Cambios en la ecología trófica de los depredadores apicales del Mar Argentino durante el Holoceno

Fabiana Saporiti

El Mar Argentino ha sufrido un impacto humano creciente desde el Holoceno medio hasta hoy en día, fruto del cual se han producido importantes cambios en los niveles más altos de la red trófica. Las actividades extractivas (caza y pesca), tanto la aborigen como la actual, tienen la tendencia a explotar las especies de mayor tamaño, produciendo el efecto conocido en gestión de pesquerías como "*fishing down the food web*". En otras palabras el impacto humano llevaría a cadenas tróficas más cortas como consecuencia de la extinción de los depredadores apicales. Sin embargo, las especies que sobreviven a la explotación, si bien reducidas drásticamente en número de individuos, permanecen en el ecosistema y desempeñan un papel trófico. En esta tesis se han analizado los cambios que ocurrieron en la red trófica del Mar Argentino durante el Holoceno medio y tardío como consecuencia de la actividad humana, centrándose principalmente en dos de sus depredadores más abundantes: el lobo marino común (*Otaria flavescens*) y el lobo marino fino (*Arctocephalus australis*). Por un lado se observó que los cazadores-recolectores no tuvieron un impacto relevante sobre los patrones de uso del hábitat y alimentación de estas dos especies, ya que durante todo el Holoceno no se produjeron apenas cambios en sus dietas. Sin embargo, sí variaron los patrones de explotación de pinnípedos por parte de los aborígenes, seguramente como consecuencia de cambios en la producción primaria marina que debido a una posible sobreexplotación de los pinnípedos. No hay duda, por el contrario, de que los cambios radicales en la dieta de ambas especies de lobos marinos observados hace unos 150 años fueron la consecuencia de su extinción virtual en el Mar Argentino entre los siglos XVIII y XX. A la vez que las dietas cambiaron, la red trófica se alargó y se hizo menos redundante. Estos sorprendentes resultados se pueden interpretar como la respuesta de los depredadores apicales a la disminución de la presión intraespecífica generada por la explotación humana. Los estudios históricos como la presente tesis pueden ayudar a comprender los mecanismos que actúan en ecosistemas perturbados por la actividad humana y ofrecer una perspectiva más amplia para su restauración.

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Changes in the trophic ecology of the apex predators of the Argentine Sea during the Holocene

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Un giovane gambero pensò: "Perchè nella mia famiglia tutti camminano all'indietro? Voglio imparare a camminare in avanti, come le rane, e mi caschi la coda se non ci riesco."

Cominciò ad esercitarsi di nascosto, tra i sassi del ruscello natio, e i primi giorni l'impresa gli costava moltissima fatica.

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(Gianni Rodari, Favole al telefono)

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Contenidos


INTRODUCCIÓN
GENERAL

1. El impacto humano en el Mar Argentino

Las actividades humanas han alterado la mayoría de los ecosistemas marinos costeros a lo largo de los siglos. La pesca industrial es sin duda la principal culpable de la degradación de los ecosistemas pelágicos y bentónicos de todo el mundo (Jackson et al. 2001, Christensen et al. 2003, Myers y Worm 2003, Lewison et al. 2004, Devine et al. 2006), causando entre otros la reducción en el tamaño de las poblaciones, cambios en la distribución geográfica de las especies, pérdida de diversidad, biomasa, y en definitiva alterando el funcionamiento del ecosistema (Caddy 1998, Pauly et al. 1998, Jackson et al. 2001, Devine et al. 2006, Halpern et al. 2008, Rivadeneira et al. 2010). Según los últimos datos disponibles de la FAO, el 57,4% de los stocks mundiales se encuentra totalmente explotado, el 29,9% sobreexplotado y sólo un 12,7% se halla parcialmente explotado (FAO 2011). Sin embargo estas cifras podrían ser hasta demasiado optimistas, ya que se basan en datos de desembarques y parámetros biológicos actuales (Cadima 2003), sin una adecuada perspectiva histórica. Pero para entender hasta qué punto la intervención humana ha modelado los ecosistemas actuales, es fundamental establecer un nivel de referencia con el que comparar, ya que en muchos casos los cambios se iniciaron hace ya varios milenios (Pauly 1995, Jackson et al. 2001).

Sólo recientemente se ha propuesto investigar el registro histórico para acceder a una información previa al impacto humano moderno (Jackson et al. 2001, Lotze y Milewski 2004, Emslie y Patterson 2007, Erlandson y Rick 2010, Rivadeneira et al. 2010). En estos estudios se evidencia no sólo el ingente cambio demográfico en las poblaciones de las especies pescadas, inimaginable si sólo se considerasen los datos recientes, sino también los cambios funcionales en los ejemplares no pescados y en las especies no explotadas. En muchos casos la magnitud de los cambios es tal que, si el sistema alcanzara un nuevo estado estable, podría verse impedida la restauración de su dinámica inicial, incluso aunque cesase la explotación humana (Petraitis y Dudgeon 2004).

Recientes estudios arqueológicos han demostrado que el impacto humano sobre los ecosistemas marinos es mucho más antiguo y severo de lo que se pensaba, contradiciendo la opinión común que el hombre prehistórico vivía en equilibrio con el ambiente a su alrededor (Erlandson y Rick 2010). Ejemplo claros de extinción se encuentran en las islas de la Polinesia donde el hombre extirpó masivamente, y en tan sólo 3000 años, las especies de aves marinas que allí vivían (Steadman 2006). Siempre en el Pacífico, se atribuye a los maorís no sólo la desaparición de las aves moas, sino la aniquilación de los lobos marinos de Nueva Zelanda (*Arctocephalus forsteri*) y de aves marinas nidificantes (Smith 1989, Anderson 2008). En las costas orientales del Pacífico Norte existen evidencias del impacto ecológico que tuvo la explotación sobre pinnípedos y nutrias marinas por parte de los cazadores-recolectores de las islas Aleutianas, de las costas de Washington, Oregón y California (Braje y Rick 2011). En las islas del Canal de California hay evidencias de cascadas tróficas de origen antropogénico en los bosques de kelp alrededor de 8000 años AP, junto con una reducción sustancial en el tamaño de las conchas de moluscos usados por el hombre durante siglos y el agotamiento local de las poblaciones de peces (Erlandson y Rick 2010). Sin embargo no todas las poblaciones antiguas que vivían en la costa de forma más o menos estable provocaron cambios tan radicales en el ambiente marino, ya que sus densidades no eran suficiente elevadas como para alterar los recursos o alternaban el uso de recursos marinos con recursos terrestres o ambas cosas (Gómez Otero 2006, Gómez Otero 2007, Rivadeneira et al. 2010, Orquera et al. 2011).

La explotación de los recursos marinos, tanto la aborigen como la industrial, se caracteriza por la eliminación preferencial de las especies más grandes (Jackson et al. 2001, Christensen et al. 2003, Myers y Worm 2003, Lewison et al. 2004, Erlandson y Rick 2010, Lotze et al. 2011), un proceso que en principio debería llevar a la reducción de la longitud de las cadenas tróficas (Wainwright y Barton 1995, Pauly et al. 1998, Becker y Beissinger 2006, Gómez-Campos et al. 2011). Sin embargo, el resultado habitual de la sobrepesca de la megafauna es el colapso de las poblaciones y la rarefacción de los depredadores apicales, en lugar de una verdadera extinción (Worm et al. 2006, Dulvy et al. 2009, McClenachan et al. 2012). La diferencia entre rareza y extinción es relevante, ya que las especies extintas ya no pertenecen a la red trófica local, mientras que las especies que se han vuelto escasas continúan existiendo, aunque a densidad muy baja (Sala 2004, Lotze et al. 2011). Por lo tanto, el papel de estos depredadores apicales se posiblemente muy diferente del original, debido a la existencia de fenómenos densodependientes. Reconstruir las abundancias originales, las dietas y las funciones ecológicas de los animales marinos en épocas prístinas es especialmente complejo ya que sus restos se hallan hundidos en el fondo del mar y sólo excepcionalmente salen a luz. Una metodología cada vez más utilizada en zooarqueología es el análisis de concheros, o fogones, particulares y prominentes elementos paisajísticos creados por el hombre en los últimos 140.000 años y compuestos principalmente de conchas, otros restos marinos y artefactos (Alvarez et al. 2011). Aunque al principio de su descubrimiento los concheros tenían un uso puramente antropológico, muy pronto se convirtieron en una herramienta interdisciplinaria para estudios paleoambientales, paleoecológicos y zooarqueológicos. En los últimos años, junto a los clásicos estudios de diversidad y abundancias, el análisis de isótopos estables (principalmente de carbono, nitrógeno y oxígeno) en restos óseos se ha convertido en una técnica ampliamente utilizada para reconstruir el uso de hábitat, la dieta y el nivel trófico de los organismos marinos que vivieron en el pasado, así como para realizar reconstrucciones medioambientales (Burton et al. 2001, Bailey et al. 2008, Barrett et al. 2008, Corbett et al. 2008).

El Mar Argentino se presta ampliamente a estudios de cambios temporales en ecosistemas marinos ya que desde el Holoceno medio (Cruz y Caracotche 2008) ha sufrido un impacto humano creciente que dura hoy en día. El extremo meridional de América del Sur fue colonizado por los humanos hace más de 12.000 años AP (Miotti et al. 2003, Dillehay et al. 2008, Orquera et al. 2011), pero la explotación regular de recursos marinos no se desarrolló hasta alrededor de 6000 ^{14}C años AP en el norte de la Patagonia (Gómez Otero 2007, Favier Dubois et al. 2009), 6300-5150 años en el sur de Patagonia (Orquera y Gómez Otero 2007) y 6400 ^{14}C años AP en el Canal de Beagle (Orquera y Piana 1999). Aunque los patrones de empleo de recursos marinos varían notablemente de una región a otra, en todo el litoral los recursos marinos cumplieron un papel importante en la subsistencia de los cazadores-recolectores.

Figura.1. Conchero, o fogón, en Puerto Deseado (Argentina).

Junto con moluscos, aves marinas y peces, los pinnípedos fueron presas especialmente importantes tanto para los cazadores-recolectores que vivían en el Canal Beagle como los que habitaban la costa sur de Chile, pues ambos basaban su vida en los recursos marinos (Schiavini 1993, Orquera y Piana 1999, Yesner et al. 2003, Orquera et al. 2011, Tivoli y Zangrando 2011). También fueron explotados por los pobladores del centro y del norte de la Patagonia, aunque estos últimos eran sólo parcialmente dependientes de los recursos marinos (Borrero y Barberena 2006, Gómez Otero 2006, Castro et al. 2007, Moreno 2008, Favier Dubois et al. 2009, Belardi et al. 2011). De acuerdo con el registro zooarqueológico, las poblaciones humanas que habitaban en el Canal Beagle aproximadamente 6000 años AP eran altamente dependientes de los lobos marinos finos (*Arctocephalus australis*), siendo esta especie la principal fuente de alimento y materia prima durante varios milenios (Orquera y Piana 1999, Orquera et al. 2011, Tivoli y Zangrando 2011). En cambio, los humanos que habitaban en el norte y centro de la Patagonia explotaban tanto recursos terrestres como marinos y la explotación de los pinnípedos, especialmente del lobo marino común (*Otaria flavescens*), se desarrolló aproximadamente hace 3000 años AP, cuando se establecieron asentamientos estacionales cerca de las loberías (Gómez Otero 2006, Favier Dubois et al. 2009). La explotación de lobos marinos fue intensa en el norte de la provincia de Río Negro desde 3100 hasta 2200 años AP, seguida por un período de explotación moderada desde 1500 hasta 420 años AP (Favier Dubois et al. 2009). Por el contrario, la explotación de lobos marinos en la provincia de Chubut fue moderada desde 3000 hasta 1000 años AP y se intensificó en el período comprendido entre 1000 y 350 años AP (Gómez Otero 2006, Gómez Otero 2007), mientras que en la costa norte de Santa Cruz, Golfo de San Jorge y Cabo Vírgenes, la explotación de pinnípedos fue intensa durante todo el Holoceno tardío, aunque de una forma discontínua (Borrero y Barberena 2006, Castro et al. 2007, Moreno et al. 2011).

Figura 2. Grupo de Yámanas canoeros del Canal del Beagle. A finales del siglo XIX, los pinnípedos ya no jugaban ningún papel relevante en su economía.

A pesar de estos datos, hasta el momento no hay evidencias de que el uso de recursos marinos por parte de los cazadores-recolectores del Holoceno medio y tardío tuviese un impacto sustancial sobre el ecosistema marino, o al menos sobre los pinnípedos (Schiavini 1993, Orquera et al. 2011). Recientemente, Zangrando y colaboradores han propuesto cambios en el uso del hábitat y en el tamaño del lobo fino del Canal de Beagle durante el Holoceno tardío como consecuencia de la explotación indígena, basándose en estudios isotópicos y en el análisis de las clases de edad y talla en el registro zooarqueológico (Zangrando et al. 2013). Sin embargo no es posible considerar estos resultados como concluyentes ya que, al analizar los cambios de comportamiento trófico en los lobos no se consideran las posibles variaciones en la línea de base isotópica (Casey y Post 2011).

