Grau and Acuña 1998; Beauplet *et al*. 2006; Boyd *et al.* 1999; Wickens and York 1997). Taking $\theta = 4N_e\mu$ (Kuhner 2006; Hartl and Clark 2007). Also, we calculated the effective inmigrants per year (g), where $g = 4N_em = \theta M$, m is the chance for a lineage to immigrate per generation and M = m/μ (Beerli and Felsenstein 1999).

We also tested for a possible recent genetic bottleneck for the sea lion populations in Chile, using the program BOTTLENECK version 1.2.02 (Piry *et al.* 1996). Populations that have experienced a recent reduction of their effective population size exhibit a faster reduction in allele numbers and in gene diversity at polymorphic loci. Because of that, in bottlenecked populations the observed gene diversity is less than the expected equilibrium gene diversity under the assumption of mutation-drift equilibrium (Luikart *et al.* 2008). Using coalescent simulations in BOTTLENECK, we compared the sample heterozygosity (H_e) at each locus against the values expected for a sample of equal size and number of alleles, and taken from a population under neutrality and in equilibrium conditions (H_{eq}). In a population at mutation-drift equilibrium (e.g. where the effective population size has remained constant in the recent past), there is approximately an equal probability that a locus shows a H_e excess or deficit. But if a population has suffered a recent bottleneck, the mutation-drift equilibrium is transiently disrupted and the measured heterozygosity will exceed the expected under mutation-drift equilibrium. To determine whether a population exhibits a significant H_e excess, we employed the Wilcoxon signed-rank and the sign test estimators (Cornuet and Luikart 1997). The calculations were based on 1000 simulations performed under Stepwise (SMM) and Two-Phase (TPM) mutations models of microsatellite evolution. The TPM model implemented consists of mostly one-step mutations, but with a 30% of multi-step changes. Another approach used was the mode-shift indicator of allele distribution, based on the idea that when a population passes through a recent bottleneck, rare alleles are more likely to be lost, which inflates the frequencies of common alleles. Because of that, the assumption behind this test is that a population under mutation-drift equilibrium is expected to have a large proportion of alleles in low frequencies (Luikart *et al*. 1997).

Additionally, we evaluated the genetic condition of the population and contrasted the results of the bottleneck analysis by calculating the ratio N_e/N, where N represents the census adult population size. This index help to visualize the genetic status of populations, because it measures the loss of genetic variation in relation to the demographic population size (Nunney 1995). For the estimation of N we used the 2007 census values (Bartheld *et al*. 2007; Oliva *et al*. 2007; Sepúlveda *et al*. 2007a).

8.3.- RESULTS

8.3.1.- *mt*DNA control region sequence analysis

For the studied populations of the South American sea lion the 28 sequences from the *mt*DNA control region accessible from a total of 72 individuals (Table 1), are distributed as follow: 24 are present in the 58 individuals sampled north of 33°S and 7 haplotypes in the 14 individuals south of 40°S (Figure 1). The individual sampled between those latitudes, in Cobquecura at 36°S, has a unique haplotype not shared with the southern and northern groups. Between these groups we found 3 shared haplotypes (Ot-1, Ot-4 and Ot-5), being one of them (Ot-1) the most frequent haplotype found in the northern group, in the south, however, this haplotype was found at the same frequency as the others haplotypes.

Haplotype diversity of sea lion colonies did not show a significant correlation with population size (r=-0,20, p=0,53), indicating that population size is not determining the genetic diversity due to possible genetic drift and bottleneck effects.

Regarding the population genetic structure, GENELAND results, which are based in the spatial configuration of the haplotype frequency estimations, show the existence of 2 genetic clusters (Figure 2), separated approximately at 50°S, with the southern cluster including only

Isla Marta in the Magellan Strait (this colony has only 2 samples, one of them is associated to the Argentinean clade).

Results of the Mantel test, indicate that there is no correlation between genetic and geographic distance, neither when the analysis is run for all individuals sampled from colonies (reproductive or not) along the Chilean Pacific coast (z=12416434, p= 0,63), or when only females (n=24) from reproductive colonies are considered (z = 1390043, p = 0,3197). This non-significant correlation between genetic distance and geographic distance indicate that gene flow is not taking place in a stepwise fashion between colonies. To see if the non-significance of this relation is due to the genetic differentiation between clusters, and for the *mt*DNA D-loop sequences, we analyzed the correlation between genetic and geographic distance for the cluster north of the 50°S and for the cluster south of this latitude.. The Mantel test was also non-significant: z = 4607861 (p = 0,381, n=60) and z = 189765,4 (p = 0,353, n=12), for the north and south cluster respectively. Similarly, molecular diversity was similar when both cluster are compared. For the northern cluster the haplotype diversity was h = 0,928 +/- 0.017 and the nucleotide diversity p = 0,008 +/- 0,005 (n=60), while for the south cluster, h = 0,924 +/- 0,048 and p = 0,010 +/- 0,006 (n=12).

8.3.2.- Microsatellite analysis

Due to difficulties in DNA extraction from hair, only 63 samples distributed in 18 colonies were successfully genotypes by a total of eight loci (Table 1). Population structure, evaluated using GENELAND, evidenced the existence of two geographic genetic clusters separated approximately at 40°S (Fig.3), with a fixation index of population differentiation of

F_{st} = 0,045 (p<0,001).

The average gene diversity over loci for the northern cluster was 0,766 +/- 0,408, and 0,791 +/- 0,437 for the southern one. The rarefaction analysis shows that for both, the northern and the southern clusters, the allelic richness do not reach a plateau, but a constant and moderate increase with sample size (Figure 4), indicating that the observed genetic diversity may be slightly underestimated due to sampling effort. The private allelic richness stabilized at approximately 10 samples for each clusters. When the northern and southern clusters are combined, it increases constantly with sample size, not reaching a plateau (Figure 5). These results indicate that despite the fact that the northern and southern clusters shared a significant number of alleles, the sample size for each cluster is enough to assess genetic diversity and private allelic richness.

The correlation of pairwise genetic distance (eight microsatellite loci) between individuals and geographic distance was not significant within both clusters (Mantel´s test z = 7451854781, p = 0,41 with n = 50 and z = 561192464 p = 0,47 with n =13, for the northern and the southern clusters respectively). As with the sequence of *mt*DNA, these results indicate that gene flow is not taking place in a stepwise fashion inside clusters, but there is exchange among all populations within a cluster.

The coalescence based estimates of the parameter Theta (ϴ) for the northern and southern clusters are 24,64 and 14,97, respectively. The immigration rate for the northern cluster is M = 0,68 and M = 1,49 for the southern cluster. With those population parameters estimates, we infer N_e = 12.320 individuals in the north and N_e = 7.475 individuals in the south. Also, the estimates for the effective immigrants per year from the north to the south cluster were 2,24 individuals and from the south to the north one it is of 1,67 individuals.

For the estimation of N_e/N, we calculate the values of N in 41.571 and 32.571 adult individuals, for the northern and the southern clusters, respectively, from the 2007 census data (Sepúlveda et al. 2007a; Bartheld et al. 2007; Oliva et al. 2007). The ratio N_e/N is 0,296 in the north and 0,229 in the south.

8.3.2.1.- *Recent genetic bottleneck*

Bottleneck detection using Wilcoxon signed-rank and sign tests, under both mutations models of microsatellite evolution (SMM and TPM), indicates that the null hypothesis of mutation-drift equilibrium cannot be rejected for both genetic clusters with an expected number of loci with heterozygosity excess between 4 to 5 out of 8 ($p > 0,05$). Additionally, the allele frequency distribution as revealed by the mode-shift indicator test has a normal L-shaped distribution for both genetic clusters (Figure 6), indicating a large proportion of low frequency allele in both areas. These results lends further support to the lack of a recent genetic bottleneck for the Chilean populations of *O. flavescens*.

8.4.- DISCUSSION

8.4.1.- Genetic structure

Our hypothesis that there would be a spatial genetic structure in *O. flavescens* along the Chilean coast, which would parallel the current biogeographic province distribution was only partially supported. Our results show that the South American sea lion in Chile is characterized by low genetic differentiation between colonies and by the existence of two main clusters. The microsatellite analysis showed very clearly two main genetic clusters for the Chilean coast, divided at 41°S. The *mt*DNA control region analysis, however, integrated all the Pacific Chilean colonies in one cluster and the southernmost Chilean colony, located in the Magellan Strait (Isla Marta, in front of the city of Punta Arenas) in another cluster. The colony of Isla Marta is represented by only 2 samples for the *mt*DNA analysis, one of them with a haplotype that belong to the phylogenetic clade found in Argentina (Chapter I *of this Thesis*). The discrepancy between the results of both markers could be an artifact of the smaller resolution associated to the *mt*DNA analysis, due to genetic sample size. Results of microsatellites are statistically more powerful, because the genetic sample size increases by the fact that these markers are diploids and we evaluated eight loci. Because of that, in the analysis of microsatellites, each sample represents sixteen genetic samples. Also, microsatellites have higher mutation rates, showing more contemporary changes that *mt*DNA markers (Goldstein and Pollock 1997; Ho *et al*. 2005; Ho *et al*. 2007), being more powerful for the determination of actual genetic structure of populations.

The genetic spatial subdivision observed in *O. flavescens* at 41°S, is consistent with the existence of a major geophysical, oceanographic and biogeographic discontinuity in the South Pacific coast at 41-42°S (Strub *et al.* 1998; Camus 2001; Escribano *et al.* 2003). At this latitude the West Wind Drift (WWD) divides into the Humboldt Current to the north and the Cape Horn Current to the south (Strub *et al.* 1998; Escribano *et al.* 2003). Also, north of this latitude, the Chilean coast is characterized by a straight continental line and at approximately 41°S, there is a sharp change to an ecosystem conformed by fjords and austral channels (Camus 2001). In that sense, this major biogeographic break divides the Magellan province to the south (from ~42° to 56°S) from the north, were the Chilean coast could be divided in two more biogeographic units: the Peruvian province (from Perú to ~30°S) with year-round upwelling and the Intermediate area (~30° to 41°S) with seasonal upwelling (Camus 2001). These two northern provinces, in turn, are separated by the tropical convergence zone (29° to 32°S) and an abrupt narrowing of the continental shelf (Strub *et al.* 1998; Thiel *et al.* 2009). At this latitude important discontinuities in species abundance, diversity and recruitment of several pelagic and benthonic species have been documented (Camus 2001; Escribano *et al.* 2003, Navarrete et al. 2005).

The genetic structure analysis of the South American sea lion did not show any discontinuities at latitude 30°S. Despite this, not in this exact latitude but near it, at approximately 24°S, the coastal area shows discontinuities in the abundance of breeding colonies (Figure 7) and different population growth tendencies for the reproductive season of 2006-2007 as compared to the colonies found to the south and to the north of this latitude. In the area between 18° to 24ºS, the population size of the South American sea lion was estimated in 62.281 individuals census and 32 breeding colonies, with a positive tendency for population growth rate since 1996 (Bartheld *et al.* 2007). Between 24°S and 41°S, population size seems to remain constant and relatively low (Sepúlveda et al. 2012). And between 41°S and 48°S, despite the total increase in population size, the population growth shows a tendency of decline (Oliva et al. 2007). For latitudes between 32° and 40°S, the total population was estimated to be 18.179 individuals by Sepúlveda et al. (2007a), having remained constant since 1997, when the previous census was made by Aguayo et al. (1998), but there has been a sustained decrease in the number of breeding colonies (Chapter III of this Thesis). Afterwards, between latitudes 40° and 48°S, the population size amounted 45743 individuals, and 33 breeding colonies (Oliva *et al.* 2007), remaining constant since 1998 (Oporto et al. 1999), but with a decreasing growth tendency (Oliva *et al.* 2007). Further south, population size was estimated in 5689 sea lions in the 2001 census (Venegas *et al.* 2002), showing population decline since the previous census (Sielfeld 1978), with a population size estimate of 13620. It is also interesting to mention that the other sea lion of the Chilean coast, *Arthocephalus australis*, is completely absent between 28° to 43°S, in the Intermediate Biogeographic zone (Aguayo and Maturana 1973; Aguayo *et al.* 1998; Sielfeld *et al.* 1997; Oporto *et al*. 1999; Venegas 2002; Sepúlveda *et al.* 2007a; Bartheld *et al*. 2007).

The genetic structure of Chilean marine mammals has only been determined before for the marine otter *Lontra felina*. This species is represented by two genetic clades, one for Peru and one for Chile. In Chile, *L. felina* is structured in five Management Units with long sandy beaches acting as barriers to dispersal (Vianna *et al*. 2010), instead of biogeographic barrier as in the Southern sea lion. Sandy beaches as physical barriers for *L. felina* can be explained by the lower dispersal capacity of this species (Vianna *et al*. 2010).

The mechanism accounting for the observed population spatial structure in *O. flavescens* and its association with the biogeographic break found at 41 - 42°S remains unknown, mainly because these animals are good swimmers capable of traveling long distances (up to 860 km) (Campagna *et al*. 2001), which makes difficult to think of oceanographic conditions as physical barriers to dispersal. Instead of that, we hypothesize that the observed genetic structure is a reflection of differences in biotic composition and prey availability (Montecino and Lange 2009). Changes on sea lion preys may affect the foraging and feeding behavior of these animals (e.g. Sielfeld 1999 for latitude difference in the diet of the South American sea lion; Thompson *et al*. 1998 and Naya *et al*. 2002 for changes in the diet of *A. australis* in relation to food availability; Soto *et al*. 2006 for the effects of food availability on the feeding behavior of the South American sea lions). In that sense, Laptikhovsky (2009) found a positive relation between the distribution of *A. australis* around the Falkland Islands before the breeding season and the oceanographic conditions that determine the distribution of its prey species. This positive correlation had also been found in others species of otariids (e.g. Boyd *et al*. 1994; Boyd 1996; Lea *et al*. 2006 for *Arctocephalus gazella*).

Beside this, and taking into account the management unit (MU) concept of Moritz (1994), the genetic clusters found to each side of the biogeographic break represent two different MUs, but with sufficient gene flow between them to maintain only a moderate genetic differentiation. On the other hand, non-genetic structure between colonies inside MUs has important implications. This high genetic relatedness could not be asserted because of low sample size, but it could be proposed considering that this tendency is common also for others otariids species, despite the existence of philopatric behaviour (Pomeroy *et al*. 1994, Twiss *et al*. 1994, Cassini 1999, 2000, Pomeroy *et al*. 2000, Harkonen and Harding 200, Hoffman *et al*. 2006*b,* Wolf and Trillmich 2007), which is associated to a high degree of genetic population structuring. Our results, as well as others studies (Túnez *et al*. (2010) and Feijoo *et al*. (2011) for *O. flavescens*, Dickerson *et al*. (2010) for *Callorhinus ursinus* and Hoffman *et al*. (2006a, 2009) for *E. jubatus*), indicate little genetic differentiation between colonies inside MU's. This general pattern suggests that philopatry is not dominating the spatial distribution of most of these species, neither for females nor for males (little genetic differentiation for *mt*DNA and microsatellite markers). Instead of that, dispersion seems to be a common behavior, corroborated by the fact that most population are growing and expanding, as seems to be the case of most otariids species in the last half century (York *et al*. 1996; Wickens and York 1997; Raum-Suryan *et al*. 2002; Dans *et al.* 2004; Hucke-Gaete *et al*. 2004; Harrison *et al*. 2006; Grandi *et al*. 2008). Thus, supporting the metapopulation structure for these species.

Assuming that the two MUs found in Chile represent two metapopulations, it is important to emphasize the results of the Mantel Test analysis. These results evidence the non-linearity of the dispersion kernel and therefore, that the connectivity between colonies may be driven by factors others than just geographic distance.

8.4.2.- Dispersal between MUs

One problem with most indirect estimates of gene flow is that effects of recent gene flow on gene frequencies are often confounded with historical gene flow. If isolation is recent, populations might appear to have high gene flow even if they are completely isolated because molecular differences have not had time to accumulate (Slatkin 1985; Neigel 1997). Many estimators of gene flow are based on populations being at migration-drift equilibrium, where population size and number of successful migrants have not changed dramatically for many generations. These conditions are not typical in many settings in which resource managers wish to estimate gene flow. Thus, estimates of gene flow, while useful in a relative sense, should be regarded with some caution (Oyler-McCance and Leberg 2005). The South American sea lion in Chile experienced recent, drastic and cycling change in population size by sealing (Sielfeld 1999) and by changes in climate conditions (Sielfeld and Guzmán 2002; Soto *et al*. 2006). Also, investigations shows the influence of population size in the expansion process of the species (Cassini 2000; Cassini and Fernández-Juricic 2003; Grandi *et al*. 2008), indicating the existence of a positive correlation between migration rates and population size. In that manner, those MUs could be recently isolated and present historical gene flow. Because of that, the analysis of the coalescent estimate of dispersion rate between the north and south MUs could not be interpreted as an exact quantitative results. Instead, these results indicate that the effective dispersion of two individuals per year between MUs, represents enough gene flow to account for the low genetic differentiation between both clusters. If genetic differentiation between both MUs is due to historical gene flow, then less or none recent time migration exist. Consequently, it can be said that there is little gene flow between both clusters, emphasizing the existence of two different MUs.