Con la llegada de los europeos a principios del siglo XVI, pero sobre todo con el establecimiento de los primeros asentamientos en los siglos XVIII-XIX, el aparente equilibrio entre hombre y recursos marinos cambió radicalmente. Por un lado los indígenas del norte de la Patagonia abandonaron poco a poco la dieta marítima para dedicarse a la caza de animales terrestres, facilitados por la introducción del caballo (Gómez Otero 2007, Moreno y Videla 2008, Favier Dubois et al. 2009). Por el otro, los europeos empezaron a explotar de forma masiva la megafauna marina local por su piel y grasa, empezando por el lobo fino (desde el 1515) y la ballena austral (*Eubalaena australis*), desde el 1602, diezmados durante los siglo XVIII y XIX (Ellis, 1969; Tønnessen y Johnsen, 1982; Reeves et al., 1992; Bastida y Rodríguez 2003). Sucesivamente se explotaron el lobo común, cuya población se vio reducida drásticamente durante la primera mitad del siglo XX (Godoy 1963, Crespo y Pedraza 1991, Dans et al. 2004), el elefante marino y varias especies de cetáceos. Finalmente la pesca industrial, principalmente dirigida a la merluza (*Merluccius hubbsi*) y a otras especies demersales, empezó a desarrollarse en la década 1960, aunque los desembarques aumentaron sensiblemente más tarde, en las décadas de 1970 y 1980, para luego volver a bajar en la década de 1990, cuando fueron necesarias medidas de protección (Bertolotti et al. 2001). Actualmente los stocks de merluza se encuentran sobreexplotados, así como los del abadejo (*Genypterus blacodes*), mientras que la merluza austral (*Merluccius australis*), la corvina rubia (*Micropogonias furneri*) y el calamar (*Illex argentinus*) están entre totalmente explotados y sobreexplotados (Milessi y Jaureguizar 2013). El langostino (*Pleoticus mulleri*) está clasificado como totalmente explotado y al parecer que sólo la anchoíta (*Engraulis anchoíta*) está subexplotada (FAO 2011). Todo esto, junto con la llegada de diversas especies de algas invasoras que ahora dominan la comunidad en amplias zonas (Casas et al. 2004), ha provocado una reorganización del ecosistema que incluye un cambio continuo de la estructura de la comunidad de depredadores apicales. La población del pingüino de Magallanes (*Spheniscus magellanicus*), por ejemplo, al no haber sido explotada sistemáticamente como otras especies, ha incrementado en el transcurso del siglo XX (Boersma y Williams 1995, Cruz et al. 2004), ocupando aparentemente recursos tróficos dejados vacantes por otras especies como el lobo marino común (Crespo y Pedraza 1991).

2. Tres depredadores apicales del Mar Argentino: el lobo común, el lobo fino y el pingüino de Magallanes.

Para este trabajo se escogieron el lobo común, el lobo fino y el pingüino de Magallanes como representantes de depredadores apicales del Mar Argentino por varias razones. En primer lugar porque sus poblaciones sufrieron muchos cambios a lo largo del tiempo, debido principalmente a la intervención humana (directa o indirecta), y hoy en día su distribución y abundancia están muy lejos de las originales. Además las tres especies se encuentran entre las más emblemáticas de la fauna marina de la región y muchos estudios en la literatura se han dedicado a describir, cada vez con más detalle, su biología, ecología e historia natural. Por ello se ha intentado reconstruir la ecología trófica de cada uno de ellas y su papel en las redes tróficas a lo largo del Holoceno medio y tardío, lo que debería permitir una previsión hacia donde debería dirigirse la evolución del ecosistema en caso de querer restaurarlo.

2.1. El lobo común

Figura 3. Lobos marinos comunes (*Otaria flavescens*)

El lobo común (*Otaria flavescens*) es el mamífero marino más abundante y más fácil de observar en Argentina, contando con numerosos apostaderos continentales e insulares que utiliza para reproducirse y/o como lugares de asentamiento invernal (Reyes et al. 1999, Dans et al. 2004, Schiavini et al. 2004). Es uno de los otáridos más grandes y dimórficos que existen (Cappozzo y Perrin 2009), alcanzando los machos un volumen corporal mucho mayor que las hembras (aproximadamente 350 kg *vs* 150 kg). Su distribución atlántica abarca desde Torres (sur de Brasil – 29º20'S) hasta Cabo de Hornos, incluyendo las islas Falklands/Malvinas, para luego llegar hasta Zorritos (norte de Perù 3º30'S) en el Pacífico (Cappozzo y Perrin 2009). La población mundial estimada es superior a los 250.000 individuos, con aproximadamente 150.000 individuos a lo largo de la costa pacífica y aproximadamente 120.000 individuos a lo largo de la costa atlántica, principalmente concentrados en Argentina (Cappozzo y Perrin 2009, IUCN 2009).

La especie fue objeto de explotación por su piel y grasa en todo el litoral Argentino, sobre todo en Península Valdés (Patagonia norte) y Tierra del Fuego (Crespo y Pedraza 1991), desde comienzo de la colonización europea. Sin embargo la mayor explotación del lobo común se produjo entre 1920 y 1950 (Godoy, 1963), habiéndose reducido la población a menos del 10% de su tamaño original en el momento del cese de la caza, en la década de los 1960 (Crespo y Pedraza 1991, Reyes et al. 1999, Schiavini et al. 2004). Aunque en el norte de Argentina nunca hubo explotación comercial de lobo común, las colonias de las que se tiene constancia desde por lo menos el 1581 han desaparecido como consecuencia de las actividades humanas (Rodriguez y Bastida 1998). Actualmente, la población de lobo común en el norte de Patagonia está aumentando anualmente en un 5,7% y cuenta con unos 50.000 individuos (Dans et al. 2004), mientras que los datos de Uruguay indican una reducción anual de un 4,5% desde el 1995, año en que la explotación cesó (Páez 2006). En la Patagonia meridional, Tierra del Fuego e islas Malvinas/Falklands no hay datos disponibles sobre tendencias actuales y, aunque hasta los años 1990 las poblaciones se encontraban en fuerte reducción por razones desconocidas, en los últimos años se vislumbra alguna señal de recuperación (Schiavini et al. 2004, Thompson et al. 2005).

Costa y colaboradores sostienen que los otáridos con dieta principalmente bentónico-demersal experimentan una recuperación más lenta tras el cese de la caza, en comparación con los que se alimentan de presas pelágicas ya que, por un lado, su capacidad de buceo se encuentra al límite fisiológico y, por el otro, tienen que competir con la pesca demersal industrial, desarrollada a partir de la segunda mitad del siglo XX (Costa et al. 2004, Costa et al. 2006). El lobo común es considerado un depredador oportunista de amplio espectro (Vaz-Ferreira 1982b), siendo las presas demersales preferidas con respecto a las pelágicas (Koen Alonso et al. 2000, Zenteno et al. unpublished); sin embargo estas últimas se consuman en grandes cantidades cuanto más abundantes sean en el medio (Soto et al. 2006, Romero et al. 2011) y/o cuanto más densa sea la población de lobo, como por ejemplo en Península Valdés (norte de Patagonia) (Drago et al. 2009).

2.2. El lobo fino

Figura 4. Lobos marinos finos (*Arctocephalus australis*).

El lobo marino fino (*Arctocephalus australis*) se extiende desde Perú hasta Uruguay (Vaz-Ferreira 1982a), aproximadamente el mismo rango geográfico que el lobo marino común con el que se solapa a menudo. Sus principales poblaciones se encuentran en el Atlántico sur, principalmente al norte y al sur de su área de distribución, allí donde más estrecha es la plataforma continental y hay disponibilidad de islas y comida (Túnez et al. 2008). Al igual que otros pinnípedos, el lobo fino fue explotado intensamente en toda su área de distribución (Vaz-Ferreira 1982a, Arnould 2008). En Uruguay, el nadir de la población se alcanzó en los años 1940, pero desde entonces la población uruguaya de lobo fino aumentó de manera constante, a pesar de que la caza comercial continuara hasta el 1991

(Vaz-Ferreira 1982a, Páez 2006). En la actualidad, las mayores colonias del mundo se encuentran en Uruguay (Naya et al. 2002), mientras que la información referida al resto del litoral es escasa, sobre todo debido a la dificultad para acceder a las loberías tanto en Tierra del Fuego como en la Isla de los Estados (Schiavini 1987, Parera et al. 1997, Niekisch y Schiavini 1998).

La ecología trófica del lobo fino ha sido estudiada en Perú, Chile, Isla Lobos (Uruguay), Malvinas/Falklands y en la zona del Río de la Plata y cercanías (Majluf 1992, Zavalaga et al. 1998, Naya et al. 2002, Arias 2003, Laptikhovsky 2009, Hernández 2012, Vales et al. 2013). Es opinión general de que se trate de un animal generalista y oportunista, consumiendo las presas más abundantes dentro de su área de forrajeo (Naya et al. 2002, Arias 2003, Hernández 2012). Sin embargo, tanto en Perú como en Isla Lobos y en la zona de la pluma del Río de la Plata se han identificado los pequeños peces pelágicos (*Engraulis ringens* en Perú y *Engraulis anchoita* en Uruguay y Río de la Plata) y los calamares como los componentes básicos de su dieta (Muck y Fuentes 1987, Zavalaga et al. 1998, Naya et al. 2002, Vales et al. 2013). Por otra parte, allí donde se estudió durante un tiempo suficientemente largo, la dieta del lobo fino no ha cambiado en paralelo al desarrollo de pesquerías industriales (Vales et al. 2013). Sin embargo Zangrando y colaboradores han documentado posibles cambios en la dieta de la especie en el Canal de Beagle durante el Holoceno tardío en respuesta a la presión aborigen (Zangrando et al. 2013).

2.3. El pingüino de Magallanes

Figura 5. Pingüino de Magallanes (*Spheniscus magellanicus*)

El pingüino de Magallanes (*Spheniscus magellanicus*) es la más abundante de las tres especies de pingüino que nidifican en Argentina. Se reproduce en las costas atlántica y pacífica de América del Sur, abarcando Argentina (63 colonias), Chile (al menos 10 colonias) y las Islas Falklands/Malvinas (90 colonias), y alcanzando una población estimada de un mínimo de 950.000 parejas reproductoras entre Chubut y Santa Cruz

(Pütz et al. 2000, Schiavini et al. 2005). El pingüino de Magallanes efectúa migraciones hacia el norte en otoño y los que se reproducen en las colonias más septentrionales de Argentina (Río Negro), en invierno llegan hasta las costas de Brasil (Frere et al. 1996b). Tienen un ciclo reproductivo estacional, regresando a las colonias de cría entre Agosto y Septiembre. La puesta se realiza en Octubre y consta de dos huevos. La crianza de los pichones se extiende hasta Enero y Febrero. En ese momento se produce la muda, tanto de adultos como de pichones, y se inicia la migración entre Marzo y Abril. Ambos padres ayudan a defender el nido, a incubar los huevos y a alimentar a los pollos (Boersma et al. 1990). La dieta del pingüino de Magallanes presenta variaciones latitudinales, aunque a lo largo de toda su distribución reproductiva se alimenta fundamentalmente de peces pelágicos (*E. anchoita, S. fueguensis, M. hubbsi, S. brasiliensis…*) (Frere et al. 1996a), con un aporte importante de calamares (*Illex* sp*., Loligo sp.*, *Doryteuthis pleii*) en algunas localidades y temporadas (Schiavini et al. 2005, Pinto et al. 2007, Silva et al. 2014). Se han encontrado diferencias en la estrategias de forrajeo entre machos y hembras durante la época migratoria (Abril-Agosto), probablemente debidas al diferentes uso de las áreas de invernada (Silva et al. 2014).

No se tienen noticias de explotación humana directa y masiva en época moderna, como en el caso de los pinnípedos, aunque sí se solían matar para obtener provisiones para los barcos (Silva, comunicación personal).

La información sobre las tendencias poblacionales sugiere que, mientras en algunos sectores costeros el número de individuos reproductivos de pingüino de Magallanes ha disminuido, en otros ha aumentado. El dato más interesante es probablemente la expansión geográfica de esta especie hacia el norte durante el siglo XX, probablemente aprovechando de la liberación de recursos como la anchoíta por parte de los lobos (Boersma et al. 1990, Cruz et al. 2004).

3. Uso de isótopos estables en ecología trófica y paleoecología

Los isotopos estables (Cuadro 1), especialmente los de carbono (^{13}C y ^{12}C) y nitrógeno (^{15}N y ^{14}N), se utilizan cada vez más en la ecología trófica, gracias al hecho de que las relaciones isotópicas en las proteínas de los consumidores reflejan las de las proteínas de su dieta de una manera predecible (Hobson y Clark 1992, Post 2002b). La abundancia relativa del isótopo pesado con respecto al ligero, o razón isotópica, varía en función del origen del alimento y del nivel trófico. La razón isotópica en el depredador está enriquecida globalmente respeto a su **dieta** de un 0-1‰, en el caso del $\delta^{13}C$, y alrededor de 3-5‰, en el caso del $\delta^{15}N$ (Hobson et al. 1996, Roth y Hobson 2000, Kurle y Worthy 2002), pero este enriquecimiento, o factor de discriminación, varía según la especie, el tejido, el lugar, la condición nutricional y la ontogenia (Caut et al. 2009). Por lo tanto, para relacionar las concentraciones de isótopos en un tejido del consumidor con las de su dieta, es necesario establecer los valores de fraccionamiento isotópico para cada una de estas variables. Idealmente, dicha información se obtiene mediante experimentos controlados en cautividad bajo dieta constante, pero esto resulta imposible para especies de vida larga y difíciles de mantener en cautividad. Este punto es el más crítico en la mayoría de los estudios de dieta, ya que el factor de fraccionamiento es desconocido para la mayor parte de las especies estudiadas, sobre todo si se hallan amenazadas y/o son de difícil captura y baja tasa de crecimiento.

Ahora bien, determinar la composición de la dieta no es la única utilidad de los isótopos estables en ecología. Por un lado el carbono es un buen indicador del **hábitat**, debido a la diferente concentración de ^{13}C entre fitoplancton y algas. Por lo tanto en ambiente marino el $\delta^{13}C$ es capaz de discriminar el hábitat pelágico del bentónico por la más rápida difusión de la CO_2 en la membrana celular del fitoplancton en comparación con la de los macrófitos (France 1995). Debido a ello y al hecho de que las plantas prefieren utilizar CO_2 que lleva ^{12}C, las especies de los ecosistemas pelágicos se caracterizarán por valores de $\delta^{13}C$ inferiores al de losde las especies bentónicas.

Por otro lado el nitrógeno, es un buen indicador del **nivel trófico** de una especie, ya que el valor del $\delta^{15}N$ aumenta de forma predecible de presa a depredador (Michener y Schell 1994). Además hay que destacar que en ambiente marino la productividad primaria en las zonas costeras depende por lo general de la disponibilidad de nitrógeno, que aumenta debido a la aportación de agua dulce, a la mezcla vertical y al afloramiento de aguas profundas (Gruber 2008). Todos estos procesos también promueven el reciclado de nitrógeno sobre la fijación y por lo tanto modifican la abundancia relativa de ^{15}N en los tejidos de los productores primarios (Calvert et al. 1992, Wu et al. 1997, Waser et al. 2000). En resumen el valor del $\delta^{15}N$ en las plantas y herbívoros marinos es también un buen indicador de la **producción primaria marina**.