8.4.3.- Populations genetic condition

Despite the drastic decline in population size that experienced the South American sea lion in Chile during the last two centuries (Sielfeld 1999), we found no evidence of a recent genetic bottleneck using eight microsatellite markers. This finding applies also to the analysis of the *mt*DNA control region (Chapter I of this Thesis). The fact that there is no evidence of the drastic population declines accrued due to sealing, together with the low degree of population structuring detected inside each MU of the species, suggest that metapopulation dynamics may be dominated by high dispersal between colonies and possibly an important role of isolated and preserved colonies in the recolonization process.

Further, effective population sizes of 12.320 and 7.475 individuals, for the northern and southern cluster, respectively, are well above the critical N_e (~ 1.000 to 5.000) for a genetically secure population based on empirical and theoretical estimation (Lynch and Lande 1997). Also, these values are well above the minimum viable levels of N_e (~ 1.800 individuals) for vertebrates (Reed *et al*. 2003) and for others pinnipeds populations classified as in danger of extinction, despite the laking of N_e estimations for this taxonomic group. For example, the N_e for the Peruvian population of the South American fur seal, *Arctocephalus australis*, was estimated in 2.153 individuals, after the population declined by 72%, as a result of low food availability during the El Niño in 1997–1998 (Oliveira *et al*. 2009). Contrary and also very far from the N_e estimated for *O. flavescens*, the Antarctic fur seal, *Arctocephalus gazella* presents a high value of N_e (mean = 744 000) Hoffman *et al.* (2011). This species has also suffered a bottleneck at the first decades of the past century, but seem to be very well recovered. Similarly, the Antarctic Phocids present values of N_e of the order of magnitude of 100.000 (Curtis et al., 2009; 2011), instead of the 10.000 obtained for *O. flavescens*. The three species of antarctic seals, the Weddell seal (*Leptonychotes weddellii*), the Crabeater seal (*Lobodon carcinophaga*) and the Ross seal (*Ommatophoca rossii*), did not present any signature of recent genetic bottleneck, even though population size estimates (N) for the Weddel and Crabeater seals are much higher than the values estimated for N_e by different genetic markers, *mt*DNA sequences (Curtis et al., 2009) and microsatellites (Curtis et al., 2011). The effective population size of the Weddel seal was estimated in 111.200 and 151.200 with *mt*DNA and microsatellites, respectively; with a census size of 800.000. For Crabeater seal, N_e(*mt*DNA)=853.400 and N_e(micsat)=880.200, with N=15.000.000. The Ross seal is the only one whose estimations of the effective population size differ between genetic markers: N_e(*mt*DNA)=130.400 and N_e(micsat)=254.200 (Curtis et al., 2009; 2011). Also, population size of this species seems to be smaller than the estimations of the N_e (N=220.000), explained by underestimation of real population size due to the difficult access to its habitat (Curtis et al., 2011). In that manner, female effective population size for *O. flavescens* in Chile is higher than for endangered species, but not so high as for pinnipeds well recovered from past sealing.

Estimations of the ratio N_e/N, using ecological data (Nunney and Elam 1994; Nunney 1995) and also theoretical expectation (Nunney 1991, 1993, 1996), are generally close to 0.5 for populations with overlapping generations. These authors also found that it takes rather special circumstances for N_e/N to be outside the range of about 0,25-0,75. N_e/N was 0,296 and 0,229 for the north and the south MUs, respectively. The value for the northern cluster is in the lower boundary of the normal range and for the southern cluster it is slightly outside this range. Despite that, Nunney (1995) exposed that population that can run into problems from a loss of genetic variation, present values for N_e/N markedly below 0,1. In that sense, the Southern sea lion in Chile is not now in danger of extinction by loss of genetic variability.

Despite that, Vucetich *et al.* (1997) demonstrated, using ecological data, that temporal fluctuations in population size affect this ratio: as the variation in populations size increase (measured as the coefficient of variation of population size and also as the standard deviation of the log-transformed population size), N_e/N decrease. Fluctuations in population size are sufficient to depress N_e/N to very low values (Vucetich *et al.* 1997). In that manner, this ratio should have a low value in scenarios of constant bottlenecks. This fact could be masking the genetic bottleneck signature, because continuous disturbances prevent the population to recover and genetic drift to act. Despite this, the effective population size (N_e north = 12.320 and N_e south =7.475 individual) and the demographic population size (N north = 41571 and N south = 32571 adult individuals), do not differ in orders of magnitude. This pattern is observed in populations near the equilibrium, suggesting that both management units are in mutation-drift equilibrium (Hartl and Clark 2007).

8.4.4.- Conclusion and conservation perspective

Our results show that the South American sea lion, *O. flavescens*, in Chile, has a moderate degree of spatial structure composed of two main management units that may treated separately, each located on one side of 40°S latitude and consistent with the major biogeographic break of the Chilean coast (Camus 2001). Despite the high genetic diversity and the absence of genetic bottleneck signal, the values of the N_e/N ratio, exposed these fragility of the species in case of strong and constant population size fluctuation (Nunney 1995, Vucetich *et al.* 1997), as could be the case if past sealing in Chile had not been interrupted for long periods of sealing closure. To that effect, our results suggests that to foster adequate management of the South American sea lion, strategies that avoid drastic population size fluctuation and that take into account the negative effects of ENSO events in population size, must be carry out. In that sense, it is important to take into account the dependence of the sea lion populations with resource abundance (Sielfeld and Guzmán 2002, Soto et al. 2004, 2006), together with the decline of representative sea lion preys (Aguayo and Maturana 1973, Nacimento et al. 1985 and Sielfeld et al. 1997) by fishery industry during last decades (Moreno and Fedele 2008). Also, it is essential to consider the metapopulations behavior of the speciess, in order to maintain connectivity between colonies, and hence avoiding extinction of the species in part of its distribution range. Investigation of biotic and abiotic factors determining the spatial structure of the species distribution and those factors affecting the connectivity of its populations will be of great importance for future management decisions.

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8.6.- TABLES AND FIGURES

T**able 1:** Sample locations of *Otaria flavescens* in Chile, with they reproductive state and sample size for the analysis of the *mt*DNA control region and for the analysis of microsatellite loci.

F**igure 1:** Map of Chile with *Otaria flavescens* sample locations for this study in red. Relative frequencies of haplotypes for the *mt*DNA control region are specified for each sample location. Each color represents a different haplotype and the size of the circles are proportional to the sample size.

F**igure 2:** Map of GENELAND posterior probability to belong to cluster 1 for K(clusters)=2, derived from the analysis of the control region *mt*DNA sequence (555bp) and using 72 *O. flavescens* individual calculated for all pixels along the Chilean coast. The Y coordinates are latitude and X coordinates are longitude in UTM. The highest population membership values are in light yellow and the lowest in red. The level curves illustrate the spatial changes in assignment values. The plot is based on the run with the highest-probability at that value of K. The probability to belong to cluster 2 are inversely proportional to the displayed probabilities (i.e. probability to belong to cluster 1), being the highest population membership values in red and the lowest in light yellow.

F**igure 3:** Map of GENELAND posterior probability to belong to cluster 1 for K(clusters)=2, derived from the analysis of the control region *mt*DNA sequence (555bp) and using 72 *O. flavescens* individual calculated for all pixels along the Chilean coast. The Y coordinates are latitude and X coordinates are longitude in UTM. The highest population membership values are in light yellow and the lowest in red. The level curves illustrate the spatial changes in assignment values. The plot is based on the run with the highest-probability at that value of K. The probability to belong to cluster 2 are inversely proportional to the displayed probabilities (i.e. probability to belong to cluster 1), being the highest population membership values in red and the lowest in light yellow.

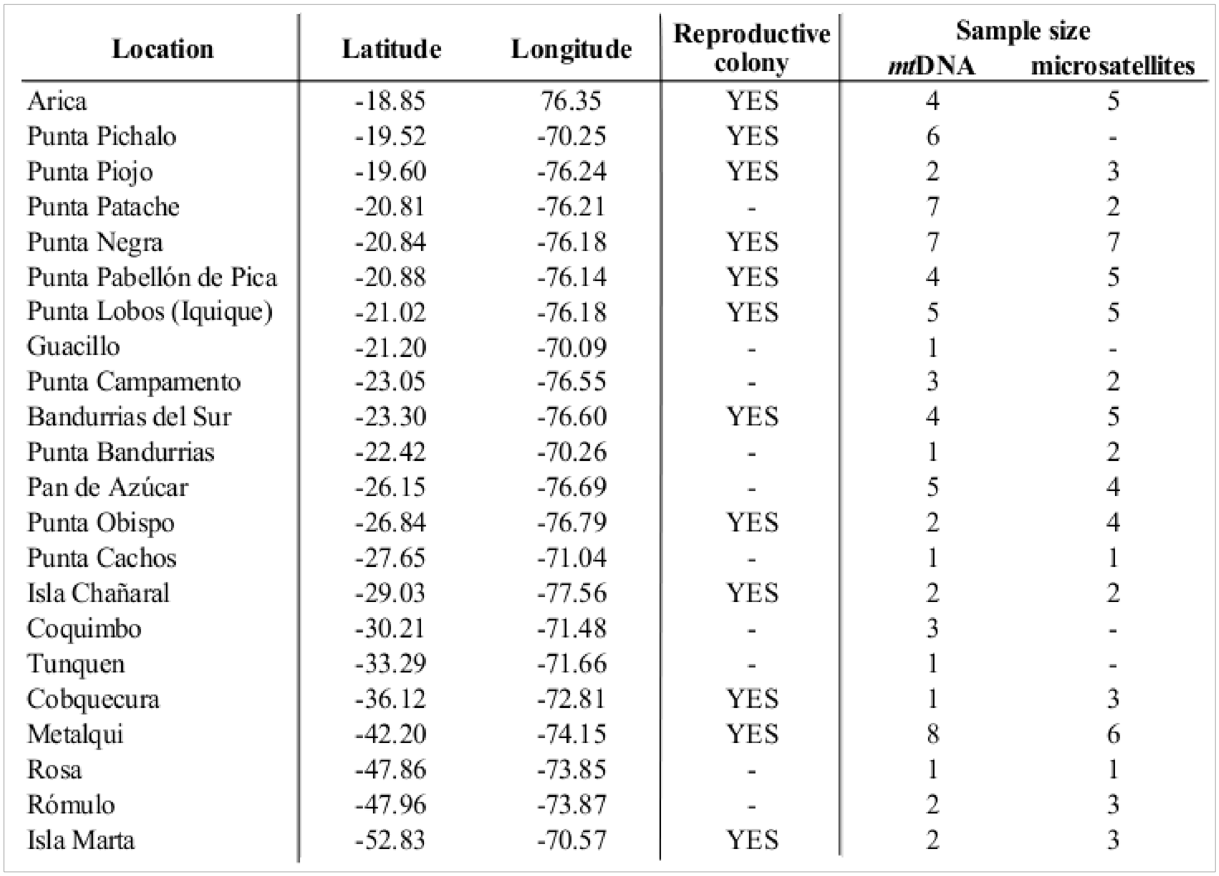
Figure 4: Rarefaction curve of allelic richness, for the cluster north of 40°S (North), for the cluster south of 40°S (South) and for both clusters together (All). Figure shows the mean value for eight loci and associated standard error.

Figure 5: Rarefaction curve of private allelic richness, for the cluster north of 40°S (North), for cluster south of 40°S (South) and for both clusters together (All). Figure shows the mean value for eight loci and associated standard error.

Figure 6: Mode-shift indicator test of allele distribution pattern for the north (grey) a south (black) genetic groups of the Chilean common sea lion. The analysis is based on eight microsatellite loci from 63 individuals (50 from the north and 13 from the south).

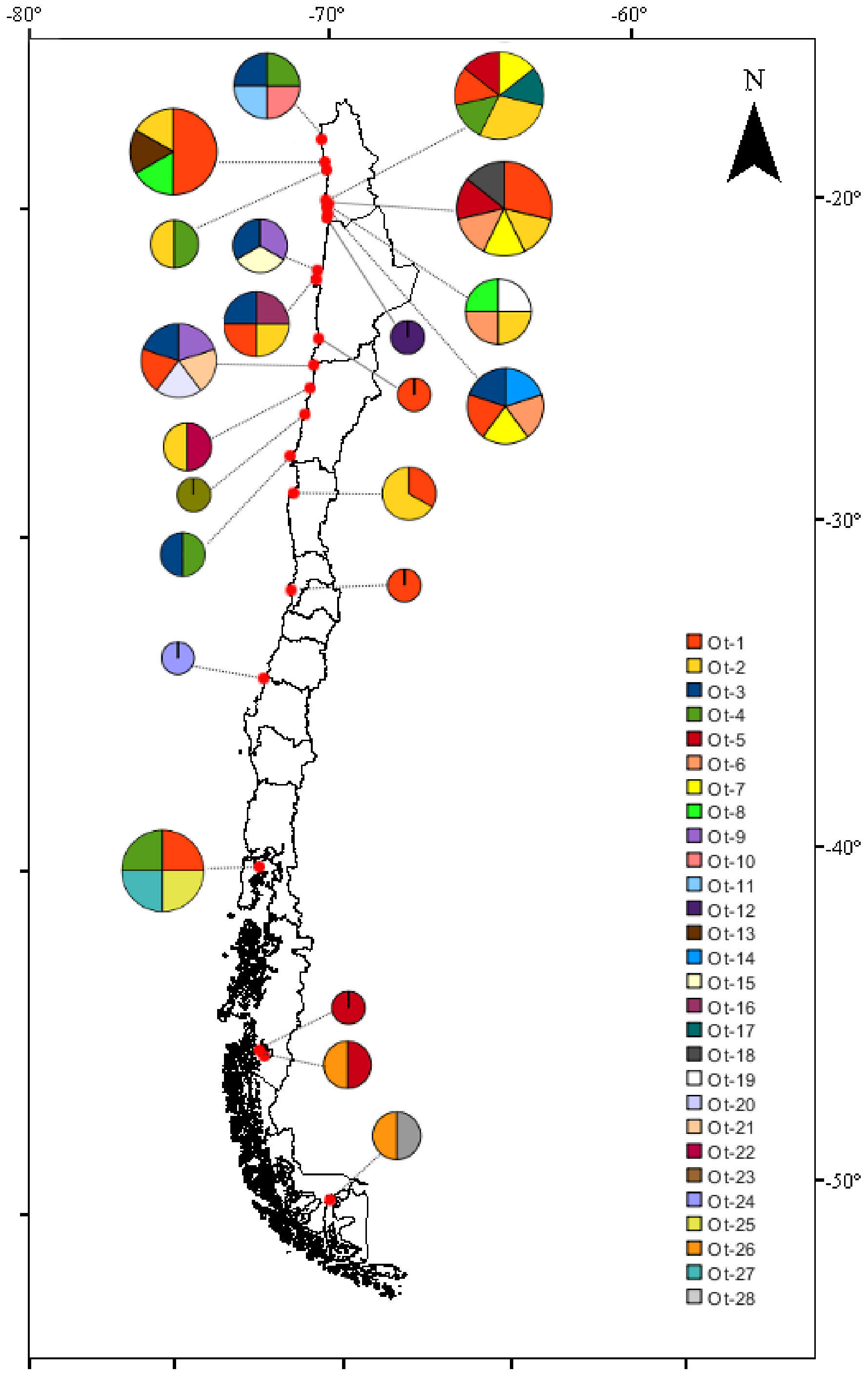
Figure 7: Map of Chile showing the breeding colonies of *O. flavescens* for breeding season 2006-2007.