Isótopos estables. Los isótopos son formas diferentes de un elemento químico que difieren entre sí por el número de neutrones en el núcleo, y por lo tanto por su masa atómica. Cada elemento posee uno o más isótopos, que puede ser estable o inestable (radioactivo), dependiendo de su tiempo de neutralización (Hoefs 2004). En ecología se utilizan los isótopos estables de hidrógeno, carbono, nitrógeno, oxígeno, y azufre, es decir los que están más relacionados con la biosfera. Los isótopos son presentes en ella en diferentes proporciones, aunque el isótopo más ligero siempre es el más abundante. Muchos procesos naturales causan una distribución desigual de isótopos pesados y ligeros llamada fraccionamiento. El fraccionamiento se da porque los isótopos ligeros forman enlaces químicos que requieren menos energía para romperse, por lo tanto reaccionan más rápido y se quedan más concentrados en los productos (Dawson y Brooks 2001). Esta capacidad de concentrarse de formas diferentes según el proceso convierte los isótopos estables en excelentes trazadores naturales.

El método más común de cuantificar los isótopos estables es mediante un espectrómetro de masa de relación isotópica, que proporciona con gran exactitud la estimación de la proporción isótopo pesado/isótopo ligero en una muestra con respecto a un estándar. La abundancia de isótopos estables relativa al estándar se expresa en partes por mil (‰) de acuerdo con la siguiente expresión:

$$\delta^{H}X = [(R\ \text{muestra}/R\ \text{estándar}) - 1] \times 10^{3}$$

En esta definición, la notación δ, que es la ratio entre muestra y estándar, se especifica para un elemento particular (X = H, C, N, O o S), el superíndice H da la masa isótopo pesado de ese elemento (^{2}H, ^{13}C, ^{15}N, ^{18}O, o ^{34}S), y R es la relación del isótopo pesado/isótopo ligero para el elemento (Fry 2006). Debido a que los estándares internacionales son arbitrarios, algunas proporciones de isótopos son positivas (es decir, enriquecidas en el isótopo pesado con respecto al estándar) y otras son negativas (es decir, empobrecidas en el isótopo pesado con respecto al estándar).

Cuadro 1. Isótopos estables

Por otra parte, la abundancia relativa de los isótopos estables del oxígeno (^{18}O y ^{16}O) permiten reconstruir las condiciones de temperatura y salinidad en que vive el organismo. Las proporciones de isótopos de oxígeno en las valvas de bivalvos son actualmente los indicadores más robustos para la reconstrucción de la **temperatura superficial del mar** (SST) y muy probablemente no se ven afectados por los cambios ontogenéticos durante el crecimiento de los bivalvos (Schone et al. 2004). Sin embargo, la razón isotópica de oxígeno en las valvas, utilizada para la reconstrucción de palaeotemperaturas, se ve alterada asimismo por variaciones en la salinidad (Epstein et al. 1951, Wefer et al. 1991, Schone et al. 2004, LeGrande y Schmidt 2006), ya que los valores de $\delta^{18}O$ del agua de mar están influenciados tanto por la temperatura como por la salinidad (Bowen 2010). En consecuencia, en zonas de alta aportación de agua dulce, como por ejemplo en el Canal del Beagle (Tierra de Fuego), hay que ser prudentes en la interpretación de los resultados, aunque en zonas sin aportes relevantes de agua dulce, la temperatura sería la principal fuente de la variación de $\delta^{18}O$.

Finalmente, destacar que en los últimos 10 años, han surgido una serie de métodos cuantitativos basados en la información proporcionada por los isótopos estables que están mejorando significativamente la comprensión de las **redes tróficas**. Gracias a ellos es posible cuantificar de forma relativamente sencilla la longitud de la red trófica, la dimensión y el solapamiento de nicho trófico de diferentes especies y otros descriptores de la estructura de la comunidad (Bearhop et al. 2004, Layman et al. 2007a, Layman et al. 2007b, Schmidt et al. 2007, Layman et al. 2012). El método analítico utilizado en esta tesis, llamado SIBER, tiene muchas ventajas en comparación con otros métodos cuantitativos, ya que es capaz de cuantificar el tamaño del nicho trófico de una especie o de un grupo funcional a través de elipses que tienen en cuenta la incertidumbre del muestreo y además contempla una corrección de tamaño para comparar pequeñas muestras (Jackson et al., 2011). Finalmente calcula las medidas propuestas por Layman para describir la topología de una red trófica (Layman et al. 2007a) propagando la incertidumbre desde los datos hasta el resultado (Jackson et al. 2011).

OBJETIVOS

La presente tesis doctoral tiene como **objetivo principal** la reconstrucción de los cambios ocurridos en la estructura trófica del ecosistema marino costero del Mar Argentino a lo largo del Holoceno medio y tardío, como consecuencia de la explotación secuencial de sus recursos por parte del hombre.

La hipótesis de partida es que la explotación secuencial por parte de los colonizadores europeos, primero del lobo fino, después del lobo común y finalmente de las poblaciones de peces demersales, ha llevado el ecosistema a un nuevo estado de equilibrio donde los pingüinos, entre otros, habrían ocupado un nicho diferente del original. Si esto fuera cierto se debería observar un cambio en las dietas/posiciones tróficas de los tres depredadores en el tiempo, ya que la sobreexplotación de cada uno de ellos liberaría recursos que serían utilizados por los otros. A la vez deberían haber cambiado las características intrínsecas de la red trófica estudiada, como por ejemplo la longitud y la redundancia.

Para poder hacer esto se han reconstruido las condiciones paleoambientales durante los últimos 6.000 años. Este paso ha sido necesario para poder excluir que los eventuales cambios ecológicos observados fueran consecuencia de variaciones de factores ambientales, como la temperatura o la productividad. Por lo tanto en el **primer capítulo** se han analizado las razones isotópicas de oxígeno y nitrógeno en valvas procedentes de fogones situados en el norte de Patagonia y en Tierra del Fuego para verificar: i) si la temperatura marina ha cambiado o no a lo largo del Holoceno medio y tardío; ii) si la productividad del mar ha cambiado en la mismo período y iii) si estos cambios han coincidido o no con cambios en la abundancia de los pinnípedos en el registro zooarqueológico.

Una vez comprendido el papel de los factores ambientales en los patrones de explotación de los pinnípedos por parte de las poblaciones aborígenes, se aborda el análisis de los cambios en las dietas del lobo común y lobo fino durante el Holoceno medio y tardío en el **segundo capítulo.** Para ello se analizaron los isótopos estables de carbono y nitrógeno en hueso de lobo común y lobo fino procedentes del registro zooarqueológico y de colecciones científicas del siglo XX. A estos valores se aplicó una corrección basada en los cambios observados a lo largo del Holoceno medio y tardío en los valores de δ^{13}C y el δ^{15}N de las valvas de moluscos, indicadores de los cambios en el nivel de la base isotópica del ecosistema (Casey y Post 2011). En este apartado se hizo uso del análisis bayesiano SIAR, contenido en el paquete de R SIAR (Parnell y Jackson 2013).

Finalmente en el último apartado (**tercer capítulo)** se analizó la estructura de la red trófica actual en tres sectores del litoral argentino, con especial énfasis en las relaciones entre el lobo común, el lobo fino y el pingüino de Magallanes, y se reconstruyó la estructura de las tróficas antiguas para comparar, por un lado sus topologías y por el otro los nichos tróficos de los depredadores apicales objeto de estudio. Para hacer esto, primero se analizaron las razones isotópicas de carbono y nitrógeno de huesos de lobo común, lobo fino y de pingüino de Magallanes actuales para ver si la repartición de los recursos entre ellos es debida sobre todo a su morfología (masa corporal y tamaño de la boca/pico) o variaba en función de la zona. En este apartado se hizo especialmente uso del análisis bayesiano SIBER, contenido en el paquete de R SIAR (Jackson et al. 2011, Parnell y Jackson 2013). Por otro lado se analizaron las razones isotópicas de carbono y nitrógeno en diferentes tejidos de animales y vegetales recolectados a lo largo del litoral, desde el sur del Brasil (29ºS aproximadamente) hasta Tierra del Fuego (55ºS aproximadamente), desde productores primarios hasta depredadores apicales. De esta forma pudimos verificar: i) si la red trófica actual presenta algún patrón latitudinal; ii) si este patrón está acoplado a algún patrón ambiental, como por ejemplo la temperatura o la productividad marinas; iii) si este patrón sigue el gradiente de explotación humana. Una vez establecidas las características de la red actual se pasó a caracterizar las redes antiguas, una en el norte de Patagonia y la otra en Tierra de Fuego. Para hacer esto se analizaron los isótopos estables de carbono y nitrógeno en valvas y huesos, por ser este el único material arqueológico existente. Las valvas de moluscos informaban de las variaciones de la línea de base isotópica, mientras los huesos informan de los depredadores apicales. De esta forma pudimos verificar: i) si las redes antiguas tienen la misma topología que las modernas; ii) si los cambios temporales observados se verifican en las redes de ambas zonas y finalmente iii) si estos cambios pueden estar explicados por un gradiente temporal de creciente impacto humano. En este apartado se hizo especialmente uso del análisis bayesiano SIBER, contenido en el paquete de R SIAR (Parnell y Jackson 2013).

ESTRUCTURA DE LA TESIS

Capítulo 1. Influencia de la temperatura y de la productividad marina sobre la abundancia de pinnípedos en el Mar Argentino durante el Holoceno medio y tardío.

1.1. Changing patterns of marine resource exploitation by hunter-gatherers throughout the late Holocene of Argentina are uncorrelated to sea surface temperatura [Los cambios en los patrones de explotación de recursos marinos por los cazadores-recolectores durante el Holoceno tardío en Argentina no están correlacionados con la temperatura superficial del mar].

✍ **F. Saporiti**, L.O. Bala, E.A. Crespo, J. Gómez Otero, A.F.J. Zangrando, A. Aguilar, L. Cardona, 2013. *Quaternary International*, 299:108-115.

1.2. *Paleoindian pinniped exploitation in South America was driven by oceanic productivity* [La explotación de pinnípedos por parte de los cazadores-recolectores en América del Sur fue impulsada por la productividad oceánica].

✍ **F. Saporiti**, L.O. Bala, J. Gómez Otero, E.A. Crespo, E.L. Piana, A. Aguilar, L. Cardona, 2014. *Quaternary International*, n/a: n/a.

Capítulo 2. Cambios en la dieta de dos depredadores apicales (el lobo común y el lobo fino) en el Mar Argentino durante el Holoceno.

2.1. Shifting niches of the South American sea lion (Otaria flavescens) in the southwestern Atlantic since the late Holocene [Cambios en el nicho del lobo marino común (*Otaria flavescens*) en el Atlántico sud-occidental desde finales del Holoceno].

✍ L. Zenteno, F. Borella, J. Gómez Otero, E. Piana, J.B. Belardi, L.A. Borrero, **F. Saporiti,** L.Cardona**,** E. Crespo. *Paleobiology*, submitted (Marzo 2014).

2.2. Reconstructing the diet of South American fur seals in the south-western Atlantic since the middle Holocene [Reconstrucción de la dieta de los lobos marinos finos sudamericanos en el Atlántico sudoccidental desde el Holoceno medio].

✍ D.G. Vales, L. Cardona, A.F. Zangrando, F. Borella, **F. Saporiti**, R.N.P. Goodall, E.A. Crespo. En preparación.

Capítulo 3. Cambios en las redes tróficas y en la ecología trófica de los depredadores apicales del Mar Argentino en consecuencia al impacto humano.

3.1. Morphology or species identity? A stable isotope analysis about resource partitioning between air-breathing predators [¿Morfología o identidad de la especie? Un análisis de isótopos estables sobre la repartición de recursos entre los depredadores de respiración aérea].

✍ **F. Saporiti**, S. Bearhop, D.G. Vales, L. Silva, L. Zenteno, M. Tavares, E.A. Crespo, L. Cardona. *Marine ecology: an evolutionary perspective*, enviado (Mayo 2014).

3.2. Latitudinal changes in the structure of marine food webs in the south-western Atlantic Ocean [Cambios latitudinales en la estructura de las redes tróficas marinas en el Océano Atlántico sur-oeste].

✍ **F. Saporiti**, S. Bearhop, D.G. Vales, L. Silva, L. Zenteno, M. Tavares, E.A. Crespo, L. Cardona. *Marine Ecology Progress Series*, enviado (Julio 2014).

3.3. Longer and less overlapped food webs in anthropogenically disturbed marine ecosystems: confirmations from the past [Redes tróficas más largas y menos solapadas en los ecosistemas marinos alterados por el hombre: confirmaciones del pasado].

✍ **F. Saporiti**, S. Bearhop, L. Silva, D. Vales, L. Zenteno, E.A. Crespo, A. Aguilar, L. Cardona. *PLos ONE*, aceptado (Junio 2014).

Informe de los directores

Los directores de la presente Tesis, el **Dr. Luis Cardona Pascual** y el **Dr. Luis Oscar Bala** certifican que **Fabiana Saporiti** ha participado activamente en el desarrollo del trabajo asociada a cada uno de los artículos presentados en esta Tesis Doctoral, así como en su elaboración. En concreto, su participación en cada uno de los artículos ha consistido en:

- Planteamiento de los objetivos.
- Planificación y ejecución de los experimentos, tanto en cuanto a trabajo de campo (allí donde ha sido posible) como en el laboratorio.
- Procesado y análisis de las muestras obtenidas.
- Redacción de los artículos y seguimiento del proceso de revisión de los mismos.

A continuación se detalla la contribución que ha realizado el doctorando y los otros coautores en cada uno de los artículos, así como el factor de impacto de cada uno de ellos, tal y como están publicados por el *Institute for Scientific Information (ISI)* y listados en el *Journal Citation Reports (JCR)* correspondiente a 2012:

1.1 Changing patterns of marine resource exploitation by hunter-gatherers throughout the late Holocene of Argentina are uncorrelated to sea surface temperature. F. Saporiti, L.O. Bala, E.A. Crespo, J. Gómez Otero, A.F.J. Zangrando, A. Aguilar, L. Cardona, 2013.
Quaternary International, 299:108-115. 5-year impact factor: 2.150.
Diseño del trabajo: LC, AA, EAC, FS
Muestreo: JGO, AFJZ, FS, LOB
Análisis de las muestras: FS
Redacción: FS, LC

1.2 Paleoindian pinniped exploitation in South America was driven by oceanic productivity. F. Saporiti, L.O. Bala, J. Gómez Otero, E.A. Crespo, E.L. Piana, A. Aguilar, L. Cardona, 2014.
Quaternary International, n/a: n/a. 5-year impact factor: 2.150.
Diseño del trabajo: LC, AA, EAC, FS

Muestreo: JGO, ELP, FS, LOB

Análisis de las muestras: FS

Redacción: FS, LC

2.1 **Shifting niches of the South American sea lion (*Otaria flavescens*) in the southwestern Atlantic since the late Holocene.** L. Zenteno, F. Borella, J. Gómez Otero, E. Piana, J.B. Belardi, L.A. Borrero, F. Saporiti, L.Cardona, E. A. Crespo. *Paleobiology*, enviado. 5-year impact factor: 3.213.