Table I



Location	Latitude	Longitude	Reproductive colony	Sample size	
				*mt*DNA	microsatellites
Arica	-18.85	76.35	YES	4	5
Punta Pichalo	-19.52	-70.25	YES	6	-
Punta Piojo	-19.60	-76.24	YES	2	3
Punta Patache	-20.81	-76.21	-	7	2
Punta Negra	-20.84	-76.18	YES	7	7
Punta Pabellón de Pica	-20.88	-76.14	YES	4	5
Punta Lobos (Iquique)	-21.02	-76.18	YES	5	5
Guacillo	-21.20	-70.09	-	1	-
Punta Campamento	-23.05	-76.55	-	3	2
Bandurrias del Sur	-23.30	-76.60	YES	4	5
Punta Bandurrias	-22.42	-70.26	-	1	2
Pan de Azúcar	-26.15	-76.69	-	5	4
Punta Obispo	-26.84	-76.79	YES	2	4
Punta Cachos	-27.65	-71.04	-	1	1
Isla Chañaral	-29.03	-77.56	YES	2	2
Coquimbo	-30.21	-71.48	-	3	-
Tunquen	-33.29	-71.66	-	1	-
Cobquecura	-36.12	-72.81	YES	1	3
Metalqui	-42.20	-74.15	YES	8	6
Rosa	-47.86	-73.85	-	1	1
Rómulo	-47.96	-73.87	-	2	3
Isla Marta	-52.83	-70.57	YES	2	3

Figure 1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-70°
-60°
N
-20°
-30°
-40°
-50°
Ot-1
Ot-2
Ot-3
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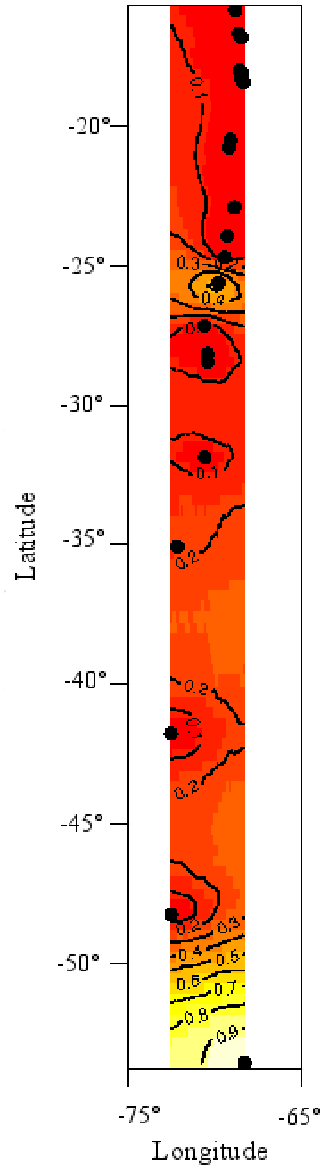
Figure 2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0.2
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0.6
0.7
0.8
0.9
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Latitude
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-65°
Longitude

Figure 3

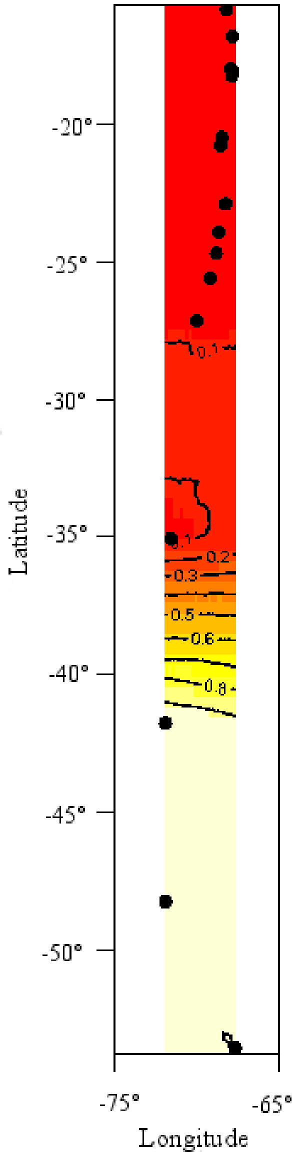


Figure 4

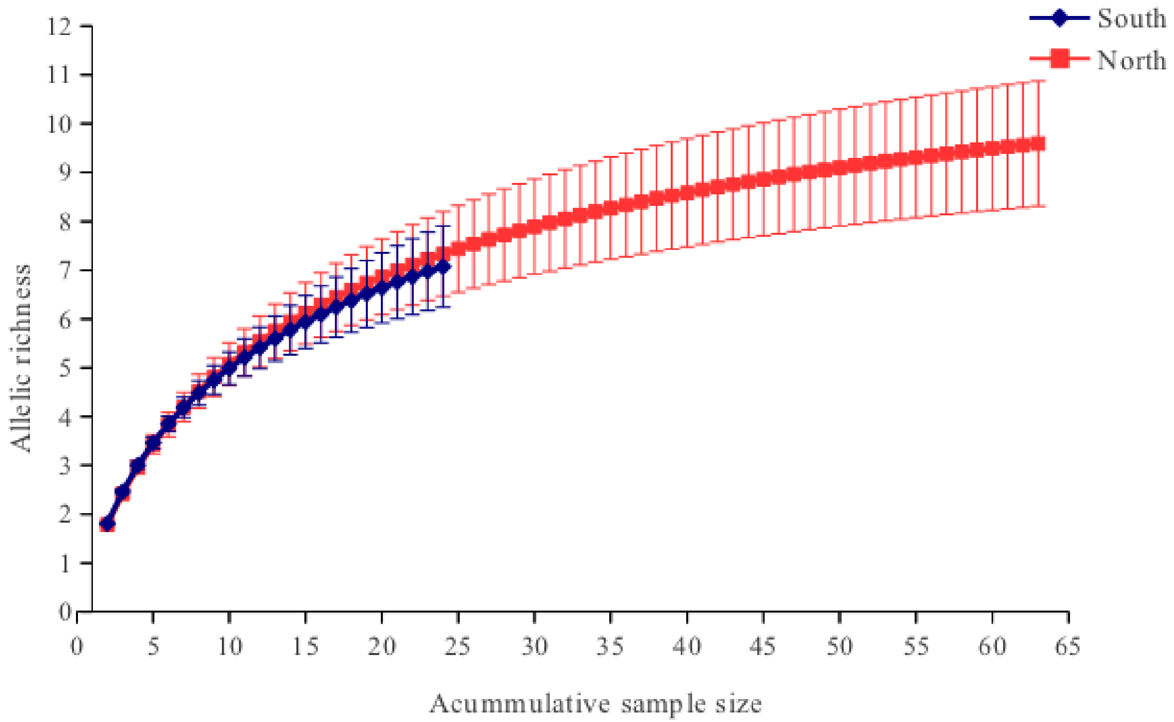
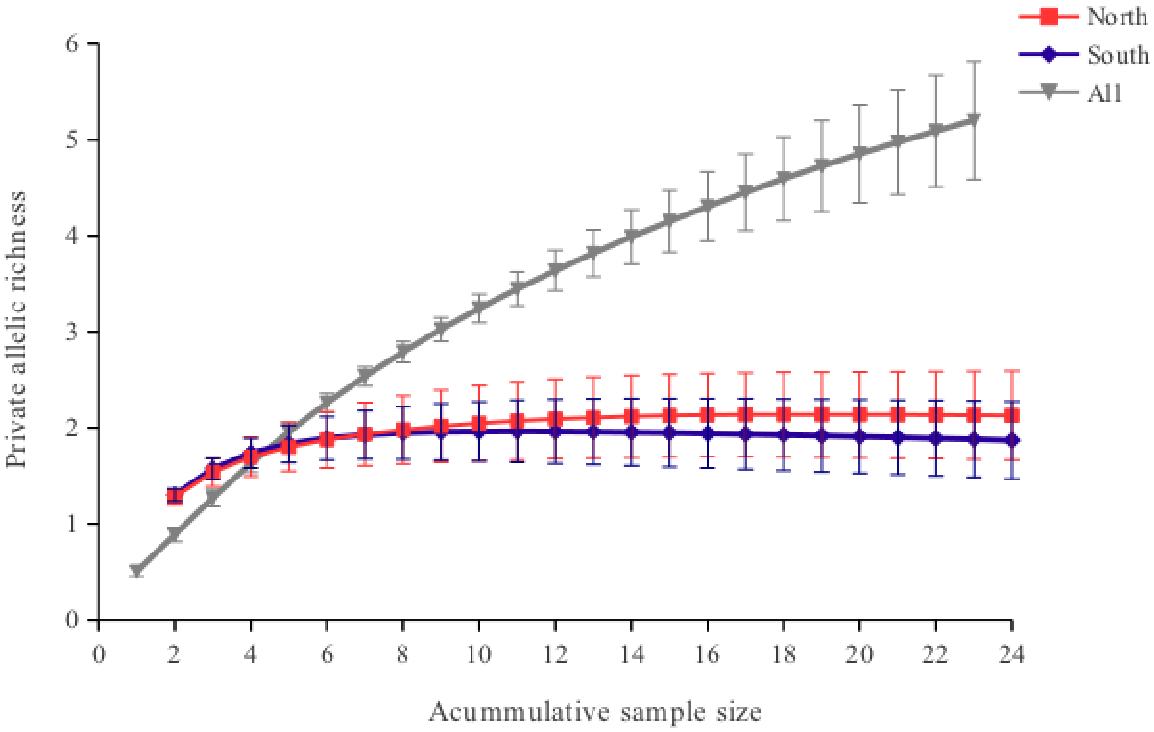

South
North
Allelic richness
12
11
10
9
8
7
6
5
4
3
2
1
0
0
5
10
15
20
25
30
35
40
45
50
55
60
65
Acummulative sample size

Figure 5


North
South
All
Private allelic richness
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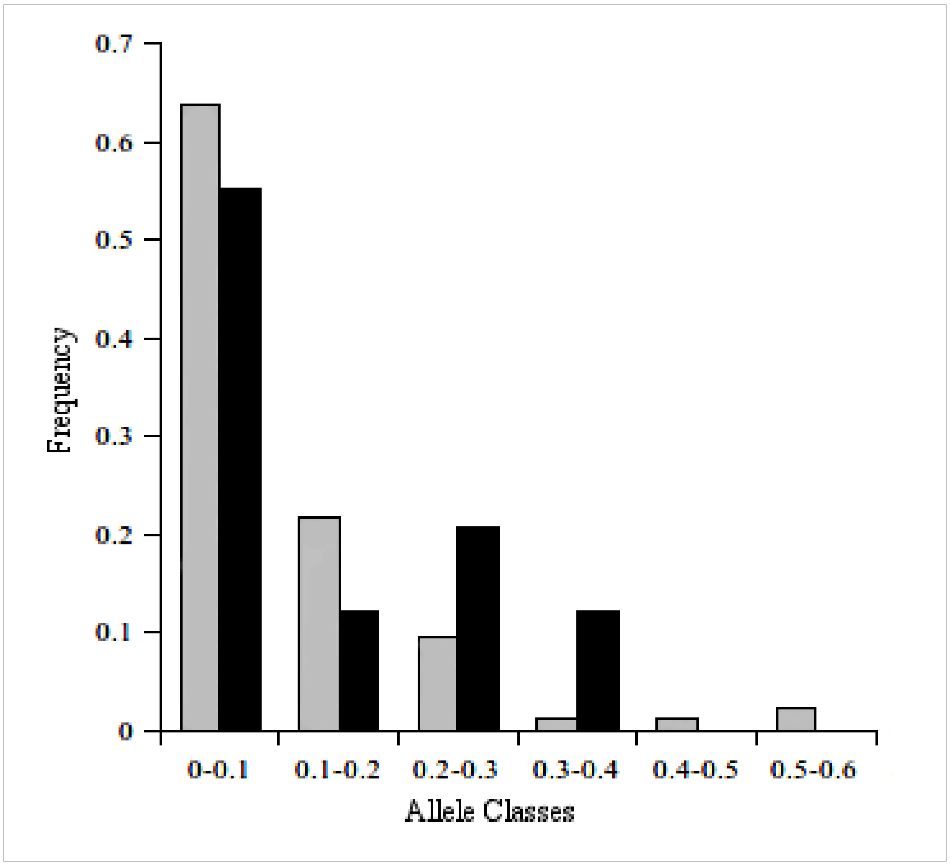
1
2
3
4
5
6
0
2
4
6
8
10
12
14
16
18
20
22
24
Acummulative sample size

Figure 6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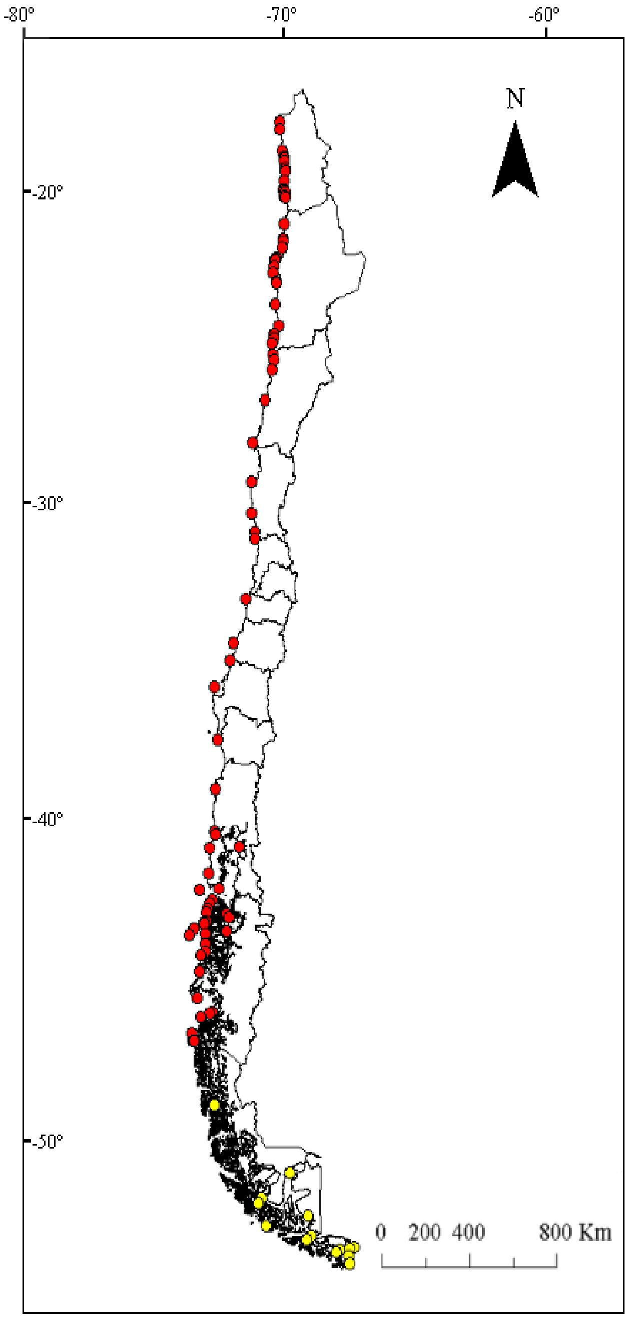
0.6
0.5
0.4
0.3
0.2
0.1
0
Frequency
0-0.1
0.1-0.2
0.2-0.3
0.3-0.4
0.4-0.5
0.5-0.6
Allele Classes

Figure 7



9.- CAPÍTULO III

Distribución espacial y conectividad de las poblaciones del lobo marino común, *Otaria flavescens*, en Chile

Spatial distribution and connectivity of the Southern sea lion, *Otaria flavescens*, populations in Chile

9.1.- INTRODUCTION

The South American sea lion (*Otaria flavescens*) is the most common species of otariids in Chile and, together with *Arctocephalus australis,* represents the most abundant and the widest geographically distributed otariid species in South America (Oliveira *et al*. 2012). Its global distribution is limited to South America, as inferred by its common name, and goes from the Southwestern Atlantic Ocean at Torres, Brazil (29°20S, 49°43W) (Scheffer 1958; Bonner and Laws 1964; Vaz-Ferreira 1976) to Cape Horn in the extreme south of South America, to Zorritos-Peru (34°00S, 80°34W) in the Southeastern Pacific Ocean (Tovar and Fuentes 1984). Due to its trophic habit, *O. flavescens* interfere with fisheries, leading to a conflict between them in almost its entire distributional range, with indirect and direct competition for resources, with negative consequences for fisheries (e.g. Szteren ans Páez 2002; Oliva et al. 2003; Hückstädt and Antezana 2003; Hückstädt and Krautz 2004; Sepúlveda *et al*. 2007b; Oliva et al. 2007; Goetz et al. 2008; Riet-Sapriza et al. 2012) and also for sea lions (Reyes et al 2013).