Diseño del trabajo: LC, EAC, LZ

Muestreo: LZ, EAC, FB, JGO, EP, JBB, LAB

Análisis de las muestras: LZ, FS

Redacción: LZ, LC, FS

2.2 **Reconstructing the diet of South American fur seals in the south-western Atlantic since the middle Holocene.** D.G. Vales, L. Cardona, A.F. Zangrando, F. Borella, F. Saporiti, R.N.P. Goodall, E.A. Crespo.

En preparación.

Diseño del trabajo: LC, EAC, DGV

Muestreo: DGV, AFZ, FB, RNPG, EAC

Análisis de las muestras: DGV, FS

Redacción: DGV, LC, FS

3.1 **Morphology or species identity? A stable isotope analysis about resource partitioning between air-breathing predators**. F. Saporiti, S. Bearhop, D.G. Vales, L. Silva, L. Zenteno, M. Tavares, E.A. Crespo, L. Cardona.

Marine ecology: an evolutionary perspective: enviado. 5-year impact factor: 2.257.

Diseño del trabajo: LC, FS, SB, EAC

Muestreo: FS, DGV, LS, LZ, MT

Análisis de las muestras: FS, DGV, LS, LZ

Redacción: FS, LC

3.2 **Latitudinal changes in the structure of marine food webs in the south-western Atlantic Ocean.** F. Saporiti, S. Bearhop, D.G. Vales, L. Silva, L. Zenteno, M. Tavares, E.A. Crespo, L. Cardona.

Marine Ecology Progress Series: enviado. 5-year impact factor: 3.160.

Diseño del trabajo: LC, FS, SB, EAC

Muestreo: FS, DGV, LS, LZ, MT

Análisis de las muestras: FS, DGV, LS, LZ

Redacción: FS, LC

3.3 **Longer and less overlapping food webs in anthropogenically disturbed marine ecosystems: confirmations from the past**. F. Saporiti, S. Bearhop, L. Silva, D. Vales, L. Zenteno, E.A. Crespo, A. Aguilar, L. Cardona.

PLos ONE, aceptado. 5-year impact factor: 4.244.

Diseño del trabajo: LC, AA, FS, EAC, SB

Muestreo: FS, LS, DV, LZ

Análisis de las muestras: FS, LS, DV, LZ

Redacción: FS, LC, SB, AA

Barcelona, a 14 de Julio de 2014

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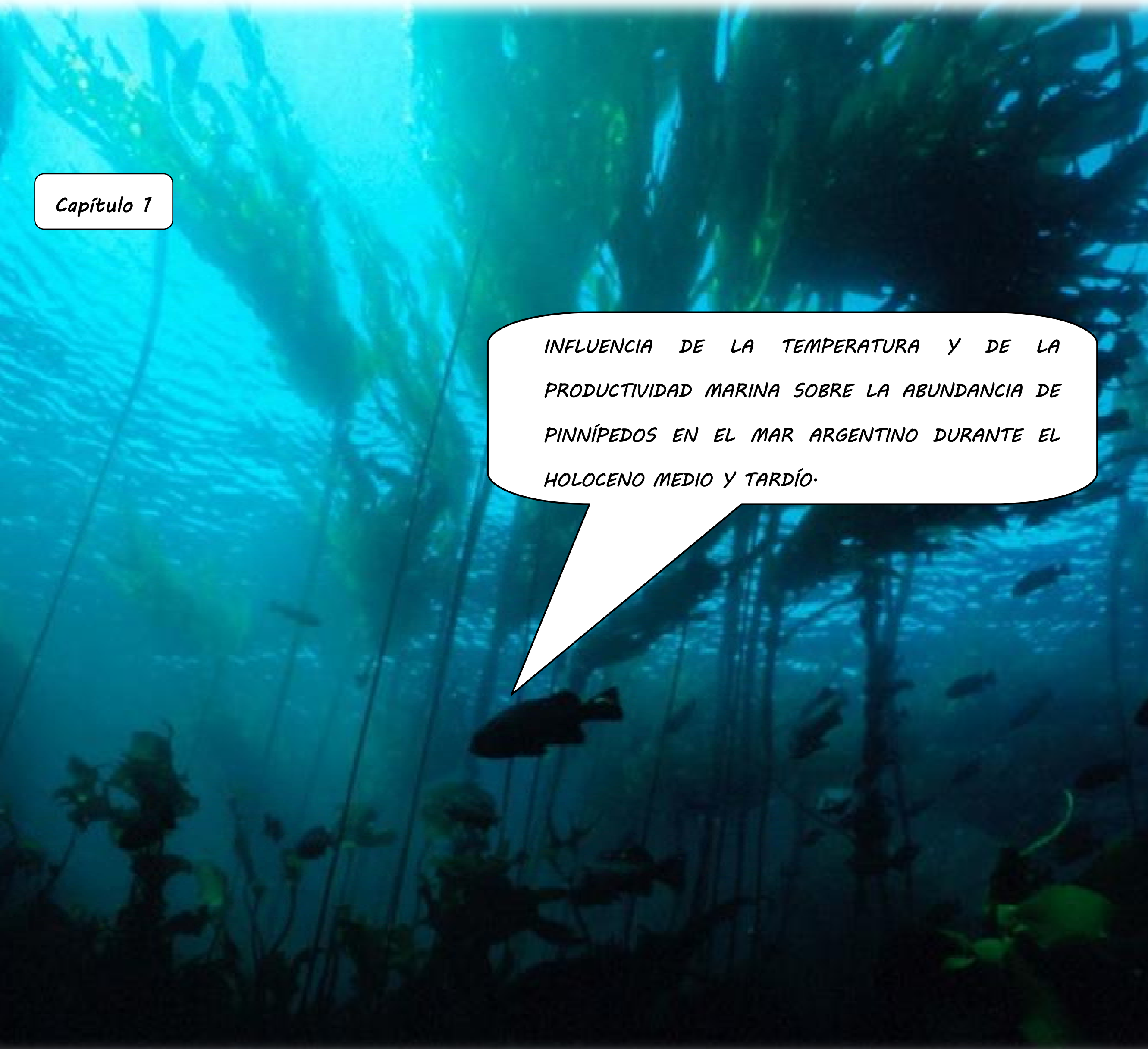

Capítulo 1

INFLUENCIA DE LA TEMPERATURA Y DE LA PRODUCTIVIDAD MARINA SOBRE LA ABUNDANCIA DE PINNÍPEDOS EN EL MAR ARGENTINO DURANTE EL HOLOCENO MEDIO Y TARDÍO.

1.1 Los cambios en los patrones de explotación de recursos marinos por los cazadores-recolectores durante el Holoceno tardío en Argentina no están correlacionados con la temperatura superficial del mar.

RESUMEN. Durante el Holoceno tardío, los recursos marinos costeros del extremo meridional de América del Sur fueron explotados tanto por los canoeros que vivían en el Canal del Beagle y en el archipiélago chileno como por los cazadores-recolectores terrestres que habitaron en diferentes asentamientos costeros. Aunque las dos culturas diferían en la tecnología y en los patrones históricos de explotación, ambos utilizaron otáridos, moluscos, peces y aves marinas como fuente de alimentos y de materias primas durante siglos. Finalmente, el uso de estos recursos, en particular de los otáridos, declinó fuertemente en diferentes momentos. La sobreexplotación ha sido indicada como la principal causa de este patrón, por lo menos en el Canal de Beagle, pero descensos similares en el Pacífico norte se han atribuido a un aumento de la temperatura superficial del mar (SST). El presente trabajo examina esta última hipótesis usando el $\delta^{18}O$ de valvas de moluscos (*Aulacomya atra atra* y *Mytilus edulis*), recogidos en sitios arqueológicos de Argentina, como indicador de la SST y comparándolo con los patrones de explotación de recursos por parte de los cazadores-recolectores. Las muestras se recolectaron en las costas del Canal del Beagle y de la Patagonia centro-norte (al norte de 43ºS) para generar dos conjuntos de datos comparables. Los resultados sugieren que la SST aumentó en ambas áreas al inicio del Holoceno tardío y que fue ligeramente más alta que en la actualidad durante todo ese período, excepto durante la Pequeña Edad de Hielo, cuando se registraron valores similares a los registrados al final del Holoceno medio. La importancia relativa de otáridos, principalmente *Arctocephalus australis*, en la economía de los habitantes del Canal del Beagle declinó al aumentar de la SST, pero la explotación de otáridos no se intensificó nuevamente durante la Pequeña Edad de Hielo. Por el contrario, la intensidad de la explotación de otáridos, principalmente *Otaria flavescens*, en el centro-norte de Patagonia no estuvo relacionada con los cambios en $\delta^{18}O$. Por lo tanto, parece poco probable que los cambios en la SST fueron el principal motor de estos patrones de explotación de los recursos.

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Changing patterns of marine resource exploitation by hunter-gatherers throughout the late Holocene of Argentina are uncorrelated to sea surface temperature

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Abstract

During the late Holocene, the coastal marine resources of southern South America were exploited by both marine hunter-gatherers with aquatic mobility in the Beagle Channel and the Chilean archipelago and terrestrial hunter-gatherers who inhabited various coastal settings in Argentina. Although the two cultures differed in technology and in historical exploitation patterns, they both used otariids, molluscs, fishes and sea birds as sources of food and raw materials for centuries. Ultimately, their use of these resources, particularly of otariids, declined strongly at different times. Overexploitation has been suggested as the main reason for this pattern, at least in the Beagle Channel, but similar declines in the north Pacific have been attributed to an increase in sea surface temperature (SST). The present paper tests the latter hypothesis in southern South America by using the $\delta^{18}O$ of bivalve shells (*Aulacomya atra atra* and *Mytilus edulis*) collected at archaeological sites as a proxy for SST and comparing the patterns of $\delta^{18}O$ with the patterns of resource exploitation by hunter-gatherers. Samples were collected from the Beagle Channel and the central-northern Patagonian coast (north to 43º S) to generate two comparable datasets. The results suggest that SST increased in both areas at the beginning of the late Holocene and was slightly higher than at present during most of that period, except during the Little Ice Age, when values similar to those recorded at the end of the middle Holocene were found. The relative importance of otariids, mainly *Arctocephalus australis*, in the economy of the inhabitants of the Beagle Channel declined as SST increased, but otariid exploitation did not intensify again during the Little Ice Age. On the contrary, the intensity of otariid exploitation in central-northern Patagonia, mainly *Otaria flavescens*, was unrelated to the changes in $\delta^{18}O$. Thus, changes in SST are unlikely to be the major driver of these resource-exploitation patterns.

1. Introduction

Concern about the conservation of marine resources has increased during recent decades as evidence that human exploitation has caused major changes in most marine ecosystems has grown (Pauly et al., 1998; Jackson et al., 2001; Pauly et al., 2005). Although recent examples of fisheries recovering after collapse certainly exist (Worm et al., 2009), marine resource exploitation has increased dramatically worldwide during recent centuries (Pauly et al., 2005), and few marine regions remain unaffected by anthropogenic impacts (Halpern et al., 2008).

Modern industrial fishing is solely responsible for the alteration of offshore and deep-sea ecosystems (Christensen et al., 2003; Myers andWorm, 2003; Lewison et al., 2004; Devine et al., 2006), but overfishing and the ecological extinction of coastal marine megafauna are thought to predate industrialized fishing in many cases. The historical record clearly demonstrates that pre-industrialized European societies overexploited coastal marine mammals (Dulvy et al., 2009) and that European settlement triggered the overexploitation of coastal marine megafauna on other continents (Jackson et al., 2001). However, the impact of other pre industrialized cultures on coastal marine resources remains contentious. An increasing number of multidisciplinary studies examining the interactions between prehistoric peoples and their environments suggest that, at least in some cases, ancient peoples caused cumulative and often irreversible impacts on natural land- scapes and biotic resources worldwide (Kirch, 2005).

Humans have exploited marine resources for at least 120,000 years (Marean et al., 2007), but fully maritime cultures (*sensu* Lyman, 1991; Orquera and Piana, 1999; Bjerck, 2009) developed only later, during the Holocene. Such cultures were found in the Arctic (Corbett et al., 2008; Hill, 2011), the Pacific coast of the Americas (Gifford Gonzales et al., 2005; Rick et al., 2011) and the Strait of Magellan and the adjoining Fuegian and Chilean archipelagos (Orquera and Piana,1999; Yesner et al., 2003; Orquera et al., 2011; Tivoli and Zangrando, 2011), among other regions.

Humans colonized the Americas from southern Siberia at the end of the Pleistocene, most likely following two independent dispersal routes (Keeferet al., 1998; Sandweiss et al., 1998; Miotti and Salemme, 2003; Erlandson et al., 2007; Dillehay et al., 2008; Meltzer, 2009; Erlandson et al., 2011). Human groups dispersing along the Pacific coastline possessed the technology required to exploit marine resources, notably fish, birds and molluscs, but the zooarchaeological record suggests that only a few of them had truly maritime economies and that a strong reliance on marine mammals, primarily pinnipeds, developed only much later, during the Holocene (Keefer et al.,1998; Sandweiss et al.,1998; Yesner et al., 2003; Dillehay et al., 2008; Betts et al.,2011; Erlandsonet al.,2011; Gifford-Gonzalez,2011;McKechnie and Wigen, 2011; Moss and Losey, 2011; Orquera et al., 2011; Tivoli and Zangrando, 2011;Whitaker and Hildebrandt, 2011).