The interference exerted by *O. flavescens* seems to be greater with local small-scale artisanal fisheries, damaging their fishing gear and removing part of the catch (Szteren ans Páez 2002; Oliva et al. 2003; Sepúlveda *et al*. 2007b*;* Oliva et al. 2007; Goetz et al. 2008). But, there is also interference with industrial fisheries (e.g. Huckstadt and Antezana 2003; Huckstadt and Krautz 2004, Riet-Sapriza et al. 2012) and with the salmon farms in southern Chile (Oliva et al. 2003; Sepúlveda and Oliva 2005; Oliva et al. 2007; Vilata et al. 2010). This situation, together with the hunting of individuals for oil production in the past, has led to a cyclic dynamic of overexploitation and subsequent protection of the species during the 19th century (Sielfeld 1999). Since 2004 the sea lion exploitation in Chile is prohibited, but the fishery and seal oil industry pressures are mounting. Because of these demands, the government have undertaken an estimation of species' population status, determining its size and spatial distribution, with the main focus of defining culling quotas.

In order to respond to that request, the Chilean government, through *Fondo de Investigación Pesquera y Acuicultura* (FIP), financed the execution of two complete censuses of *O. flavescens* along the country. The first census was conducted between 1996-2000 (Sielfeld et al. 1997, Aguayo et al. 1998, Oporto et al. 1999, Venegas et al. 2001) and the second on 2007 (Bartheld *et al*. 2007, Oliva *et al*. 2007, Sepúlveda *et al*. 2007b). Dans et al. (2012) described the major findings of these FIP censuses. Between 18º - 32º S the total population was estimated in 70,286 individuals by Bartheld et al. (2007). Latitudes 18º to 25ºS had 88% of the population estimated for this area, which represents 54% of the total population in Chile (about 130,000 individuals). In relation to the previous estimates of Sielfeld *et al*. (1997), this area shows an increase in population size and in the number of breeding colonies. For latitudes between 32° and 40°S, the total population was estimated to be 18,179 individuals by Sepúlveda *et al*. (2007a), having remained constant since 1997, when the previous census was made by Aguayo *et al*. (1998), but there has been a sustained decrease in the number of breeding colonies in the south of Chile. In the census performed by Oliva *et al*. (2007) between 40°S and 49°S, population amounted to approximately 45,000 individuals, remaining constant since 1998, when Oporto *et al.* (1999) recorded 44.806 individuals.

In terms of total numbers, *O. flavescens* seems to be doing well with population well above thresholds sizes that may compromise its viability and accrue a high rate of extinction. These estimations, however, should be taken with caution, since as shown in this thesis (Chapter 2, 3) there is evidence that point out to the existence of spatial structuring or metapopulation type dynamics as a consequence of the trade-off between philopatric and dispersal behavior in pinnipeds (Cassini 2000; Cassini and Fernández-Juricic 2003). Considerations of these two aspects have provided ground for envisioning otariids as conforming metapopulations, as for example in the Steller sea lion (York *et al*. 1996; Raum-Suryan *et al*. 2002), whereby local breeding populations (rookeries) interchange individuals among them with the potential of affecting local dynamics (Levin 1974, Hanski and Simberloff 1997). Metapopulation dynamics require to take into account the role that the spatial structure plays on the population dynamics of the species (Hanski and Simberloff 1997, Marquet 2002), and failure for their inclusion could lead to wrong management and conservation decisions, with possible tragic consequences, like the management strategies applied during the 19th century for *O. flavescens* in Chile (Sielfeld 1999).

Female pinnipeds, seals and sea lions, show high site fidelity to their natal colonies along the rocky shores, and they tend to return to these patches in order to reproduce and bear (e.g. *Halichoerus grypus* (Pomeroy et al. 1994, 2000; Hoffman et al. 2006); *Zalophus wollebaeki* (Wolf and Trillmich 2007); *Phoca vitulina* (Harkonen and Harding 2001); *Leptonychotes weddellii* (Cameron et al. 2007); *Arctocephalus gazella* (Hoffman and Forcada 2012)). This philopatric behavior has also been reported for some male pinnipeds (e.g. *H. grypus (*Twiss *et al*. 1994, Pomeroy *et al*. 2000); *Z. wollebaeki* (Wolf and Trillmich 2007); *Arctocephalus Gazella* (Hoffman *et al*. 2006b)). This tendency has also been reported for females of *O. flavescens* (Cassini 1999, 2000), although the philopatric behavior is unknown for males of the species. Moreover, dispersal between colonies from other pinnipeds species evidence a metapopulation structure (e.g. *E. jubatus* (Raum-Suryan et al. 2002; Hoffman et al. 2006a; Fay 2004)). Also, evidence of patch colonization and patch extinction for *O. flavescens* reasserts those dynamics (e.g. Rodriguez and Bastida 1998, in Argentina; Thompson et al. 2005, in Malvinas-Falkland Islands). The main mechanisms driving these spatial dynamic are thought to be related to density-dependent population effects.

The gregarious and philopatric behavior of pinnipeds leads to a constant increment of individuals within a patch, an aspect that at high densities, entails an increment of pup mortality by density-dependent factors (e.g. *A. australis* (Harcourt 1992); *A. gazella* (Doidge *et al*. 1984); *M. leonine* (Le Boeuf and Briggs (1977)). This situation seems to emerge as a consequence of the greater aggressiveness of females due to space competition, and of males, as they augment the competition in order to gain access to bigger territories that contain more females, due to the polygynous nature of the species. More aggressive males show signals of infanticide and greater rage in male-female interactions that tend to injure females (Cassini and Fernandez-Juricic 2003).

Within this context, Baldi *et al*. (1996) found that the dispersal rate of *M. leonina* females in the Argentinean coasts diminished the number of aggressive female-female interactions, augmenting pup survival. In this manner, taking both the philopatric and dispersal behavior of pinnipeds together, it is hypothesized that dispersion of individuals decrease with distance between colonies, creating a tendency where the kinship of individuals diminishes with distance between patches. In that sense, Harrison *et al*. (2006) found that for *H. grypus,* the best movement probability model follows a negative lineal tendency with distance. Furthermore, by means of population genetics techniques on this species, Gaggiotti *et al*. (2002, 2004) found that both density and geographic distance are the responsible factors that account for the colonization of new patches.

In species with patchy and heterogeneous distribution as pinnipeds, the estimation of the dispersion kernel is necessary to understand its metapopulation structure and dynamics (Hanski and Ovaskainen 2003, Harrison et al. 2006). In otariids, population dynamics is mediated principally by females (Lima and Páez 1997). Females dispersion would be a key element in metapopulation dynamics, because breeding colonies are mainly form by females with relative few males (Cassini 1999). There is not a direct estimation of the dispersion kernel for any otariid species, but in pinnipeds there is an estimate for the grey seal, *H. grypus* (Harrison et al. 2006). Those authors found that movement probabilities decreased with increasing distance between colonies and that seals were attracted towards the larger colonies. For some otariids species it has been identified the maximum foraging distance during the breeding season (e.g. Merrick and Loughlin 1997, for Steller sea lion (*Eumetopias jubatus*);

Staniland et al. 2011, for Antartic fur seal (*Arctocephalus gazella*)). This distance can be regarded as an approach to dispersion distance, because of individuals of these species seem to stay in a particular area around the breeding colony (Baylis et al. 2011; Russel et al. 2013), keeping their movement trajectories (e.g. Riet-Sapriza et al. 2012), probably due to philopatric behavior (Pomeroy *et al*. 1994, 2000; Twiss *et al*. 1994; Cassini 1999, 2000; Harkonen and Harding 2001; Hoffman *et al*. 2006*b*; Wolf and Trillmich 2007). For the Southern sea lion, studies estimated the foraging movement patterns principally for lactating females (Thompson et al. 1998 for Falkland Island; Campagna et al. 2001 for Patagonian Argentina and Riet-Sapriza et al. 2012 and Rodriguez et al. 2012 for Uruguay). These authors found that the mean foraging distance from breeding colonies are generally within 45 and 60 km, but occasionally some trips extend to approximately 150 km from breeding sites. Dispersion distance may be important for the system connectivity. In that sense, we hypothesized the genetic break observed for the species at ~40°S may be influenced by colonies separation at more than this dispersion distance.

Given all these insights about the importance of analyzing pinnipeds population within a spatially dynamic framework, we used both *O. flavescens*' FIP censuses along the Chilean coast (Sielfeld et al. 1997, Aguayo et al. 1998, Oporto et al. 1999, Venegas et al. 2001, Bartheld *et al*. 2007, Oliva *et al*. 2007, Sepúlveda *et al*. 2007b), in order to determine spatial patterns and landscape dynamics of the species' metapopulation and propose conservation actions. In particular, we hypothesize that: 1) The spatial distribution of abundance in *O. flavescens* has an important spatial component forming clusters of spatially autocorrelated abundances at short distances as a consequence of philopatric behavior and 2) the observed spatial discontinuity in the genetic make up of *O. flavescens* colonies shown to occur at 40°S in Chapter II of this Thesis, and which separates colonies into two major clusters at 40°S, is mostly the result of a sharp change in the connectivity of populations at this latitude. For these analysis we will used spatial statistics and graph theory, which is suitable for connectivity analyses (Urban and Keitt 2001, Galpern *et al*. 2011). A graph is a set of nodes or vertices with connections between them, called links (or edges, or lines). In landscape ecology, nodes typically represent patches, and links indicate either dispersal capacity or dispersal frequency between patches. Such representations of the relations that occur between patch habitats are known as "patch-based graphs", and assume a metapopulation type of spatial structuring (Urban and Keitt 2001; Urban *et al*. 2009; Galpern *et al*. 2011). With this approach, different analysis can be applied to provide new insights on the population status. For instance, subtle modifications to the graph structure, which traduces into dispersal changes between patches, can completely affect the dynamical behavior of the entire metapopulations (Watts and Strogatz 1998, Artzy-Randrup and Stone 2010, Besozzi et al 2010). Moreover, graph theory allows detecting node's relevancy to the system connectivity, pointing out to proper evaluation of the metapopulation dynamic (Urban and Keitt 2001; Galpern *et al*. 2011).

9.2.- METHODS

To assess the spatial pattern of abundance and connectivity among colonies of the species, we compiled and compared the information of the two complete FIP censuses. The first one between 1996 and 2000 (Sielfeld et al. 1997, for Regions I-IV; Aguayo et al. 1998, for Regions V-IX; Oporto et al. 1999, for Region X and XI; and Venegas et al. 2001, for Region XII) and the second one in 2007 (Bartheld et al. 2007, for Regions I-IV; Sepúlveda et al. 2007a, for Regions V-IX; and Oliva et al. 2007, for Region X and XI).

For the estimation of the dispersion pattern we used eight microsatellite loci obtained from 47 samples of the Southern sea lion from thirteen colonies from northern Chile (~18°S – 30°S) (obtained and described in Chapter II *of this Thesis*). This information was used to calculate the relatedness matrix between individuals in MLRelatedness (Kalinowski et al. 2006). We calculated the geographic distance matrix using the library bioDist for R (Gentleman et al. 2004, R Development Core Team, 2011). For these matrices a Mantel test was done (Chessel et al. 2004) to assess the relationship between genetic relatedness and distance.

We also did an incremental spatial autocorrelation analysis for individuals abundance in breeding colonies for the 2007 census data, using the ArcGIS 10.1 software. This analysis measures spatial autocorrelation (Moran's Index) for a series of euclidean geographic distances, from 10 km to 280 km, with an increase of 10 km between iterations. The z-scores reflect the intensity of spatial clustering, and statistically significant peak z-scores indicate distances where spatial processes promoting clustering are most pronounced.

After that, we executed a network analysis with the R package sna (Butts, 2010), using euclidean geographic distance between all the colonies of the southern sea lion in Chile for the 2007 census. This analysis was done to describe the connectivity of the sea lion Chilean metapopulation, through the examination of the spatial proximity on the potential connection between nodes (colonies). For those networks, topological (i.e., number of isolated components, see below) and node weight measures (i.e., number of cutpoints, see below) were applied to quantify connectivity, defined as the minimum number of nodes whose removal renders the graph disconnected (Rayfield et al. 2011).

We chose to use a simple metric: the number of isolated components of the network as the threshold or critical distance to consider two nodes connected increases. To do this, the distance matrix between colonies was used to construct an adjacency matrix in function of the critical distance that is being evaluated (distances ranging from zero to 500 km). For each of these adjacency matrices, we determined the isolated components (the clusters of connected colonies). On the other hand, we evaluated the importance of nodes (colonies) for the maintenance of each network configurations that occur as the threshold distance is varied, through the cutpoint metric. A vertex is a cutpoint if when removed, the number of isolated components of the network increase, indicating that this point is important to keep the connectivity of the evaluated network. Thus, connectivity increases when the number of isolated components decreases. Similarly, the contribution of a given colony to the overall system connectivity is large when its cutpoint number is large for given distances.

9.3.- RESULTS

The comparison of the two censuses available for *Otaria flavescens* (1996-1999) vs 2007, shows that there was an increase of 14 breeding colonies in Chile between 18 - 48°S, with 65 breeding colonies for 1996- 1999 (Figure 1) and 79 in 2007. The increase is not randomly distributed within the country, but concentrates in northern Chile between 18 - 24°S, with an increase of 32 colonies. Between ~32 - 41°S, in central Chile, there is a decrease of 11 breeding colonies, reaching 18 breeding colonies for 2007. In southern Chile, about 41- 48°S, there is a replacement of colonies and the emergence of new ones, but with a final decrease of 11 breeding colonies. South of 48°S, census only for the first census in 2001, there is a tendency for the aggregation of the breeding colonies in the Strait of Magellan and Cape Horn, with a total of 14 breeding colonies.

From the first census to the 2007 census an increase of females, pups and juveniles abundance in north (to ~24°S) breeding colonies occurs (Figure 2). This increase is mainly for juveniles (Figure 2c). In the south, from 1999 to 2007, female abundance increased in the largest breeding colony of Chile (Metalqui, at 42°19'S). Near it a new important colony (3725 individuals census, 2344 females) emerged (Punta Chaiguaco 43°S) and other one (Doña

Sebastiana, 41°75'S) increase its size in almost 1000 individuals, reaching 3322 individuals. In the others south breeding colonies, the females abundance decreased (from ~41 – 48°S) (Figure 2a). The same negative tendency was observed for pups and juveniles (Figure 2b, c). Between latitudes 24 - 41°S, the spatial individuals abundance distribution in breeding colonies remains relatively constant between both census. But for pups, there was a significant increase in two particular colonies, Isla Lobos (31°75'S) with an increase in almost 1000 pups reaching 1337 pups for 2007. And for juveniles, there was a slightly decrease in abundance for colonies south of 36°S.

With regard to the spatial distribution of relatedness between Southern sea lion individuals in relation to geographic distance, the results show that this is highly variable and no trend can be detected (Figure 3). This qualitative results are confirmed by the results of the Mantel test, which was not significant when all individuals were considered and neither for males or female only comparisons: Mantel test for all the individuals sample, $z = 36178321$ ($p = 0.608$); for sampled males, $z = 4137243$ ($p = 0.995$); and for reproductive females, $z = 3278071$ ($p = 0.476$).

The incremental autocorrelation analysis for individuals abundance shows spatial clustering, with peaks of autocorrelation at similar euclidean distance for different cohorts and both sexes (Figure 4). In general, an autocorrelation peak occurs at distance of 60 km for adults females, adults males and juveniles, inferring aggregation of the Southern sea lion between colonies spaced at this distance. For adults, an autocorrelation peak at 100 km also occurs and for juveniles at 230 km. But the autocorrelation pattern for juveniles shows an increase to 60 km, after that it decline to 130 km. The autocorrelation pattern for adults females and males abruptly decline after distance of 110 km. Pup abundance did not show any autocorrelation pattern.

The number of cutpoints pronouncedly decrease until a critical distance of 400 km, where all colonies are connected without the need of particular patches to maintain this connectivity. Figure 5 shows that 230 km is the critical distance of connectivity between breeding colonies beyond which the colonies of the Southern sea lion from 18°S to 48°S are all connected. At this distance there is nine cutpoints colonies (Table 1) to keep all colonies connected in one network.

At 60 km of connectivity distance, cutpoint colonies (five) tend to be very variable in population size, with the only abundant colonies being Chucumata in the north (20,52 °S) with a total of 2256 individuals and with the highest number of juveniles (984). Despite that, the most important cutpoint colony respect to pup production is Isla Murta (117 pups), but with an intermediate population size (530 individuals) (Table 1). At 110 km of connectivity distance, cutpoint colonies (seven) are also variable in size, with 3 colonies of high individuals abundance, including Metalqui in the south (42.19 °S), the biggest colony of the species in Chile (Table 1). The cutpoint colonies for both critical distance are located in the north of Chile (north of 25 °S) and in the south (south of 43 °S), and are absent in central Chile. But, cutpoint colonies for complete connectivity (at 230 km of critical distance) and also the most frequent cutpoint colonies between analyzed distance, are located along the Chilean coast, with most of them concentrated in central Chile (Table 1). The population abundance and pup production of these colonies are also variable.

At critical distance less than 80 km the number of isolated components is high, but critical distances between 80 to 200 km produced a relative decrease in the number of isolated components of the configured networks, with variable number of cutpoints, being the minimum number at a critical distance of approximately 160 km (Figure 5).

On the other hand, Figure 6 shows that for critical connectivity distance less than 110 km, there are a relative high number of cutpoints at north (north of 26°S) and south (44 – 48°S). At critical distance up to 153 km, it can be seen the inverse pattern, where cutpoints tend to be confined to central Chile (28 – 40°S). For critical distance of 110 and 130 km, cutpoints are spread throughout the country. Important breeding colonies (23) as cutpoints are shown in Figure 7.

In Figure 8 it can be seen that for all critical connectivity distance equal or smaller than 220 km, there is a break in the network connectivity at approximately 32°S of latitude. It is also shown that northern Chile (until approximately 28°S) is well connected, been conformed by a single cluster with connectivity distance up to 110 km, and by two clusters at distance of 90 km. It is also shown that at critical distance of less than 175 km there is also a break of the network configuration at approximately 40°S and, within distance of 110 km and 175 km, colonies south of this latitude are all connected in a single network. Between those two connectivity breaks (32 - 40°S) and at critical distance lower than 175 km, it is observed a relative tendency of many isolated components, each cluster being conformed by fewer colonies, with a maximum of three colonies in one cluster.

9.4.- DISCUSION

The total population size for *Otaria flavescens* over its entire distribution is estimated in 400.000 individuals (Dans et al. 2012), from which approximately 35% are in Chile (Venegas et al. 2001, Sepúlveda et al. 2007, Bartheld et al. 2007, Oliva et al. 2007). At present, the conservation status of the Southern sea lion is classified as Least Concern (LC) in the IUCN Red List of Threatened Species (2011), with demographic attributes well above the threshold for considering a specie as endangered. The population size of the species is in the order of magnitude of others otariids with large populations, such as *Arctocephalus p. pusillus*, *A. gazella*, and *Cullorhinus ursinus* (Wickens and York 1997).

Despite that, the trends in population size are not the same along its distribution range. In the central and northern part of the Argentinean Patagonia, as well as in the Falkland Islands populations are increasing in numbers (Dans et al. 2004; Reyes 2004; Thompson et al. 2005). These increases, however, are still far from the population sizes recorded in the 1950s (Túnez et al. 2007a) and thus a complete recovery of the population to pre-collapse years can not be claimed as yet. In Uruguay, population size is decreasing at a rate of 4.5% reaching 12.000 individuals in 2004 (Páez, 2005). In Chile, the Southern sea lion experienced a total population increase of approximately 43% between 2007 and 1996-1999, with an increase in pup production of 42%. Despite that, this increase is not general for all the Chilean coast.Indeed, north of ~24°S is the most important area in terms of population growth, with the highest increase of total individuals abundance and with the 87% of total juveniles and 68% of the total pup production (Bartheld et al. 2007). Between 24°S and 41°S, population size seems to remain constant and relatively low (Sepúlveda et al. 2012). And between 41°S and 48°S, despite the total increase in population size (Oliva et al. 2007), the population growth shows a tendency of decline, due to the notorious decrease of juveniles, in all the area, and pups in the largest colony (Metalqui). In that sense, Oliva et al. (2007) estimated the intrinsic rate of population growth (λ) in this study area, finding values close to unity, suggesting that the Southern sea lion population is in a stable state, but with a slight projection to decline.

South of 48°S, Sielfeld (1978) estimated the total number of individuals in 13620. Then Venegas et al. (2001) estimated this value in 5689 ± 655, which corresponds to a decline of more than twice the total number of individuals in these two decades. Most breeding colonies of this region are confined to the Magellan Strait and Cape Horn, relatively far from the reproductive colonies from the Pacific coast. On the other hand, genetic differentiation analysis, by microsatellite markers, showed a unique genetic cluster between Southern sea lion of this zone and individuals south of ~40°S (Chapter II, *this Thesis*), but those results are not conclusive because of the small sample size in the Magellan Strait. Despite that, phylogeographic analysis showed the presence of haplotypes from both the Pacific and the Atlantic genetic clades in this area (Chapter I, *this Thesis*). Because of that, we may expect that the colonies in this area are connected by migrant individuals from both, the Atlantic and Pacific clades (Chapter I, *this Thesis)*, due to the accessibility to this area from both oceans (Diraison et al. 1997). Despite that, the Magellan Strait seems not to represent a corridor between both Southern sea lion genetic clades, because no haplotypes from the Atlantic were found in the Pacific coast (Chapter I, *this Thesis*). Similarly, no haplotypes from the Pacific have been found in the Atlantic coast (Túnez et al. 2007b, 2010; Feijoo et al. 2011). In that sense, the Magellan Strait and Cape Horn seems rather to be a mixing zone for the Southern sea lions. The lack of dispersion between colonies found in the Atlantic and Pacific oceans can be explained by considering the small population size that this species reaches in the Magellan Strait and Cape Horn, which lowers the probabilities of representative migration from this zone.

Contrary to expectations for philopatric animals, from whom dispersion is expected to be between nearby colonies and therefore genetic relatedness between individuals is supposed to decrease with geographic distance, our results do not shows any tendency in the variation of genetic relatedness with distance between colonies. This result supposes that the dispersion pattern is not between nearby colonies, and suggest instead a random pattern of migration. This conclusion, however, must be taken with caution, due to the small number of sampled individuals and because the genetic relatedness pattern may be influenced by stepping stone dispersion (Excoffier, Foll and Petit 2009). in that sense, our results showed that the emergence of new colonies tend to be more likely in the proximity to a big colony. For example, results showed that female abundance increased in the largest breeding colony of the species (Metalqui, 42.19°S, 74.14°W) from 1999 to 2007, and near it a new important colony

(3725 individuals census) emerged (Punta Chaiguaco 43°S, 74.26°W) and other one (Doña Sebastiana, 41.75°S, 73.80°W) reaching high population size (3322 individuals census). This scenario is in agreement with the idea that population growth results in the increase in the spillover or dispersion of females to nearby colonies due to density-dependent effects of the gregarious and philopatric behavior (Cassini and Fernandez-Juricic 2003), principally the increase of pup mortality (e.g. Le Boeuf and Briggs (1977) for *M. leonina*, Doidge et al. (1984) for *A. gazella* and Harcourt (1992) for *A. australis*). Despite this hypothesis should be tested, but it is consistent with the observation of a positive relationship between population growth and female dispersion in pinnipeds (Baldi et al. 1996), with colonization of new patches (Harrison et al. 2006; Gaggiotti et al. 2002, 2004) and with the spatial expansion pattern and population growth observed in *O. flavescens* (Grandi et al. 2008).

The spatial abundance autocorrelation analysis allows us to find common patterns between colonies composition. In that manner, it may be thought that colonies with similar composition present common population dynamics, assuming that they are connected by dispersion. Instead, distinct spatial trends in individual abundances suggest isolation of colonies that are under different environmental pressures (Fay and Punt 2013). For the Southern sea lion in Chile, we found a decrease of the abundance autocorrelation over colony distance of 100 km for females and males and over 60 km for juveniles. Those distance can be interpreted as a decrease of dispersion between colonies spaced over those distance. This, because abundance autocorrelation distances are consistent with foraging distance (Thompson et al. 1998, Campagna et al. 2001, Drago et al. 2010, Rodríguez et al. 2012, Riet-Saproza et al. 2012), allowing to assume those distance represent an estimation of the dispersion distance of the species. For pups, no autocorrelation was found, that may be explain by the fact that pups abundance is primary influencing by survival, which in turn is strongly dependent on local environment conditions (Beaupled et al. 2006, Lea et al. 2009, Seguel et al. 2011, Drago et al. 2011).

The spatial network analysis results show that, for dispersion distance less than 175 km, consistent with the spatial abundance autocorrelation and with movement distance, there are some general patterns: the existence of only one isolated component north of 32°S and also only one isolated component south of 40°S. Between these latitudes, colonies are more spaced, forming relatively more isolated components with a relatively abundant number cutpoints to maintain the network configuration.

The results of the network configurations are partially consistent with the abundance distribution of the Southern sea lion in Chile. Both analysis showed a demographic discontinuity at ~40 -42°S, but in the north the demographic break changed in latitude between both analysis. For the network analysis this break occurs at 32°S, and for the abundance distribution analysis, it is at 24°S. Not exact, those results are consistent with the existence of sharp discontinuities in the distribution of different types of organisms, processes and oceanographic regimes along the Chilean coast (Camus 2001, Escribano et al. 2003, Valdovinos et al. 2003, Navarrete et al. 2005), delimiting different biogeographic units (Camus 2001). According to Camus (2001), The major biogeographic break (~41°S) divides the Magellan province to the south (from ~41°S to 56°S) from the north, were the Chilean coast could be divided in two more biogeographic units: the Peruvian province (from Peru to ~30°S) with year-round upwelling and the Intermediate area (~30°S to ~ 41°S) with seasonal upwelling. These two north provinces are separated by the tropical convergence zone (~30°S) and an abrupt narrowing of the continental shelf (Strub et al. 1998; Thiel et al. 2009). Instead, the discontinuity at 41°S is associated with important geophysical and oceanographic changes; the West Wind Drift (WWD) reaches the coast and divides into the equatorward Humboldt Current to the north and the poleward Cape Horn Current (see e.g. Strub *et al*. 1998; Escribano *et al*. 2003). Thus, this latitude is associated with important discontinuities in species abundance, diversity and recruitment of several pelagic and benthonic species (Camus 2001; Navarrete et al. 2005), that may also affect the distribution of top predators such as the Southern sea lion, because of changes in prey availability (Montecino and Lange 2009). The demographic discontinuity at ~40 -42°S is consistent with the genetic population structure found for the species in Chile, through the analysis of microsatellite markers (Chapter II, *this Thesis*), showing two genetic clusters for the species, separated at ~40°. Instead of that, genetic analysis did not show any genetic break at ~30°S, implying that demographic changes at this latitude are not because of a discontinuity in the distribution of the Southern sea lion, but rather to the capacity of the environment to support a certain number of sea lions.

In terms of the conservation and management planning of the Southern sea lion in Chile, it is important to take into account the drastic discontinuity in demography of the species at 41°S, consistent with the genetic results, that emphasized the subdivision of the Chilean coast in two different Management Units (MU's) (Moritz 1994) at this latitude. Regarding the northern demographic changes, it is not clear that it does not represent a homogeneous unit, and this must be investigated further. Also, the separation of the Magellan Strait and Cape Horn zone must be confirmed.

Although, genetic (Chapter I and II *of this Thesis*) and demographic conditions of the Southern sea lion do not show a population problem in most the Chilean coast, exploitation of the species as a resource, to avoid competition with fisheries, should be taken with caution. This because the dependence of the sea lion populations with resource abundance (Sielfeld and Guzmán 2002, Soto et al. 2004, 2006), together with the decline of representative sea lion preys (Aguayo and Maturana 1973, George-Nacimento et al. 1985 and Sielfeld et al. 1997) by fishery industry during last decades (Moreno and Fedele 2008).

Conservation effort must be placed in southern Chile, because of the decline in colony number and population abundance in most colonies, and because of the prospective decline of the populations (Oliva et al. 2007). Moreover considering that in south-central Chile bottom trawling of sea lion (Reyes et al. 2013) and illegal catch records exist, mainly to obtain the sea lion fat for medicinal purposes, pup for fur pelts and meat for human consumption and for baits, especially during fishing operations south of 38°S (Sielfeld 1983, Torres et al. 1990). In that sense, the species south of 48°S is considered Vulnerable (VU) by the ”Libro rojo de vertebrados terrestres de Chile” (Glade, 1993). Some sea lion colonies in this zone are located in protected areas: Cabo de Hornos National Park, Alberto de Agostini National Park and Francisco Coloane Coastal Marine Protected Area. But, as exposed by Sielfeld (1997), only the last one helps to protect the specie, because the other ones protect only the terrestrial area. And also, without the correct supervision of those areas, illegal caches will continue. It is also important to determine the causes of decline in colony number and population abundance in most colonies, for southern Chile, investigating the possible direct effects of illegal sealing, and indirect effects of fisheries and the abrupt increase of salmon farms. For the correct management of the specie, it is also important to deeply investigate the philopatric behavior of the species. Moreover, if the species seems to show fidelity to an area, where individuals not only reproduce but also forage. On the other hand, the high population growth of the species north of 24°S must be taken with caution, because this area experiences the most drastic effects of the ENSO events (Trillmich *et al*. 1991; Guinet *et al*. 1994; Bradshaw *et al*. 2000; Sielfeld and Guzman 2002; Soto et al. 2004, 2006; Le Boeuf and Crocker 2005; Oliveira *et al*. 2006). Further, it is important to maintain monitoring and protect the largest colonies north of these latitude, because they comprises the major percentage of the population. These colonies are: Sur de Cabo Lobos (18.81°S, 70.35°W; with 5503 individuals census for 2007), Punta Lobos – Arica (18.84°S, 70.35°W, 11885 individuals census for 2007), Punta Piojos (19.72°S, 70.15°W; 8415 individuals for 2007), Piedra Parada (23.05°S, 70.56°W; 4184 individuals) and Bandurrias del Sur (23.30°S, 70.60°W; 8540 individuals).

Moreover, because important cutpoint colonies do not present any pattern of individual abundance, it is also important to protect these colonies that maintain the connectivity of the Chilean distribution of the species. In this manner, it is important to protect cutpoint colonies that keep the connectivity at distance of 60km and 110km, as a function of the results of the abundance aggregation analysis. Equally important are the breeding colonies that are cutpoints at varying distance of connectivity, being the most frequent cutpoints and thereby the most important colonies for the connectivity of the Southern sea lion metapopulation in Chile for variable dispersion scales. Also important are cutpoint colonies that allow complete connectivity of the Chilean Southern sea lion distribution (at connectivity distance >230km). Important cutpoint colonies are: Chucumata (20.52°S, 70.19°W), Punta Paquica (21.90°S, 70.19°W), Punta Guaque (22.68°S, 70.28°W), Punta Dos Reyes (24.55°S, 70.57°W), Punta Bandurrias (25.22°S, 70.43°W), Punta Cachos (27.65°S, 71.04°W), Isla Chañaral (29.04°S, 71.58°W), Centinela (30.30°S, 71.65°W), Punta Virgen (31.35°S, 71.65°W), Maintencillo (32.18°S, 71.55°W), Punta Topocalma (34.14°S, 71°W), Cabo Carranza (35.57°S, 72.62°W), Cobquecura (36.12°S, 72.81°W), Isla Santa María (36.96°S, 73.54°W), Lobería (38.66°S, 73.48°W), Dehui (40.26°S, 73.73°W), (Metalqui, 42.19°S, 74.14°W), Punta Chaiguaco (43°S, 74.26°W), Islote Murta (43.87°S, 74.17°W), Isla Gertrudiz (44.56°S, 73.90°W), Isla Paz (44.94°S, 74.63°W), Islote Seno Cornish (46.16°S, 75.03°W) and Roca este Isla Wall (46.77°S, 75.2°W) (Figure 7). Of all these breeding colonies, the colony of Isla Chañaral is the only one in a protected area (Pingüino de Humboldt National Reserve). Indeed, Tognelli et al (2009), based on the analysis of 2513 marine species of invertebrate, vertebrate and algae, show that the area between 25 and 40ºS, is particularly important for the conservation of coastal marine ecosystems as they concentrate a large number of irreplaceable sites with unique biodiversity.

9.5.- BIBLIOGRAPHY

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9.6.- FIGURES AND TABLES

T**able 1:** Important breeding colonies of the Southern sea lion, for the connectivity of the system through analysis of cutpoints, based on representative critical euclidean geographical distance of connectivity between colonies: cutpoints at 65 km and 110 km, for complete connectivity of the system (occurs at 230 km) and most frequent cutpoints from analyzed distance. Individuals abundance of these colonies for the 2007 census are shown. Indet. refers to indeterminate individuals.

F**igure 1:** Map of Chile with the breeding colonies in both FIP censuses; 1996 – 2000 or C1 and 2007 or C2. Green squares refers to the colonies that were censused only in C2. Red cycles refer to the colonies that were recorded in both C1 and C2. Yellow triangles refers to the colonies that were recorded only in C1. Orange crosses refers to the colonies recorded in C1 south of 48°S.

F**igure 2:** Latitudinal distribution of the abundance of individuals in breeding colonies within Chile. Red diamonds and continuos lines refer to the abundances found in the 2007 census and the blue squares and dashed line refer to the abundance from the 1996-2001 census. **a)** abundance of females, **b)** abundance of pups, **c)** abundance of juveniles.