The southern end of South America was colonized by humans more than 12,000 years ago (MiottiandSalemme,2003; Borrero and Miotti, 2008; Dillehay et al., 2008; Orquera et al., 2011), but the archaeological record shows that intense exploitation of marine resources did not develop until approximately 6400 ^{14}C BP in the Beagle Channel (Tierra del Fuego) and along the southern coast of Chile, where fur seals (*Arctocephalus australis*) were the primary prey (Schiavini,1993; Orquera and Piana,1999; Orquera et al., 2011; Tivoli and Zangrando, 2011). Marine resources were also exploited approximately 7000-6000 ^{14}C BP by littoral hunter-gatherers (*sensu* Lyman, 1991) inhabiting central and northern Patagonia (Gómez Otero, 2006; Moreno, 2008; Favier Dubois et al., 2009), but more ancient coastal archaeological sites may have disappeared due to rising sea levels during the middle Holocene (Ponce et al., 2011). The zooarchaeological record and analyses of carbon and nitrogen stable-isotope ratios in human samples from central and northern Patagonia have revealed major regional differences in the use of marine resources (primarily pinnipeds) during the late Holocene, although the consumption of marine resources decreased strongly in all areas after the arrival of Europeans and was completely abandoned in the 17th century (Gómez Otero, 2007; Moreno, 2008; Favier Dubois et al., 2009). Otariids, especially southern sea lions (*Otaria flavescens*), were intensely exploited throughout the late Holocene in the southern province of Santa Cruz (Moreno, 2008). Conversely, the exploitation of sea lions in Chubut province was moderate from 3000 to 1000 years ago, although it intensified from1000 to 350 years ago (Grammer, 2005; Gómez Otero, 2006, 2007). Finally, the opposite pattern occurred in the northern province of Rio Negro, where intense exploitation of sea lions from 3100 to 2200 years ago was followed by a period of moderate exploitation from 1500 to 420 years ago (Favier Dubois et al., 2009).

Although hunter-gatherers in the Beagle Channel and on the northern Patagonian coast differed dramatically in technology and in historical patterns of resource exploitation (Orquera and Piana, 1999; Moreno, 2008; Orquera and Gómez Otero, 2007; Orquera et al., 2011) (Fig. 1), the use of otariids declined strongly in both regions after a long period of exploitation (Yesner et al., 2003; Gómez Otero, 2006; Moreno, 2008; Favier Dubois et al., 2009; Tivoli and Zangrando, 2011). Similar declines in pinniped use by maritime hunter-gatherers in the north Pacific have sometimes been linked to increasing sea surface temperatures (Colten and Arnold, 1998; Betts et al., 2011) but are usually attributed to overexploitation in the absence of strong evidence for climatic forcing (Porcasi et al., 2000; Lyman, 2003; Jones et al., 2004; Newsome et al., 2007).

Available pollen and stable-isotope data from Tierra del Fuego have been interpreted as evidence of a rather constant climate through the middle and late Holocene (Heusser, 1984, 1990; Obelic et al., 1998). Accordingly, previous researchers have concluded that changes in the resource-use patterns of hunter-gatherers in the Beagle Channel were not driven by climatic variability (Orquera et al., 2011; Tivoli and Zangrando, 2011). Nevertheless, closer examination of the stable-isotope data reported by Obelic et al. (1998) reveals the prevalence of ^{18}O-enriched samples at the end of the middle Holocene and of 18O-depleted samples during most of the late Holocene, except during the Little Ice Age (Fig. 3). The lowest δ^{18}O values were recorded 2500-1500 years ago, and the pattern of resource exploitation by hunter-gatherers changed dramatically after that time (Fig. 3), suggesting that otariids were exploited more intensely during colder periods and hence that some type of environmental forcing was operative. If this hypothesis is correct, a similar pattern should be observed in central and northern Patagonia. Unfortunately, only a few shell-midden samples from this region have been analysed to date (Lanata et al., 2004; Favier Dubois et al., 2009), and the δ^{18}Odata set is not comparable to that from the Beagle Channel (Obelic et al., 1998). This paper aims to test the hypothesis that the changing patterns of marine resource exploitation by hunter-gatherers along the south-western Atlantic coast of Argentina were driven by climatic variability. To test this hypothesis, two comparable δ^{18}O data sets from the Beagle Channel and central and northern Patagonia are generated and compared to the patterns of marine resource exploitation reported by previous zooarchaeological researchers (Yesner et al., 2003; GómezOtero, 2006; Moreno, 2008; Favier Dubois et al., 2009; Tivoli and Zangrando, 2011).

2. Materials and methods

2.1 Bivalve shell samples

Archaeological samples of bivalves were obtained from previous samplings carried out by one of the authors (Julieta Gómez Otero) in central-northern Patagonia and by researchers from CADIC-CONICET, Ushuaia (Luis Orquera, Ernesto Piana and A. Francisco Zangrando), in the Beagle Channel, Tierra del Fuego (Fig. 2). Five shells of rubbed mussel (*Aulacomya atra atra*) were collected from different layers of shell middens in central-northern Patagonia and 5 shells of blue mussel (*Mytilus edulis*) from different layers of shell middens along the Beagle Channel. Because the samples were dated in different laboratories and using different methods, the conventional, non-calibrated radiocarbon dates will be used for all sites (Table 1). In February 2010, additional samples (n=5 for each species and site) of modern intertidal blue mussels were collected from the Beagle Channel and Buenos Aires province and rubbed mussels from the Beagle Channel and northern Patagonia. Sampling sites were selected to cover the latitudinal range of both species in the south- western Atlantic and to use current $\delta^{18}O$ values as benchmarks.

2.2 Stable isotope analysis

All bivalve samples were polished with sandpaper and a diamond wheel drill to remove impurities. They were then rinsed with distilled water, dried at 50ºC and ground into a fine powder using a mortar and pestle. The samples were heated at 200ºC for 1 h to remove all organic matter (Dutton and Lohmann, 2002), and aliquots weighing between 40 and 60 mg were acidified in 100% phosphoric acid at 70ºC for 180s in a Carbonate Kiel Device III (Thermo Finnigan) and analysed using an automated Finnigan MAT-252 isotope-ratio mass spectrometer at the Science and Technology Centres (CCiT) of the University of Barcelona. Stable-isotope values expressed in delta (δ) notation, in which the relative variations of stable-isotope ratios are expressed in per mil (‰) deviations from predefined international standards, were calculated as

$$\delta X=[(R_{sample}/R_{standard})-1] \times 10^3$$

where X is ^{18}O or ^{13}C, Rsample is the heavy-to-light isotope ratio of the sample ($^{18}O/^{16}O$; $^{13}C/^{12}C$), and $R_{standard}$ is the heavy-to-light isotope ratio in the NBS-19 reference standards ($\delta^{13}C_{PDB}$=+1.95‰ and $\delta^{18}O_{PDB}$=-2.20‰) certified by the International Atomic Energy Agency (IAEA, Vienna).

Table 1. Archaeological sites quoted in the text; the first column represents the sampling areas (see Fig.1).

Area	**Site**	**Material**	**Radiocarbon datation ($yr^{14}C$ BP)**	**Laboratory**	**Reference**
Central-northern Patagonia	Los Abanicos 1	Charcoal	380±60	LATYR-CONICET-UNLP	Gómez Otero, 2006
Central-northern Patagonia	Las Ollas conchero 1	Shells	610±60 640±60	LATYR-CONICET-UNLP	Gómez Otero, 2006
Central-northern Patagonia	Playa Las Lisas 2 - Perfil 1	Shells	2140±50	LATYR-CONICET-UNLP	Gómez Otero, 2006
Central-northern Patagonia	Cracker 8 - Nivel 3	Charcoal	5500±80	LATYR-CONICET-UNLP	Gómez Otero, 2006
		Shells	5200±70	LATYR-CONICET-UNLP	
Canal Beagle	Túnel VII	Charcoal	100±45	INGEIS (Buenos Aires)	Piana et *al.,* 1992. Quoted in Schiavini, 1993.
Canal Beagle	Shamakush X site	Charcoal	500±100	INGEIS (Buenos Aires)	Orquera and Piana, 1999. Quoted in Tivoli and Zangrando, 2011.
Canal Beagle	Mischiuen I Upper C	Charcoal	890±90	INGEIS (Buenos Aires)	Piana et *al.,* 2004. Quoted in Tivoli, 2010.
Canal Beagle	Imiwaia I (M/K)	Charcoal	5750±170	INGEIS (Buenos Aires)	Piana et *al.,* 1992. Quoted in Schiavini, 1993.
			5870±150	INGEIS (Buenos Aires)	
			5949±50	Arizona (USA)	

2.3 Archaeological collections for resource use pattern characterization

The collections from five middens excavated at three archaeological sites 40 km apart were used to characterize the pattern of resource use by hunter-gatherers inhabiting the Beagle Channel. One location was situated at Cambaceres Bay and included archaeofaunal samples from stratigraphic layers dated 5940 ^{14}C BP, 1580 ^{14}C BP and from the 19th century. The other middens were located at Estancia Remolino and were dated 4980 ^{14}C BP, 940 ^{14}C BP and 500 ^{14}C BP. There were not significant differences concerning excavation methods, as the same procedures (Orquera and Piana, 1992) were followed. See Tivoli and Zangrando (2011) and references herein for further detail about the sites, dating pro- cedures and collections. The collections from seven middens scattered along 30 km of coastline were used to characterize the pattern of resource use by hunter-gatherers inhabiting northern Patagonia (Favier Dubois et al., 2009).

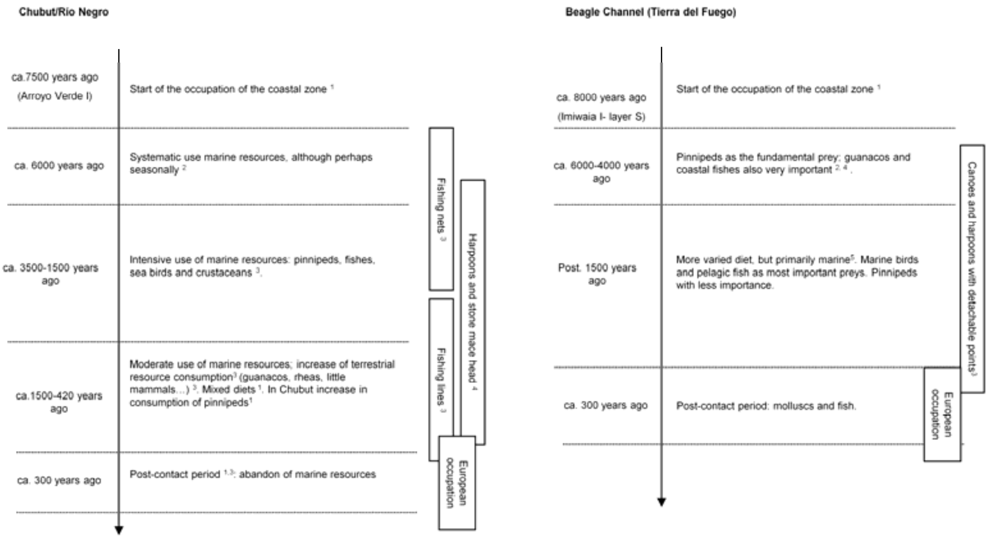

Fig. 1. Subsistence patterns of hunter-gatherers peoples of a) Northern Patagonia; [1]Gómez Otero, 2007; [2]Grammer, 2005; [3]Favier Dubois et al., 2009; [4]Moreno, 2008; and b) Tierra del Fuego; [1]Orquera and Piana, 1999; [2]Tivoli and Zangrando, 2011; [3]Orquera and Piana, 2011; [4]Schiavini, 1993; [5]Yesner et al., 2003.

2.4 Statistical analysis

The normality of the data distribution was tested using the Lilliefors test, and the homoscedasticity was tested using the Levene test. ANOVA was used for multiple comparisons when the data fit the normality and/or homoscedasticity requirements, and the non-parametric Kruskal-Wallis test was used otherwise (Zar, 1998). The non-parametric Spearman rank correlation coefficient was used to test the association of $\delta^{18}O$ values and the relative abundance of otariids in the archaeological record, which was assessed using different methods in the collections from the Beagle Channel than in those from northern Patagonia, because of their contrasting characteristics. The relative abundance of otariids was assesses as the percentage of the number of specimens identified at the species level (%NISP) in the collections from the Beagle Channel, because bone material was well preserved and the number of specimens was assessed precisely (Tivoli and Zangrando, 2011). Bone preservation was worse at the archaeological sites from northern Patagonia and therefore numbers of specimens were not assessed (Favier Dubois et al., 2009). As a consequence, the relative importance of otariids in the collections from that area was assessed by calculating the percentage of broad taxonomic groups represented by otariids (%BTG) in each collection. A single collection was analyzed from each zone (Beagle Channel and northern Patagonia) and age. All statistical analyses were conducted using the PASW Statistics 18 software package.

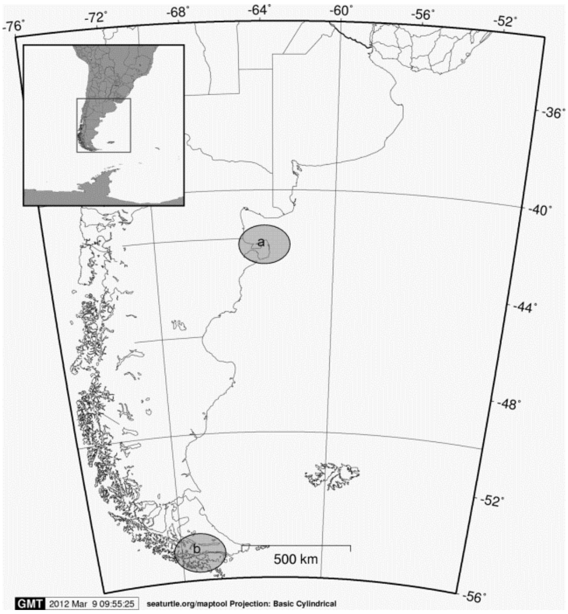

Fig. 2. Map showing approximate sampling localities: a) central-northern Patagonia and b) Beagle Channel.

3. Results

The $\delta^{18}O$ values of blue mussel shells from the Beagle Channel varied dramatically throughout the second half of the Holocene (Kruskal-Wallis test, χ^2= 22.018, df=4, N=25, p<0.001), but compared to modern blue mussels, zooarchaeological samples were often more enriched in ^{18}O, except those from the Mischiuen I site dated 890±90 ^{14}C BP (Fig. 3e). Notably, the average $\delta^{18}O$ of the blue mussels from the Mischiuen I site was much lower than that reported for modern blue mussels from the subtropical Buenos Aires province (Fig. 3e); such intense ^{18}O depletion could not be caused by a higher sea surface temperature alone. The most likely explanation is a dramatic decline in salinity, perhaps caused by increased freshwater runoff due to accelerated glacier melting in a slightly warmer climate. Under this scenario, the reconstruction the sea surface temperature based on $\delta^{18}O$ values may be highly inaccurate. Differences in the average $\delta^{18}O$ values of rubbed mussels (ancient and modern) from central-northern Patagonia throughout the past 5500 years were not statistically significant (ANOVA; $F_{4,20}$=2.056; p= 0.125) due to high variability, particularly among modern samples. However, the differences were statistically significant if only zooarchaeological samples were considered (ANOVA; $F_{3,16}$=4.726; p=0.015). Moreover, the temporal pattern was similar to that reported for the Beagle Channel, with high $\delta^{18}O$ values at the time when hunter-gatherers began to exploit coastal sites at the end of the middle Holocene, low $\delta^{18}O$ values during most of the late Holocene (2100-600 ^{14}C BP), high $\delta^{18}O$ values during the Little Ice Age and declining $\delta^{18}O$ values during recent centuries (Fig. 3f). Notably, the sea surface temperature during the cold phases corresponding to the end of the middle Holocene and the Little Ice Age was much colder than that currently observed in central-northern Patagonia and close to that currently observed in the Beagle Channel. In contrast, the sea surface temperature during the warmer period between the end of the middle Holocene and the Little Ice Age was slightly warmer than that currently observed in northern Patagonia.

Therefore, the temporal profiles of oxygen stable-isotope ratios in both areas revealed similar patterns, characterized by low temperatures at the end of the middle Holocene, high temperatures throughout most of the late Holocene, a second cold phase during the Little Ice Age and a recent warming. If the temporal changes in the resource-exploitation patterns revealed by previous zooarchaeological research were caused by climatic variability, they should be parallel in northern Patagonia and the Beagle channel, as both regions showed parallel changes in the oxygen stable-isotope ratios.

However, the resource-exploitation patterns of the Beagle Channel and northern Patagonia were rather different, because otariids occurred throughout the second half of the Holocene in the archaeological record from the Beagle Channel, but were absent from the archaeological sites older than 3000 years ago in northern Patagonia (Fig. 3). Furthermore, the relative importance of otariids in the archaeological record from the Beagle Channel declined steadily during the second half of the Holocene, whereas, the relative importance of otariids in the archaeological record from northern Patagonia increased approximately 2500 years ago, to decrease slightly 1000 years ago (Fig. 3c-d). Finally, there was no correlation between the $\delta^{18}O$ values of bivalve shells and the relative abundance of otariids in the archaeological record, either in the Beagle Channel (Rho=0.500, p=0.327, n=5) or northern Patagonia (Rho=0.154, p=0.801, n=5). Therefore, source-exploitation patterns of the two regions were quite different and varied independently, without any relationship with the oxygen stable-isotope ratios in bivalve shells (Fig. 3).

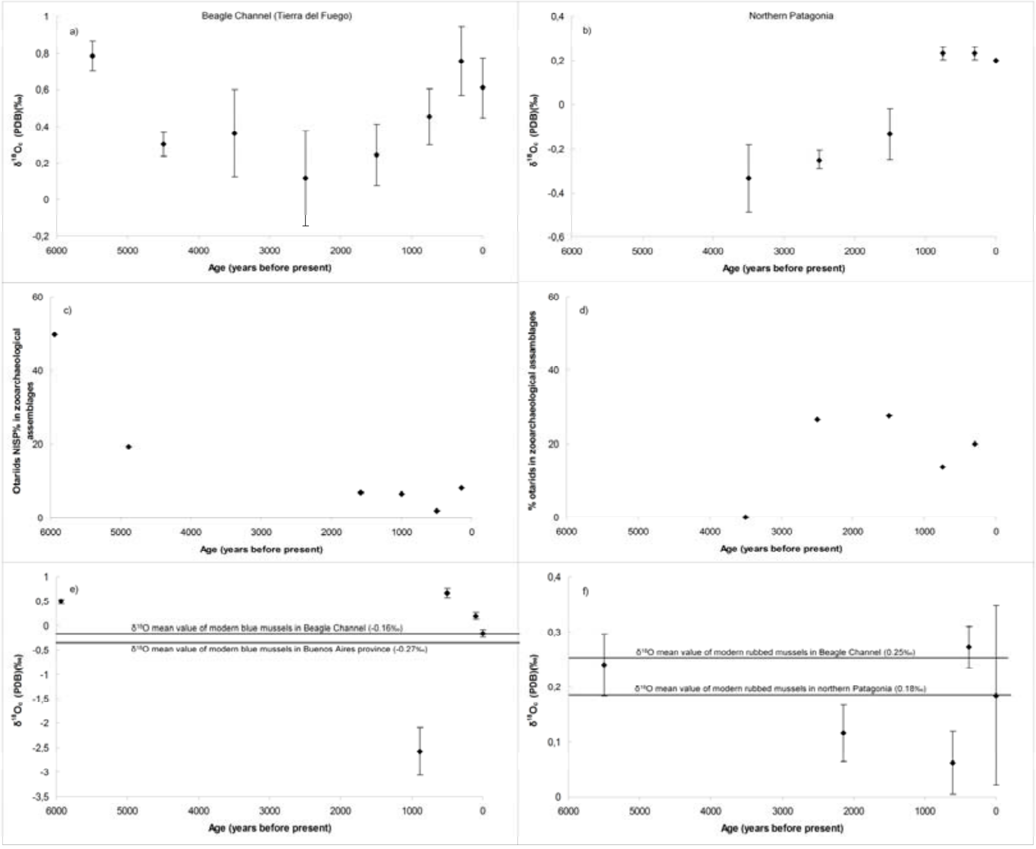

Fig. 3. a) Temporal profiles of oxygen stable isotope ratios in mytilid shells from the Beagle Channel according to Obelic et al. (1998), (b) temporal profile of oxygen stable isotope ratios in mytilid shells from Río Negro, northern Patagonia, according to Favier Dubois et al. (2009), c) temporal profiles of the relative importance of otariids in the zooarch- aeological record from the Beagle Channel according to Tivoli and Zangrando (2011), d) temporal profile of the relative importance of otariids the zooarchaeological record from Río Negro, northern Patagonia (Favier Dubois et al., 2009), e) temporal profiles of oxygen stable isotope ratios in mytilid shells from the Beagle Channel according to the present study and f) temporal profiles of oxygen stable isotope ratios in mytilid shells from central-northern Patagonia according to the present study.

4. Discussion and conclusions

The oxygen-isotope ratios of bivalve shells are currently the most robust proxies for temperature reconstructions and are most likely not affected by ontogenetic changes during bivalve growth (Schöne et al., 2004). However, the reconstruction of palaeotemperatures using the $\delta^{18}O$ values of bivalve shells can be confounded by variations in salinity (Epstein et al.,1951;Wefer and Berger, 1991; Schöne et al., 2004; LeGrande and Schmidt, 2006) because the $\delta^{18}O$ values of seawater are influenced by both temperature and salinity (Bowen, 2010). Freshwater runoff into the Beagle Channel is intense (Guerrero and Piola, 1997) and may have varied dramatically during the Holocene in response to glacier melting. Furthermore, palynological analysis has revealed wetter conditions in the Beagle Channel during the second half of the Holocene (Heusser, 1989), possibly resulting in more intense freshwater runoff.

These observations challenge the use of $\delta^{18}O$ values from bivalve shells for palaeotemperature reconstruction in the Beagle Channel, although Obelic et al. (1998) attempted to overcome this problem using samples from middens located near areas that currently contain “pure seawater”, which in the region has a salinity level of 33 g L^{-1} (Guerrero and Piola, 1997). Samples from middens located near areas that are currently flooded with brackish water were also studied but were not included in subsequent analyses. Palaeotemperature reconstruction using “marine” samples alone revealed no major changes throughout the second half of the Holocene (Obelic et al., 1998), but there is no reason to assume that the distribution of water masses of contrasting salinity within the Beagle Channel has remained unchanged throughout the second half of the Holocene. Thus, the selected middens may not actually have been representative of truly marine conditions. Furthermore, both low salinity levels and high temperatures result in low $\delta^{18}O$ values. Hence, the alternation of cold and warm periods is not obscured by changes in salinity, although the actual seawater temperature cannot be calculated, and its fluctuations may be magnified by changes in salinity.

When the full data set of Obelic et al. (1998) is considered, a clear pattern emerges, with ^{18}O-enriched samples prevailing at the end of the middle Holocene and ^{18}O-depleted samples prevailing during most of the late Holocene, except during the Little Ice Age (Fig. 3). The data reported here are consistent with this pattern and reveal a parallel pattern for the central-northern Patagonian coast, where $\delta^{18}O$ values are not confounded by variable salinity because freshwater runoff is currently very low (Guerrero and Piola, 1997) and salinity levels were similar during the middle Holocene, as suggested by a malacological analysis of Quaternary marine terraces (Aguirre et al., 2006). Accordingly, the available evidence confirms the occurrence of a warmer climate in both the Beagle Channel and central-northern Patagonia during the Mediaeval Warm Epoch (Villalba, 1990; Stine, 1994) and of a colder climate during the Little Ice Age (Villalba, 1990; Winkler, 2000; Mauquoy et al., 2004). These findings demonstrate that the climate varied simultaneously in both regions, although contemporaneous seawater temperatures were always lower in the Beagle Channel than off northern Patagonia.

Increasing sea surface temperatures coincided with the decreasing reliance of hunter-gatherers in the Beagle Channel on otariids throughout the first half of the late Holocene (Schiavini, 1993; Tivoli and Zangrando, 2011). However, a causal relationship cannot be determined for at least two reasons. Firstly, otariids consumption did not increase again during the Little Ice Age (Schiavini, 1993; Tivoli and Zangrando, 2011), when sea surface temperature declined. Western exploitation may have decimated fur seals (Arctocephalus australis) in Tierra del Fuego at the end of the 18th and beginning of the 19th century (Ratto, 1943; Schiavini, 1992), thus preventing hunter-gatherers from resuming their former exploitation levels during the Little Ice Age. However, fur seal bones were already quite rare in middens 500±100 ^{14}C BP, when the sea surface temperature had already decreased and European explorers had only recently reached the region. Secondly, male fur seals (*Arctocephalus australis*) represented most of the otariids exploited by hunter-gatherers in the Beagle Channel, and the largest population of the species in the Atlantic currently occurs in subtropical Uruguay (Túnez et al., 2008). Thus, the warm temperatures prevailing during most of the late Holocene most likely did not limit the abundance of this species. In addition, the exploitation of male fur seals would have not severely impacted the population given the high degree of polygyny in this species.

In contrast to the situation in the Beagle Channel, increasing sea surface temperatures during the late Holocene coincided with more intense exploitation of sea lions (*Otaria flavescens*) by hunter-gatherers in central and northern Patagonia, although this intensification began earlier in northern than in central Patagonia (Gómez Otero, 2006; Gómez Otero, 2007; Favier Dubois et al., 2009). Interestingly, reliance on otariids declined 1500 years ago in northern Patagonia (Favier Dubois et al., 2009) and 700 years ago in central Patagonia (Gómez Otero, 2007), although no major change in sea surface temperature was recorded at those times. Thus, the exploitation of otariids in central and northern Patagonia was high when the sea surface temperature was high (at the beginning of the

Mediaeval Warm Epoch) and low when sea surface temperature was both low (at the end of the middle Holocene) and high (at the end of the Mediaeval Warm Epoch).

In conclusion, changes in sea surface temperature played only a minor role, if any, in the changing subsistence strategies of hunter- gatherers in northern Patagonia and the Beagle Channel. However, this conclusion does not imply that the abundance of otariids in the south-western Atlantic declined as a result of prolonged exploitation by hunter-gatherers. Otariid populations can be highly sensitive to declines in food abundance and quality (Trites and Donnelly, 2003). Therefore, variations in marine primary productivity in the south-western Atlantic during the second half of the Holocene may better explain the observed variations in the relative abundance of otariids in hunter-gatherer middens, as suggested for the north Pacific (Finney et al., 2002).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2013.03.026.

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1.2 La explotación de pinnípedos por parte de los paleoindios en América del Sur fue impulsada por la productividad oceánica.

RESUMEN. Después de siglos de explotación de pinnípedos, los cazadores-recolectores de la costa atlántica del sur de Sudamérica emplearon en varias ocasiones otros recursos animales durante la segunda mitad del Holoceno. El cambio ha sido justificado por la sobreexplotación de las poblaciones de pinnípedos, aunque las variaciones de la productividad primaria marina podrían ofrecer una explicación alternativa. Este es un punto crítico, ya que actualmente las grandes poblaciones de lobos marinos y focas se encuentran únicamente en zonas donde la productividad marina es elevada. Aquí examinamos por un lado el registro zooarqueológico en el norte de Patagonia y Tierra del Fuego para evaluar la intensidad de la explotación de pinnípedos durante la segunda mitad del Holoceno, y por otro lado las razones isotópicas de nitrógeno ($\delta^{15}N$) en conchas subfósiles como indicadores de la productividad primaria marina. Los resultados revelaron grandes fluctuaciones en la productividad primaria marina y demostraron que los cazadores-recolectores empleaban intensamente los pinnípedos sólo cuando la productividad marina era alta. Este hallazgo sugiere que la disminución en la abundancia de pinnípedos que se observa en el registro zooarqueológico fue causada por un control desde abajo de la población de pinnípedos y no por la sobreexplotación de los cazadores-recolectores.

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Paleoindian pinniped exploitation in South America was driven by oceanic productivity

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Abstract

After centuries of pinniped exploitation, hunter-gatherers from the Atlantic coast of southern South America shifted in several occasions to other animal resources during the second half of the Holocene. The shift has been justified by the overexploitation of pinniped populations although changes in marine primary productivity may be an alternative explanation. This is a critical point, as currently large populations of sea lions and fur seals occur only in areas where marine productivity is high. This paper examines the zooarchaeological record to assess the intensity of pinniped exploitation and the stable isotope ratio of Nitrogen ($\delta^{15}N$) in mollusc shells collected from archaeological sites as a proxy of marine primary productivity in northern Patagonia and Tierra del Fuego during the second half of the Holocene. The results reveal major fluctuations of marine primary productivity and demonstrate that huntergatherers only relied intensely on pinnipeds when marine productivity was high. This finding suggests that the decline in pinniped abundance observed in the zooarchaeological record was caused by a bottom-up control of pinniped population and not by the overexploitation by hunter-gatherers.