F**igure 3:** Scatterplot of the relationship between genetic relatedness between all individuals sampled between ~18 - 30°S (n=50) and the geographic distance between them

Figure 4: Incremental spatial autocorrelation analysis (Moran's Index) of individuals abundance in breeding colonies of the Southern sea lion, for the 2007 census. Statistically significant z-scores are are shown. a) for pups abundance, b) for juveniles abundance, c) for females abundance and d) for males abundance.

F**igure 5:** Number of isolated components (in black) and number of cutpoints (in red) in function of the critical euclidean distance of connectivity between breeding colonies of the Southern sea lion census in 2007.

Figure 6: Assessment of the importance of breeding colonies for the connectivity of the system through analysis of cutpoints for different critical euclidean distance of connectivity between breeding colonies of the Southern sea lion census in 2007. Only cutpoint colonies are shown.

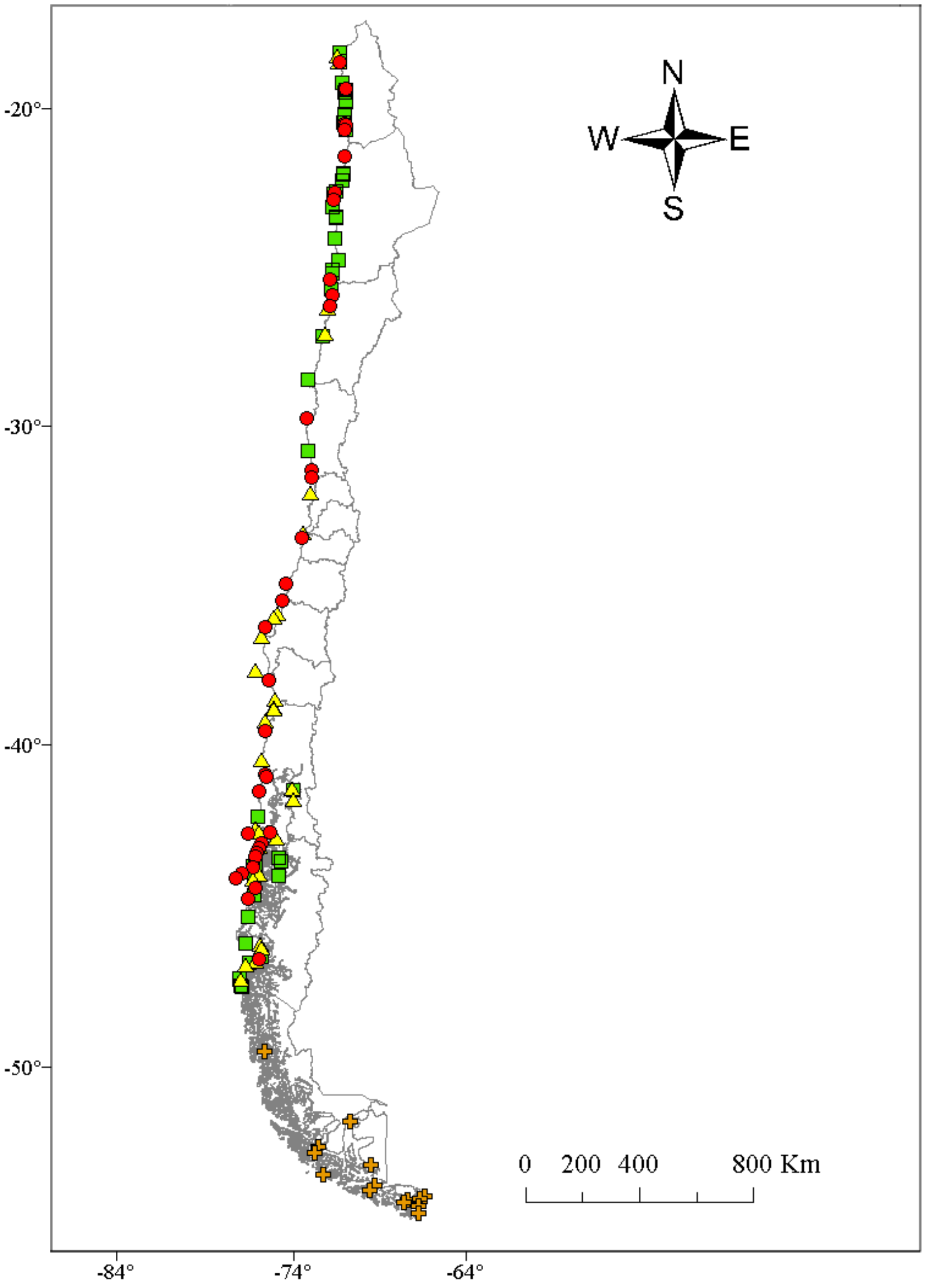
Figure 7: Map of Chile showing important breeding colonies of the Southern sea lion, for the connectivity of the system through analysis of cutpoints, based on representative critical euclidean geographical distance of connectivity between colonies: cutpoints at 65 km and 110 km, for complete connectivity of the system (occurs at 230 km) and most frequent cutpoints from analyzed distance (census in 2007).

Figure 8: Isolated components that would result at different critical euclidean distance of connectivity between breeding colonies of the Southern sea lion (census in 2007).

Table 1

CUTPOINTS		LAT (°S)	LONG (°W)	ABUNDANCE 2007					
				Males	Females	Juveniles	Pups	Indet.	Total
At distance of 60 km	Chucumata	20.52	70.186	141	744	984	43	344	2256
	Punta Guaque	22.68	70.283	15	152	119	1	33	320
	Islote Murta	43.87	74.169	41	169	73	117	130	530
	Isla Gertrudiz	44.56	73.902	7	17	12	10	32	79
	Isla Paz	44.94	74.626	8	43	3	40	36	131
At distance of 110 km	Punta Paquica	21.90	70.186	99	506	587	2	100	1294
	Punta Dos Reyes	24.55	70.573	97	71	46	2	30	247
	Punta Bandurrias	25.22	70.428	26	47	17	34	22	146
	Metalqui	42.19	74.142	2060	9290	713	4072	494	16628
	Punta Chaiguaco	43.00	74.257	292	2344	419	446	224	3725
	Islote Seno Cornish	46.16	75.025	10	28	13	32	28	112
	Roca este Isla Wall	46.77	75.214	4	13	3	9	50	78
Complete connectivity	Punta Cachos	27.65	71.04	14	58	17	59	33	182
	Isla Chañaral	29.04	71.58	190	485	117	215	116	1124
	Centinela	30.30	71.65	27	113	25	109	19	292
	Maintencillo	32.18	71.55	18	35	3	11	22	89
	Punta Topocalma	34.14	71.00	97	419	92	144	63	846
	Cabo Carranza	35.57	72.62	144	907	184	84	169	1565
	Isla Santa María	36.96	73.54	125	174	51	2	156	508
	Lobería	38.66	73.48	219	1418	355	225	130	2346
	Dehui	40.26	73.73	99	333	104	21	119	676
Most frequent	Punta Dos Reyes	24.55	70.57	97	71	46	2	30	247
	Punta Cachos	27.65	71.04	14	58	17	59	33	182
	Isla Chañaral	29.04	71.58	190	485	117	215	116	1124
	Centinela	30.30	71.65	27	113	25	109	19	292
	Punta Virgen	31.35	71.65	14	29	15	2	4	64
	Cobquecura	36.12	72.81	300	1788	184	592	129	2992
	Isla Santa María	36.96	73.54	125	174	51	2	156	508
	Lobería	38.66	73.48	219	1418	355	225	130	2346
	Dehui	40.26	73.73	99	333	104	21	119	676
	Roca este Isla Wall	46.77	75.21	4	13	3	9	50	78

Figure 1



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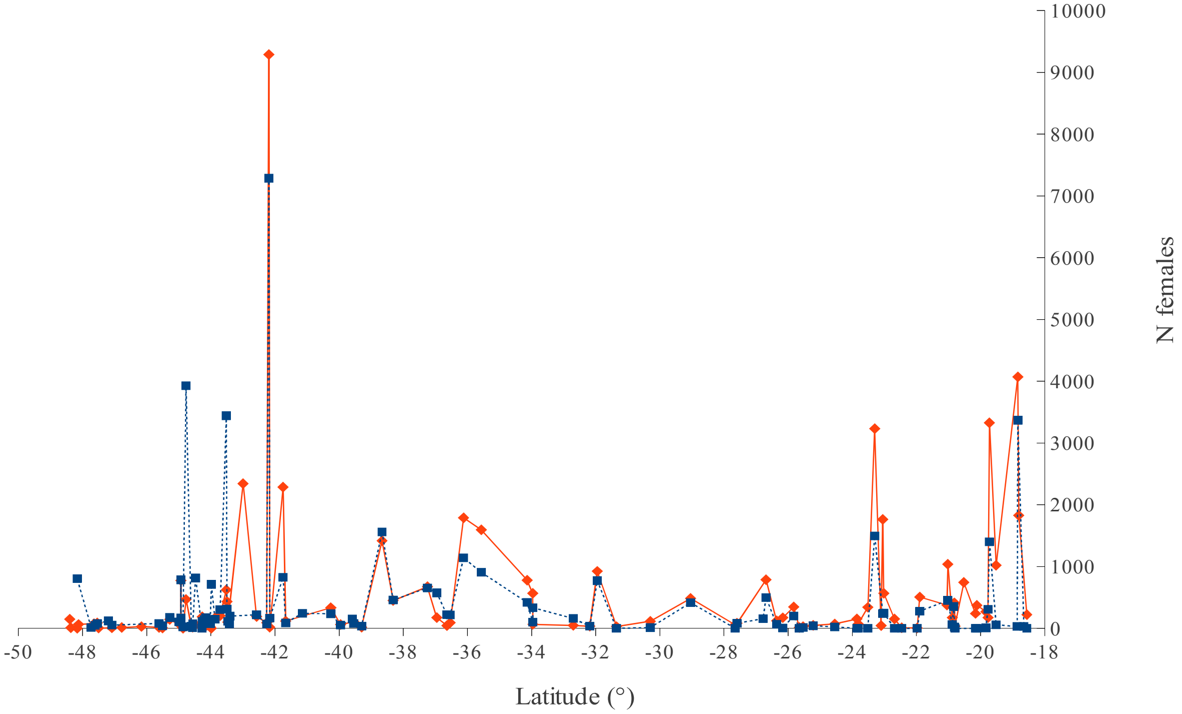
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8000
7000
6000
5000
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-48
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-42
-40
-38
-36
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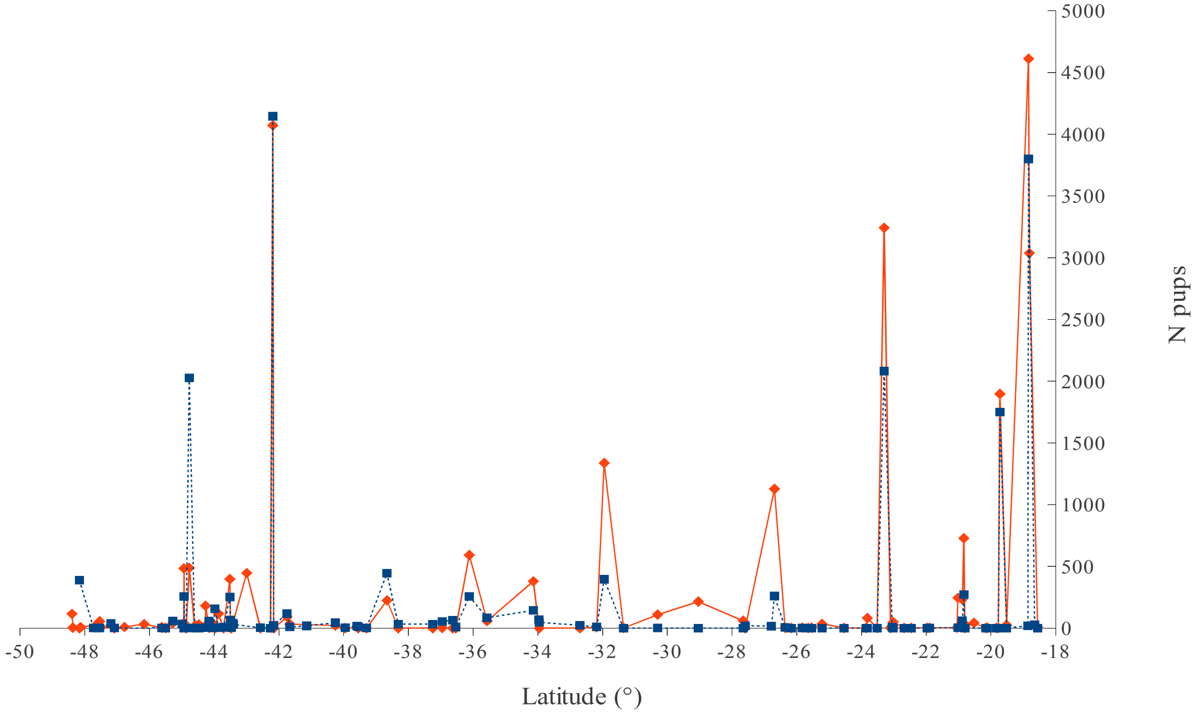
-32
-30
-28
-26
-24
-22
-20
-18
Latitude (°)

Figure 2 (b)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1500
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500
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-42
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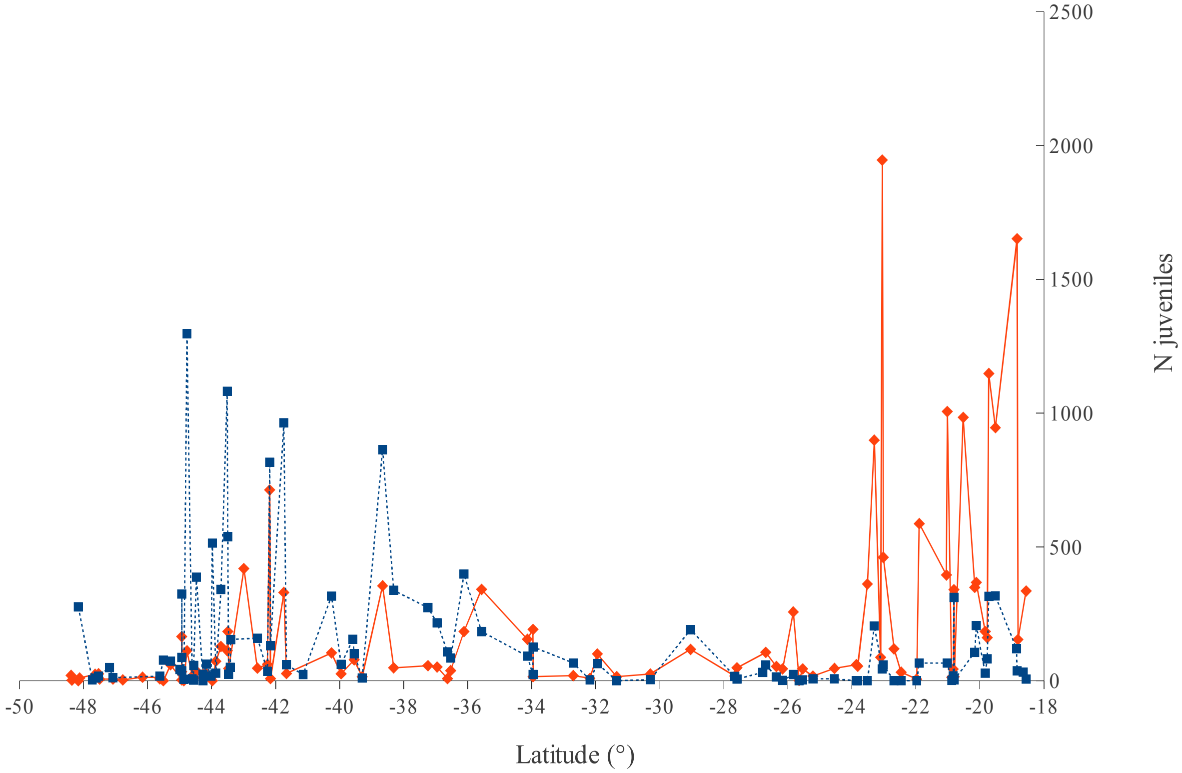
-36
-34
-32
-30
-28
-26
-24
-22
-20
-18
Latitude (°)

Figure 2 (c)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2000
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500
0
N juveniles
-50
-48
-46
-44
-42
-40
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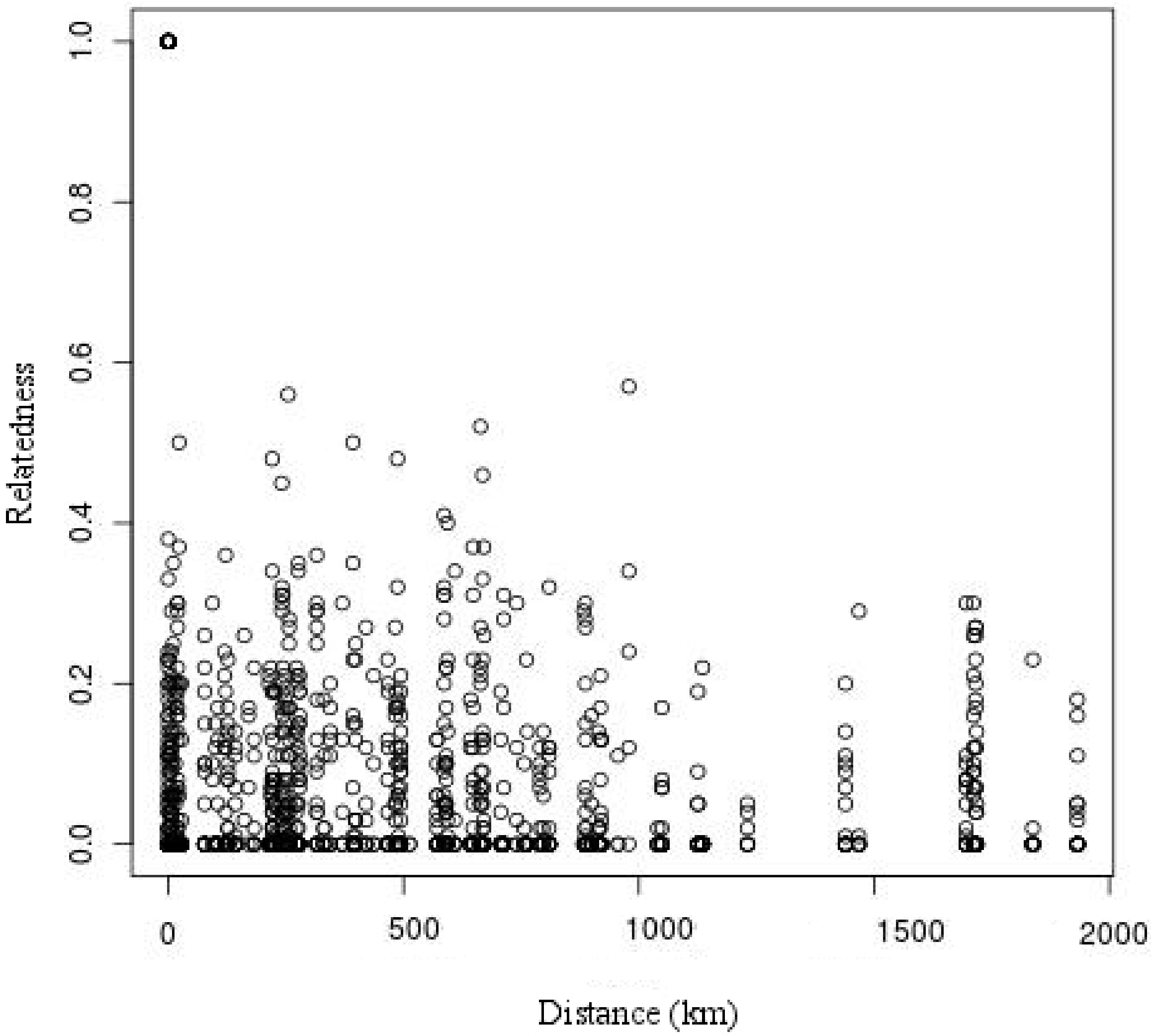
-32
-30
-28
-26
-24
-22
-20
-18
Latitude (°)

Figure 3



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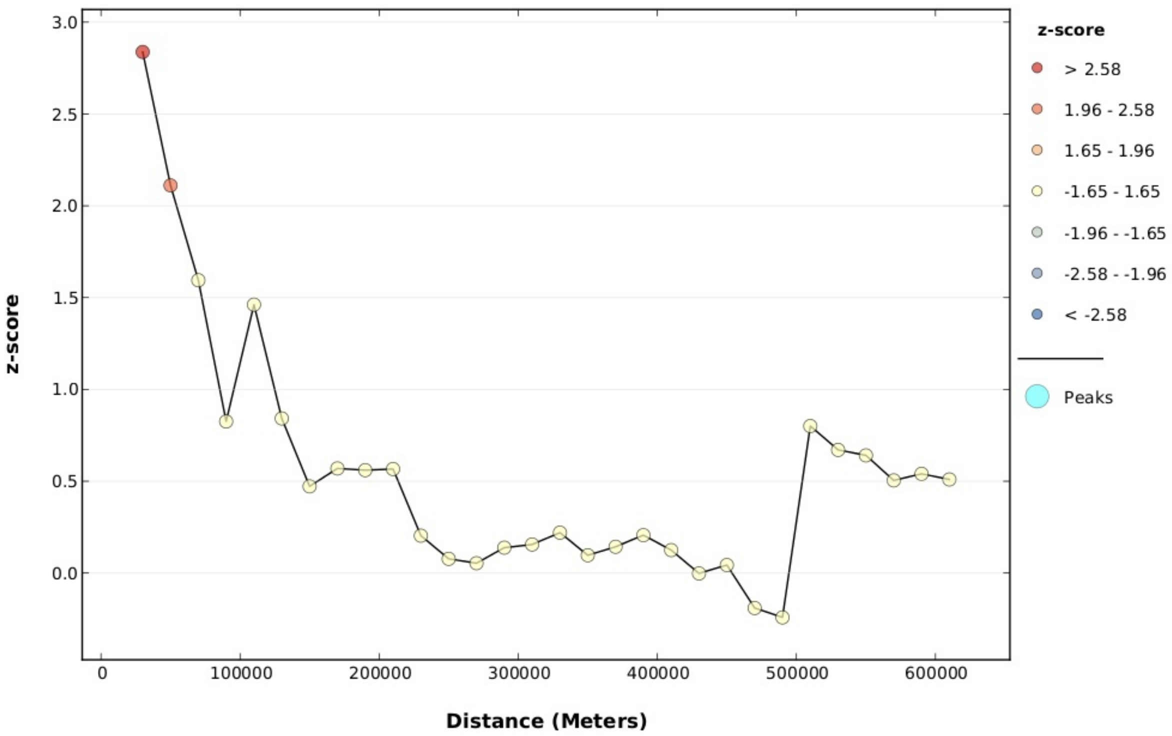
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500000
600000
Distance (Meters)
z-score
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1.96 - 2.58
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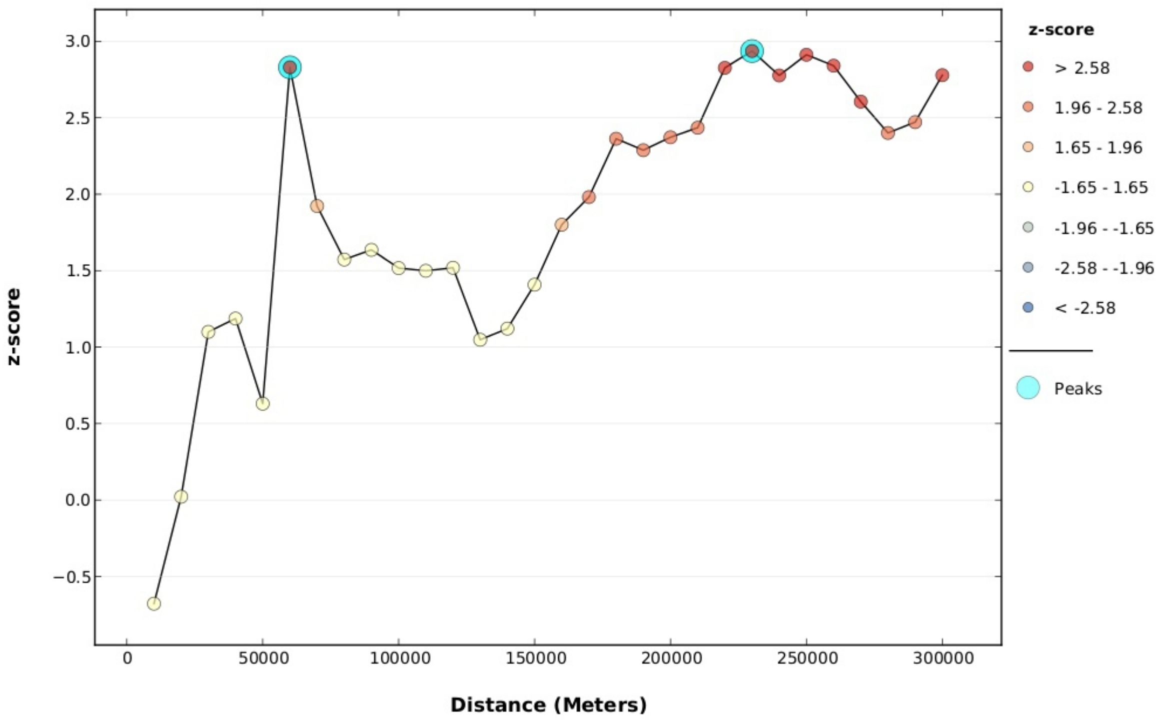
-1.65 - 1.65
-1.96 - -1.65
-2.58 - -1.96
< -2.58
Peaks

Figure 4 (b)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−0.5
0
50000
100000
150000
200000
250000
300000
Distance (Meters)
z-score
> 2.58
1.96 - 2.58
1.65 - 1.96
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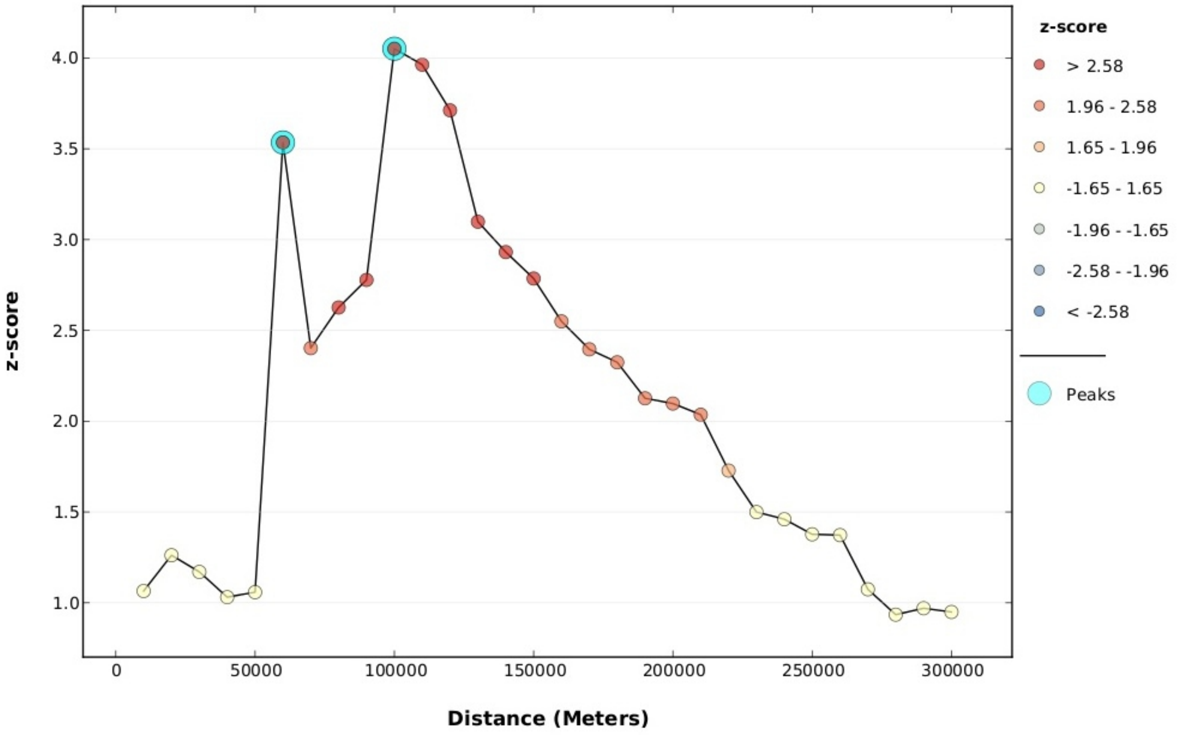
-1.96 - -1.65
-2.58 - -1.96
< -2.58
Peaks

Figure 4 (c)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Distance (Meters)
z-score
> 2.58
1.96 - 2.58
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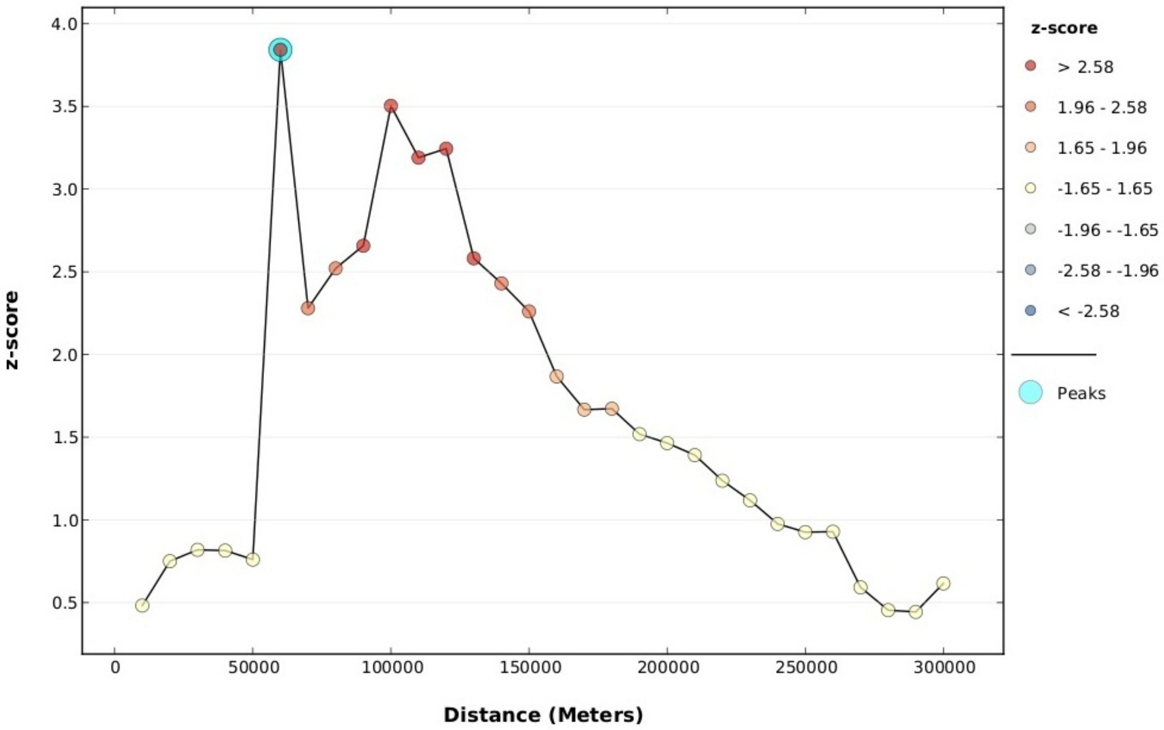
Peaks