Keywords: Nitrogen isotope; Hunter-gatherers; *Arctocephalus australis*; *Otaria flavescens*; *Aulacomya atra atra*; *Nacella magellanica***.**

1. Introduction

Concern about the conservation of marine resources has increased during recent decades as evidence that human exploitation has caused major changes in most marine ecosystems has grown (Pauly et al., 1998; Jackson et al., 2001; Pauly et al., 2005). Although recent examples of fisheries recovering after collapse certainly exist (Worm et al., 2009), marine resource exploitation has increased dramatically worldwide during recent centuries (Pauly et al., 2005), and few marine regions remain unaffected by anthropogenic impacts (Halpern et al., 2008). Although modern industrial fishing is the solely responsible for the alteration of offshore and deep-sea ecosystems (Christensen et al., 2003; Myers and Worm, 2003; Lewison et al., 2004; Devine et al., 2006), overfishing and the ecological extinction of coastal marine megafauna are thought to predate industrialized fishing in many cases. The historical record clearly demonstrates that preindustrialized European societies overexploited coastal marine mammals (Dulvy et al., 2009) and that European settlement triggered the overexploitation of coastal marine megafauna on other continents (Jackson et al., 2001). However, the impact of other preindustrialized cultures on coastal marine resources remains contentious. An increasing number of multidisciplinary studies examining the interactions between prehistoric peoples and their environments suggest that, at least in some cases, ancient peoples caused cumulative and often irreversible impacts on natural landscapes and biotic resources worldwide (Kirch, 2005).

The study of the Holocene human settlements along the Argentine coast began after 1936, as archaeologists viewed marine resources as minor dietary sources for local hunter-gatherers, who were considered primarily terrestrial (Orquera and Gómez Otero, 2007). Only since the 1980s, with the improvement of archaeological methods and based on the productivity of the seas and the high nutritional value of some marine species, was the importance of such resources recognized (Gómez Otero, 2006, 2007; Orquera and Gómez Otero, 2007; Moreno, 2008). Available evidence indicates that the southern end of South America was colonized more than 12,000 years ago by humans dispersing along the Pacific coastline of the Americas (Miotti et al., 2003; Dillehay et al., 2008; McKechnie and Wigen, 2011; Moss and Losey, 2011; Orquera et al., 2011). These humans possessed the technology to use marine resources, notably fish, birds, and molluscs (Keefer et al., 1998; Dillehay et al., 2008; Betts et al., 2011; Erlandson et al., 2011; Gifford-Gonzalez, 2011), but intense exploitation did not develop until much later, in the Middle Holocene, probably as a consequence of a technological improvement (Yesner et al., 2003; Orquera et al., 2011; Tivoli and Zangrando, 2011). However, the hypothesis that human occupation was earlier than currently thought, especially in certain sectors of the coast where the bathymetry is particularly smooth (Ponce et al., 2011), is still open (Gómez Otero, 2006).

Pinnipeds were especially important prey for both the huntergatherers inhabiting the Beagle Channel and the southern coast of Chile, who based their living on marine resources (Schiavini, 1993; Orquera and Piana, 1999; Yesner et al., 2003; Orquera et al., 2011; Tivoli and Zangrando, 2011), and those who inhabited central and northern Patagonia, only partially dependent on maritime resources (Gómez Otero, 2006; Moreno, 2008; Favier Dubois et al., 2009). According to the zooarchaeological record, the human populations inhabiting the Beagle Channel approximately 6000 BP were highly reliant on marine resources, mainly fur seals (*Arctocephalus australis*) which were the main source of food and raw material for many millennia (Orquera and Piana, 1999; Orquera et al., 2011; Tivoli and Zangrando, 2011). Conversely, people inhabiting northern and central Patagonia exploited both terrestrial and marine resources, but the exploitation of pinnipeds, especially sea lions (*Otaria flavescens*), developed approximately 3000 BP, when seasonal settlements were established close to sea lion rookeries (Gómez Otero, 2006; Favier Dubois et al., 2009). Sea lion exploitation was intense in the northern province of Rio Negro from 3100 to 2200 BP and was followed by a period of moderate exploitation from 1500 to 420 BP (Favier Dubois et al., 2009). In contrast, sea lion exploitation in Chubut province was moderate from 3000 to 1000 BP, and intensified from 1000 to 350 BP (Gómez Otero, 2006, 2007).

Although both groups of hunter-gatherers differed dramatically in technology and in historical patterns of resource exploitation (Orquera and Piana, 1999; Orquera and Gómez Otero, 2007; Moreno, 2008; Orquera et al., 2011), everywhere the zooarchaeological record reveals a general decline in the consumption of pinnipeds after several centuries of exploitation (Yesner et al., 2003; Gómez Otero, 2007; Favier Dubois et al., 2009; Tivoli and Zangrando, 2011). Similar declines in the use of pinnipeds by maritime hunter-gatherers in the north Pacific have been on occasions linked to increasing sea surface temperature (Colten and Arnold, 1998; Betts et al., 2011), but most often to overexploitation by humans in the absence of strong evidence supporting climate forcing (Porcasi et al., 2000; Lyman, 2003; Jones et al., 2004; Newsome et al., 2007). Overexploitation has also been suggested as the reason for the progressive decline in the presence of fur seals in the zooarchaeological record from the Beagle Channel (Orquera et al., 2011; Tivoli and Zangrando, 2011), as the pollen record (Heusser, 1990) and the stable oxygen isotopes (Obelic et al., 1998; Saporiti et al., 2013) suggested no relationship between climate and patterns of resources used by hunter-gatherers during the second half of the Holocene. However, nothing is known about how marine productivity varied throughout that period, a critical point because dense populations of sea lions and fur seals only thrive in highly productive environments (Bowen et al., 2009).

Primary productivity in coastal areas usually depends on nitrogen availability, which increases due to high freshwater runoff, intense vertical mixing and deep water upwelling (Gruber, 2008). All these processes also promote nitrogen recycling over nitrogen fixation and hence modify the relative abundance of heavy isotopes of nitrogen (^{15}N) in the tissues of aquatic primary producers (Calvert et al., 1992; Wu et al., 1997; Waser et al., 2000). As stable isotope ratios in prey are transferred to their predators, $\delta^{15}N$ values in herbivorous molluscs are expected to reveal $\delta^{15}N$ values in primary producers (Post, 2002) and hence inform about primary productivity. In the intertidal, mussels and limpets are prominent suspensión feeders and grazers, respectively (Bigatti and Penchaszadeh, 2008) and their shells often occur mixed with pinniped bones in huntergatherers shell middens (Gómez Otero, 2006, 2007; Orquera et al., 2011). Here, the δ^{15}N in the protein of the shell of rubbed mussels (*Aulacomya atra atra*) and limpets (*Nacella magellanica*) collected along the coast of Argentina has been measured in order to evaluate the correlation with the marine primary productivity of the wáter where they live. Once the correlation was confirmed the δ^{15}N values of the organic matter from shells collected at hunter-gatherer shell middens have been used as reliable proxies of past marine primary productivity and have been compared to the patterns of marine resource exploitation reported by previous zooarchaeological researchers (Yesner et al., 2003; Gómez Otero, 2006; Moreno, 2008; Favier Dubois et al., 2009; Tivoli and Zangrando, 2011). In this way, the hypothesis that the changing patterns of marine resource exploitation by hunter-gatherers along the south-western Atlantic coast of Argentina were driven by a bottom-up process and not by overexploitation was tested.

2. Methods

2.1. Study area and sampling

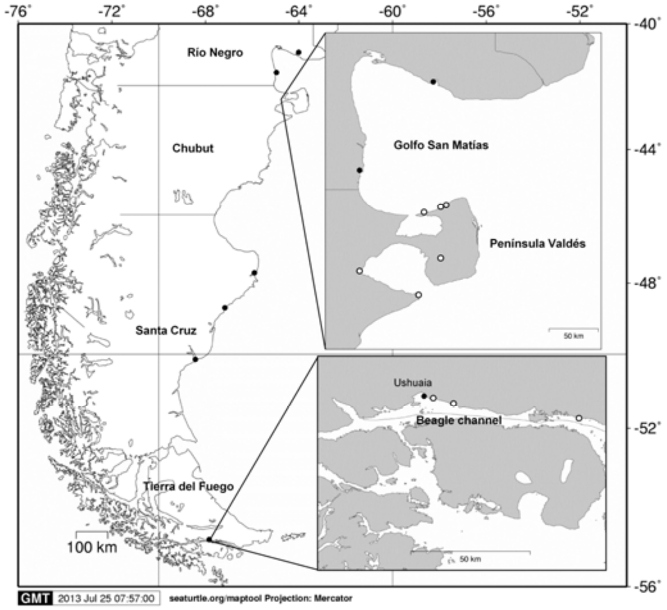

Figure 1. Map showing approximate sampling localities. Empty circles indicate the archaeological samples; the filled circles indicate the modern samples.

Modern mollusc samples (n≥5 for each species) were collected from December 2009 to February 2010 at six sites along the coastline of Argentina: two in Río Negro province (41º1.20’S-41º38.40’S; 64º10.80’W-65º1.20’W), three in Santa Cruz province (47º44.40’S-50º6.60’S; 65º50.40’W-68º27.00’W) and one in Tierra del Fuego province (54º49.20’S; 68º12.00’W) (Fig.1). The limpet *N. magellanica* was collected in five sites, and the rubbed mussel *A. atra atra* was collected in four sites (see Table 1). As remotely sensed chlorophyll concentration can be used as an index of the meanwater column chlorophyll (Smith, 1981), satellite data (SeaWiFS 9 km; http://reason.gsfc.nasa.gov/Giovanni/) were used to determine current (January 2005 to January 2010) average chlorophyll-a levels in each sampling area. Chlorophyll-a is an index of the primary productivity in the oceans (Lorenzen, 1970).

Table 1. $\delta^{15}N$ mean values (with standard deviation) of modern shells of the limpets and rubbed mussels collected along the coast of Argentina. The last column represents the chlorophyll-a levels mean values (with standard deviation) in each sample site.

Species	**Province**	**N**	**Mean $\delta^{15}N$ (‰)**	**Mean Chl-a (mg/m^3)**
Nacella magellanica	Río Negro	5	11.8 (±0.5)	1.22 (±2.33)
Nacella magellanica	Santa Cruz	5	12.1 (±0.4)	1.44 (±0.47)
Nacella magellanica	Santa Cruz	5	12.3 (±0.3)	1.55 (±0.30)
Nacella magellanica	Santa Cruz	5	13.0 (±0.5)	1.97 (±0.91)
Nacella magellanica	Tierra del Fuego	5	10.8 (±0.3)	0.86 (±0.12)
Aulacomya atra atra	Río Negro	7	11.5 (±0.3)	1.05 (±1.56)
Aulacomya atra atra	Santa Cruz	5	11.8 (±0.4)	1.44 (±0.47)
Aulacomya atra atra	Santa Cruz	5	12.5 (±0.3)	1.97 (±0.91)
Aulacomya atra atra	Tierra del Fuego	5	11.9 (±0.3)	0.86 (±0.12)

Archaeological shell samples selected for isotopic analysis come from previous fieldwork carried out by authors Julieta Gómez Otero in Golfo San Matías and Península Valdés (northern Patagonia) and Ernesto Piana and colleagues (Luis Orquera and A. Francisco Zangrando) in the Beagle Channel (Table 2). Samples size was five for each species, site, and midden layer where available (Table 3). The samples were dated in different laboratories and using different methods, in particular samples from northern Patagonia, where all dated samples were marine shells instead of charcoal. Radiocarbon ages were calibrated by the authors using the package Clam 2.2 (Blaauw, 2010) and the new curve for Southern Hemisphere ShCal13 (Hogg et al., 2013). Reservoir effects data for northern Patagonia region are emerging only recently, and they suggest variable differences between marine and terrestrial ages (Cordero et al., 2003; Favier Dubois, 2009). The regional marine reservoir effect of 266 ± 51years was included in the calibration of the shell samples (Favier Dubois, 2009).

Table 2. Archaeological sites where shells were recovered. Radiocarbon and calibrated ages were reported.. a=Gómez Otero, 2006; b= Piana et al., 1992; c= Orquera and Piana, 1999. [1]Calibration of radiocarbon ages was carried out by the authors with the program Clam 2.2 (Blaauw, 2010), using the ShCal13 curve (Hogg et al., 2013). The probability is indicated in brackets. *the regional marine reservoir effect of 266±51years was included in the calibration of the shell samples (Favier Dubois, 2009).

Area	**Site**	**Material**	**Radiocarbon age (yr^{14}C bp)**	**Calibrated age[1] (^{14}C cal yr bp (±1σ)**	**Laboratory**
Northern Patagonia	Las Ollas conchero 1[a]	Shells	610±60	268-508 (85.8%)*	LATYR-CONICET-UNLP
			640±60	278-519 (92.1%)*	
Northern Patagonia	Ecocentro Fogón 3[a]	Shells	850±150	281-798 (94.7%)*	INGEIS (Buenos Aires)
Northern Patagonia	Playa Las Lisas 2 -	Shells	2140±50	1589-1921 (95.0%)*	LATYR-CONICET-UNLP
Northern Patagonia	Playas Las Lisas 2-	Shells	2600±60	2089-2502 (90.1%)*	LATYR-CONICET-UNLP
Northern Patagonia	Cracker 8 - Nivel 3[a]	Shells	5200±70	5465-5773 (83.9%)*	LATYR-CONICET-UNLP
Beagle Channel	Túnel VII[b]	Charcoal	100±45	221-264 (17.0%)	INGEIS (Buenos Aires)
Beagle Channel	Shamakush X site[c]	Charcoal	500±100	498-518 (95.0%)	INGEIS (Buenos Aires)
Beagle Channel	Imiwaia I (M/K)[b]	Charcoal	5750±170	6187-6936 (95.0%)	INGEIS (Buenos Aires)
			5870±150	6310-6989 (95.0%)	INGEIS (Buenos Aires)
			5949±50	6631-6885 (93.8%)	Arizona (USA)

For the characterization of resource use pattern by hunter-gatherers inhabiting the Beagle Channel (Fig. 2), we relied on the collections from six middens excavated at two archaeological sites 40 km apart. One location was situated at Cambaceres Bay and included archaeofaunal samples from stratigraphic layers dated 6000 BP, 1500 BP and from the 19th century. The other middens were located at Estancia Remolino and include assemblages dated 4000 BP, 1000 BP and 500 BP. There were no significant differences concerning excavation methods, as the same procedures were followed (see Tivoli and Zangrando, 2011 and references therein for further detail about the sites, dating procedures and collections). The collections from seven middens scattered in Bajo de la Quinta, Barranco de los Concheros and between Bahía Final 1 and Saco Viejo (northern coast of San Matías gulf), dated between 3430 ± 43 and 450 ± 80 ^{14}C BP, and information about archaeological sites located in Península Valdés, were used to characterize the pattern of resource use by hunter-gatherers inhabiting northern Patagonia (Fig. 3) (Gómez Otero and Suárez, 1999; Gómez Otero, 2007; Orquera and Gómez Otero, 2007; Favier Dubois et al., 2009).