Figure 4 (d)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2.0
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250000
300000
Distance (Meters)
z-score
> 2.58
1.96 - 2.58
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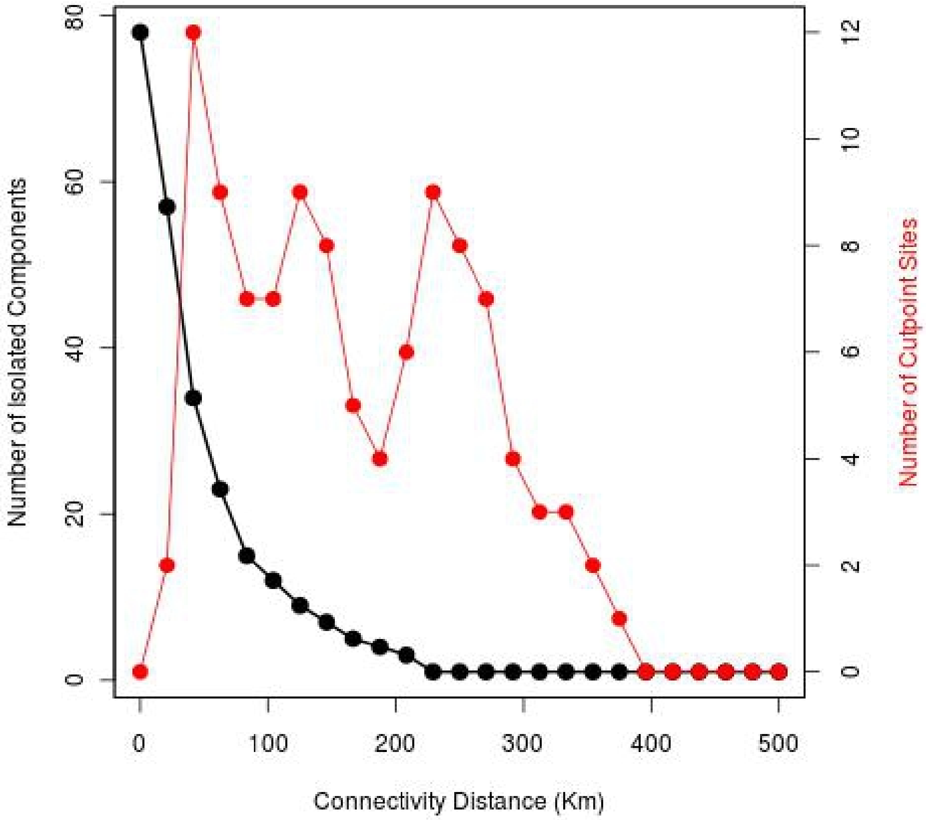
-1.96 - -1.65
-2.58 - -1.96
< -2.58
Peaks

Figure 5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40
60
80
Number of Cutpoint Sites
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2
4
6
8
10
12
0
100
200
300
400
500
Connectivity Distance (Km)

Figure 6

Latitud (°S)	43	65	90	110	130	153	175	196	218	230
19.52			X							
20.16	X									
20.52	X	X								
21.90				X	X					
22.68		X								
23.30	X									
23.51	X									
24.55			X	X	X					
25.22			X	X						
25.54	X									
25.83	X									
26.17	X									
26.36	X									
26.69					X					
27.65							X	X	X	X
29.04							X	X	X	X
30.30						X	X	X	X	X
31.35					X	X	X			
31.95			X							
32.18										X
34.14										X
35.57									X	X
36.12					X	X	X			X
36.96								X	X	X
38.66								X	X	
40.26								X	X	X
41.75					X					X
42.19				X	X					X
43.00				X	X					
43.87		X								
44.27	X									
44.56		X								
44.94	X	X								
45.28	X									
45.51	X									
46.16			X	X						
46.77				X	X	X				
47.54	X									
47.64			X							
48.13			X							

Distance (km)

Figure 7

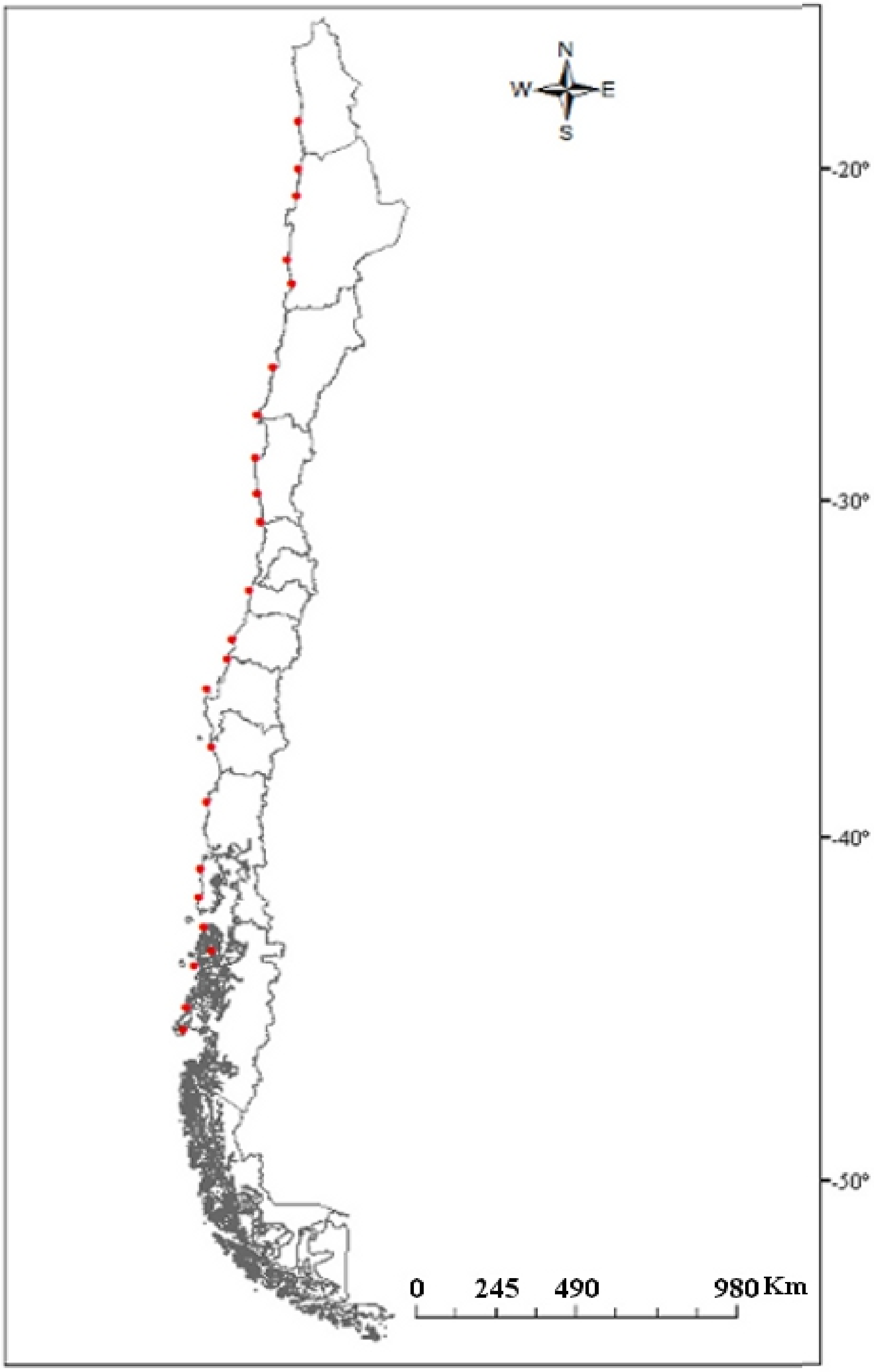
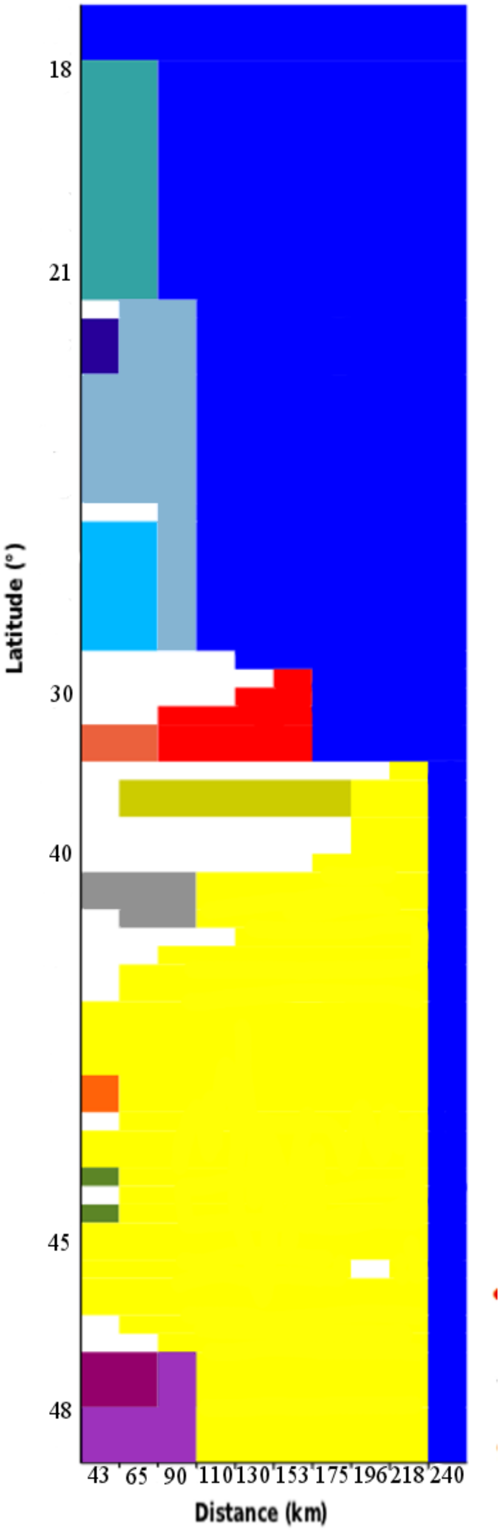


Figure 8


18
21
30
40
45
48
Latitude (°)
43
65
90
110
130
153
175
196
218
240
Distance (km)

10.- CONCLUSIONES

O*taria flavescens* se encuentra dividida en dos clados filogenéticos, el clado del Atlántico y el clado del Pacífico. conformando su distribución en la costa del océano Pacífico un único clado. Por otro lado, al sur de los 45°S, la mayoría de las colonias reproductivas se encuentran confinadas al Estrecho de Magallanes y Cabo de Hornos (al sur de 50°S). En esta área se presentan haplotipos de ambos clados, por lo que se plantea que esta zona representa un area de mezcla. El tiempo de divergencia entre ambos clados filogenéticos es aproximadamente hace 78.000 años, durante el Último Período Glacial, donde el sur de Chile se encontraba cubierto de una capa de hielo y se presentaron importantes cambios oceanográficos como el desplazamiento hacia el Ecuador del límite norte de la corriente Circumpolar Antartica (ACC), trayendo consigo cambios en la distribución de la productividad y por lo tanto de los depredadores marinos (Lamy et al., 1998, 2000; Le Boeuf and Crocker, 2005; Marchant et al., 2007; Jouzel et al., 2007).

El lobo marino común experimentó una expansión demográfica en Chile aproximadamente hace 13.000 años, según lo demuestra el análisis de la región control del ADN mitocondrial. Esta fecha coincide con el fin del Último Máximo Glacial (LGM)

(McCulloch et al. 2000). Resultados similares se encontraron para el clado Atlántico (Túnez et al. 2010, Feijoo et al., 2011), así como para otras especies acuáticas en el sur de Chile (Ruzzante et al. 2008, Cárdenas et al. 2009, Ibáñez et al. 2011).. En Chile, durante este período, se retrajeron los glaciales y se presentó un incremento en la productividad marina, y por lo tanto de los niveles tróficos superiores, debido al reforzamiento del sistema de surgencia de la Corriente de Humboldt (Romero et al., 2006).

A pesar de la drástica disminución del tamaño poblacional que experimentó *O. flavescens* durante los últimos dos siglos, mediante el análisis de la región control del *mt*ADN y de marcadores microsatelitales, no se encontraron evidencias de un cuello de botella genético reciente para las poblaciones chilenas. Este patrón también se ha visto en varias especies de otáridos (e.g. Lancaster et al. 2010, Hoffman et al. 2011). Por lo que, en función de las evidencias, se platea que luego del cuello de botella demográfico, las colonias de difícil acceso actuarían como posibles refugios para la recolonización, permitiendo la recuperación y persistencia de las metapoblaciones de la especie (Hanski 1991, Campbell et al. 2008). Además, los altos niveles de flujo génico a la que esta dinámica metapoblacional conlleva (Manel et al. 2003, Campbell et al. 2008), junto con la existencia de expansiones demográficas históricas para la mayoría de estas especies (e.g. Curtis et al. 2009, Lotze and Worm 2009), pudieran estar impidiendo detectar los efectos genéticos producidos por la cacería indiscriminada.

Los resultados del análisis de diferenciación genética, mediante microsatellites, muestran que *O. flavescenes* en Chile se encuentra separada en dos Unidades de Manejo (MU): norte y sur de ~40°S, acorde con el mayor quiebre biogeográfico de la costa de Chile (Camus 2001).

Igualmente, el análisis de la distribución de abundancias, así como el efecto de la distancia sobre la conectividad del sistema, confirman la existencia de un quiebre en la distribución de la especie a esta latitud; Además se observa un cambio en la distribución de abundancias y en la conectividad por distancia entre las colonias a ~30°S. A esta latitud también se presenta un quiebre biogeográfico, separando la Zona Intermedia (30°S to ~ 42°S) de la Provincia Peruana (desde Perú hasta 30°S) (Camus 2001), presentándose cambios en el régimen de surgencias y en la topografía de la costa, además de presenciarse una menor disponibilidad de sitios aptos para la formación de colonias de la especie (Camus 2001, Narvaez et al. 2004).

Contrario a lo esperado para animales filopátricos, mediante el análisis de diferenciación genética y parentesco entre individuos, no se observó un patrón claro de dispersión en relación a la distancia geográfica entre las colonias de la especie. A este respecto, la abundancia de individuos mostró una disminución de la autocorrelación espacial sobre los 100km, congruente con la distancia de forrageo determinada para la especie (e.g. Thompson et al. 1998, Riet-Sapriza et al. 2012, Rodríguez et al. 2012). De esta manera, se plantea que estas distancias representan la distancia de dispersión de la especie. Debido a que la mayoría de las colonias reproductivas de *O. flavescens* en Chile se encuentran distribuidas a una distancia menor a 100 km, la ausencia de un patrón genético claro de dispersión pudiera deberse a dispersión tipo “stepping stone” (Oyler-McCance and Leberg 2005, Hartl and Clark 2007).

10.1.- Manejo y conservación

A pesar de que *Otaria flavescens* está clasificada como especie de “preocupación menor” a nivel internacional (IUCN Red List of Threatened Species 2011) y las condiciones genéticas y demográficas mostraron que en la actualidad la especie en Chile se encuentra “saludable”, la explotación de la especie, con el fin de mitigar la interferencia de la misma con la pesquería, debe ser tomado con cautela. Esto debido a la dependencia de las poblaciones del lobo marino con la abundancia de recursos (Sielfeld y Guzmán 2002, Soto et al. 2004, 2006), en conjunto con el declive, durante las últimas décadas, de las poblaciones de algunas presas representativas de la dieta de *O. flavescens* por la industria pesquera (Aguayo y Maturana 1973, Nacimento et al. 1985, Sielfeld et al. 1997 y Moreno and Fedele 2008), y por la dependencia observada de la dinámica demográfica de la especie a las condiciones climáticas.

Se propone que para el manejo y conservación del lobo marino común en Chile, cada unidad de manejo debe tratarse por separado, así como también las colonias del Estrecho de Magallanes y Cabo de Hornos. A pesar de que los valores de N_e para ambas MU (N_e norte = 12,320 y N_e sur =7,475 individuos) están muy por encima del valor mínimo viable descrito para vertebrados (Reed et al. 2003) y en comparación con especies de otáridos que se encuentran catalogadas en peligro de extinción (e.g. Weber et al. 2004), esfuerzos en conservación deben ponerse principalmente en el sur de Chile, debido al valor de la razón N_e/N encontrado para la MU sur (0.229), el cual se encuentra por debajo del rango normal para especies silvestres (Nunney 1995). Este hecho advierte sobre posibles efectos de las fluctuaciones poblacionales sobre la variabilidad genética de la especie, haciéndola menos tolerante a cambios estocásticos (Nunney 2005). Por otro lado, el alto crecimiento poblacional de la especie en la MU norte debe ser tomando con cautela, debido a que la razón N_e/N (0,296) de estas poblaciones se encuentra en el límite inferior del rango normal (0,25-0,75). Además, esta zona presenta los más drásticos efectos negativos de los eventos ENSO sobre las poblaciones de otáridos (e.g. Soto et al. 2004, 2006, Le Boeuf and Crocker 2005, Oliveira *et al*. 2006). De esta manera, estrategias de manejo que conlleven a fluctuaciones poblacionales drásticas y constantes deben ser evitadas.

Es importante que en investigaciones futuras se realice un estudio más exhaustivo para la zona del Estrecho de Magallanes y Cabo de Hornos, así como de la Zona Intermedia (~30°S – 40°S). Esto con la finalidad de corroborar la existencia de una zona de mezcla entre ambos clados filogenéticos en la zona más austral de Chile y poder confirmar que las colonias de la Zona Intermedia pertenecen a la MU norte y no representan una MU por si sola o un área de mezcla entre ambas MUs. Igualmente, la determinación de los factores bióticos y abióticos que influyen en la distribución espacial de la especie,permitirían establecer decisiones de manejo a más largo plazo, por medio de las predicciones de los cambios en estas variables.

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