2.2. Analytical methods

Both the archaeological and the modern shell samples were polished with sandpaper and with a diamond wheel drill to remove impurities. Then, they were rinsed with distilled water, dried at 50ºC and ground into a fine powder by mortar and pestle. Dried powdered samples and secondary reference standards (acetanilide, urea, USGS 40 ($\delta^{15}N$ = -4.6‰), USGS 34 ($\delta^{15}N$ = -1.7‰), IAEA N2 ($\delta^{15}N$ = +20.3 ‰), IAEA N1 ($\delta^{15}N$ = +0.4‰), IAEA 600 ($\delta^{15}N$ = 1.0‰), UCGEMA F ($\delta^{15}N$ = +4.6‰)) were weighed and analyzed in a continuous flow stable isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA Thermo Finnigan) coupled with an elemental analyzer. We also employed a CO_2 absorbent for elemental analysis (CaO/NaOH) to avoid spectrometer saturation by the $CaCO_2$, which constitutes over 90% of the shell. Secondary standards were calibrated with the nitrogen international standard, atmospheric N_2. Samples were processed at Scientific and Technological Centers (CCiT) of the University of Barcelona. Stable isotope values, expressed in delta (δ) notation, in which the relative variations of stable isotope ratios are expressed in permil (‰) deviations from predefined international standards, were calculated as:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 10^3$$

where X is ^{15}N, Rsample is the heavy-to-light isotope ratio of the sample ($^{15}N/^{14}N$), and $R_{standard}$ is the heavy-to-light isotope ratio in reference standards certified by International Atomic Energy Agency (IAEA, Vienna).

Table 3. $\delta^{15}N$ mean values (with standard deviation) of archaeological shells of limpets and rubbed mussels used in the paper and collected in previous field work by two of the authors (Julieta Gómez Otero and Ernesto Piana).

Species	**Province**	**Site**	**Calibrated age (^{14}C cal yr BP (±1σ))**	**N**	**Mean $\delta^{15}N$ (‰)**
Nacella magellanica	Chubut	Ecocentro Fogón 3	281-798 (94.7%)	5	13.5 ±0.8
Nacella magellanica	Chubut	Playas Las Lisas 2-Conchero 2	2089-2502 (90.1%)	5	15.7 ±0.8
Nacella magellanica	Chubut	Cracker 8 - Nivel 3	5465-5773 (83.9%)	2	14.1 ±0.8
Nacella magellanica	Tierra del Fuego	Túnel VII	221-264 (17.0%)	5	12.5 ±0.8
Nacella magellanica	Tierra del Fuego	Shamakush X site	498-518 (95.0%)	4	12.2 ±0.8
Nacella magellanica	Tierra del Fuego	Imiwaia I (M/K)	6187-6936 (95.0%) 6310-6989 (95.0%) 6631-6885 (93.8%)	5	13.4 ±0.8
Aulacomya atra atra	Chubut	Las Ollas conchero 1	268-508 (85.8%) 278-519 (92.1%)	5	13.1 ±0.8
Aulacomya atra atra	Chubut	Playa Las Lisas 2 – Perfil 1	1589-1921 (95.0%)	5	13.7 ±0.8
Aulacomya atra atra	Chubut	Cracker 8 - Nivel 3	5465-5773 (83.9%)	5	14.1 ±0.8

2.3. Statistical methods

Normality in data distributionwas tested using the Lilliefors test and homoscedasticity using the Levene test. A linear regression was performed to investigate the correlation between modern shell $\delta^{15}N$ with chlorophyll-a. ANOVAwas used for multiple comparisons when data fit the normality and homoscedasticity requirements and the non-parametrical KruskaleWallis test was used otherwise. The percentage of the number of specimens identified at the species level (%NISP) in the collections from the Beagle Channel (Tivoli and Zangrando, 2011) was used to calculate the relative abundance of otariids. Bone preservation was worse at the archaeological sites from northern Patagonia and therefore numbers of specimens had not been assessed (Favier Dubois et al., 2009). As a consequence, the relative importance of otariids in the collections from that area was assessed by calculating the percentage of broad taxonomic groups represented by otariids (%BTG) in each collection. A single collection was analyzed from each zone (Beagle Channel and northern Patagonia) and age. All statistical analyses were conducted with the PASW Statistic 18 software package.

3. Results

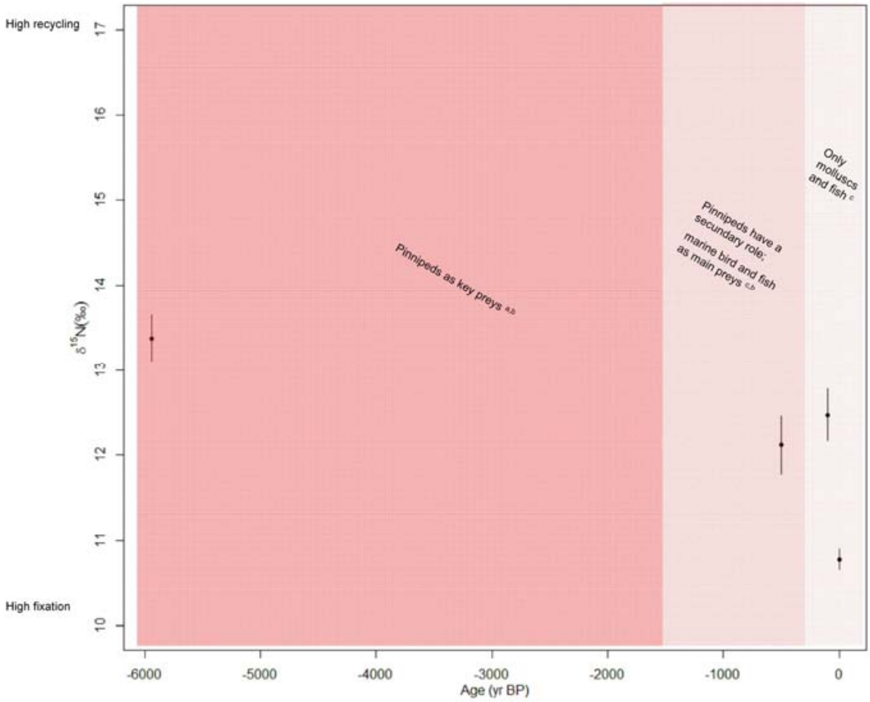

Figure 2. $\delta^{15}N$ values in the shell of limpets from the Beagle Channel during the last 6600 years, including modern samples. The background colour represents the relative abundance of pinnipeds for hunter-gatherers in the area. Vertical bars denote standard deviation (n=5). a=Tivoli and Zangrando, 2011;b=Orquera and Piana, 1999;c=Yesner et al., 2003.

As the correlation between modern shell $\delta^{15}N$ with chlorophylla was significant for both species (rubbed mussels, adjusted r-squared = 0.340, n = 22, p = 0.003; limpets, adjusted r-squared = 0.764, n = 25, p < 0.001), the $\delta^{15}N$ values of the organic matter from shells collected at hunter-gatherer shell middens have been used as reliable proxies of past marine primary productivity. The $\delta^{15}N$ values of rubbed mussel shells from hunter-gatherers shell middens from northern Patagonia were higher than those of modern samples from the same areas (Kruskal-Wallis test, χ^2 =16.42, df = 3, N = 22; p < 0.01). The same was true for the $\delta^{15}N$ values of limpet shells either in northern and central Patagonia (ANOVA $F_{3,13}$ = 22.00, p < 0.001) and the Beagle Channel (ANOVA $F_{3,15}$ = 19.97, p < 0.001). Furthermore, the $\delta^{15}N$ values of limpet shells from northern Patagonia dated 2089-2502^{14}C cal BP were significantly higher than those dated ca. 500 cal BP and modern ones. The $\delta^{15}N$ values of limpet shells from the Beagle channel dated ca. 6600 cal BP were higher than those dated

498-518 ^{14}C cal BP. Thus, stable isotopes analysis indicates that coastal primary productivity during the second half of the Holocene was higher than that currently observed in both areas, although the temporal dynamics differed between the two regions through the second half of the Holocene, as marine primary productivity was much higher at the beginning of human occupation in the Beagle Channel than in more recent periods (Fig. 2) but fluctuated off northern and central Patagonia (Fig. 3). Despite those differences, the periods of intense exploitation of pinnipeds in both regions, indicated as darker shades of colour in Figs. 2 and 3, were characterized by high values of δ^{15}N values in mollusc shells.

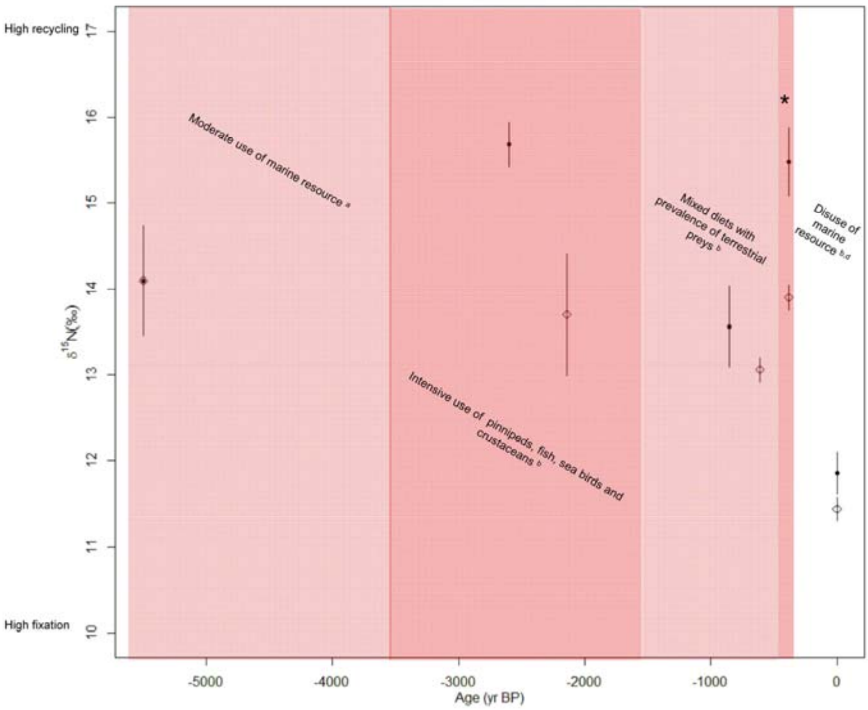

Figure 3. δ^{15}N values in the shell of limpets (solid circles) and rubbed mussels (empty diamonds) from northern Patagonia during the last 6000 years, including modern samples. The background represents the relative abundance of pinnipeds for hunter-gatherers in the area. Vertical bars denote standard deviation (n=5). a=Orquera and Gómez Otero, 2007; b=Favier Dubois et al., 2009; c=Gómez Otero and Suarez, 1999; d=Gómez Otero, 2007.

4. Discussion

Pinnipeds were exploited by hunter-gatherers since the very beginning of coastal settlement at the Beagle Channel, approximately 6400 years ago (Orquera and Piana, 1999; Tivoli and Zangrando, 2011). However, the dietary importance of pinnipeds, mainly fur seals

(*A. australis*), declined steadily through the Late Holocene and has been negligible since approximately 1500 years ago (Yesner et al., 2003; Tivoli and Zangrando, 2011), in parallel to the decline of the δ^{15}N values of limpet shells. However, this conclusion should be improved by further data for the period between approximately 6000 and 500 years ago, where there are no δ^{15}N data. It can be argued that western sealers decimated fur seals (*A. australis*) in Tierra de Fuego at the end of the 18th and beginning of the 19th century (Schiavini, 1993), and hence, impeded the ability of hunter-gatherers to resume former exploitation levels during the Little Ice Age, when d15N δ^{15}N slightly rose. However, the occurrence of fur seal bones in middens was already extremely low 500 years ago, when the marine productivity had already decreased and European explorers had just reached the region. The pattern of pinniped exploitation in northern and central Patagonia is more complex, as hunter-gatherers began the use of marine resources 7000 years ago (Orquera and Gómez Otero, 2007) but only intensified the exploitation of pinnipeds approximately 3000 years ago in Golfo San Matías (Favier Dubois et al., 2009), when the δ^{15}N values in mollusc shells increased. The intensity of pinniped exploitation in Golfo San Matías declined approximately 1500 years ago (Gómez Otero and Suárez, 1999). The δ^{15}N values of the rubbed mussels are also consistent with this pattern, although differences among Holocene samples were not statistically significant. Finally, coastal areas were abandoned following the domestication of feral horses of European origin at the beginning of the 18th century (Gómez Otero, 2006; Favier Dubois et al., 2009). In conclusion, the overall evidence suggests that intense exploitation of pinnipeds by hunter-gatherers inhabiting the coastline of the Southwest Atlantic Ocean began when marine primary productivity was high and declined when marine primary productivity decreased. Accordingly, changes in the relative abundance of pinnipeds in the zooarchaeological record more likely reflect a *bottom-up* control of pinniped populations by marine primary productivity rather than overexploitation by huntergatherers. These findings indicate that hunter-gatherers along the south-western Atlantic coast of Argentina did not have a critical role in pinniped population declines, as in other coastal areas of New Zealand and northern Pacific (Anderson, 2008). This is a major advancement in the archaeology of the Patagonia and revealed that, despite the different mechanisms of livelihood observed in local populations, they had only a minor impact on pinnipeds. In contrast, the prolonged hunt by European sealers was the sole cause of their near extinction in the twentieth century.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2014.05.015.

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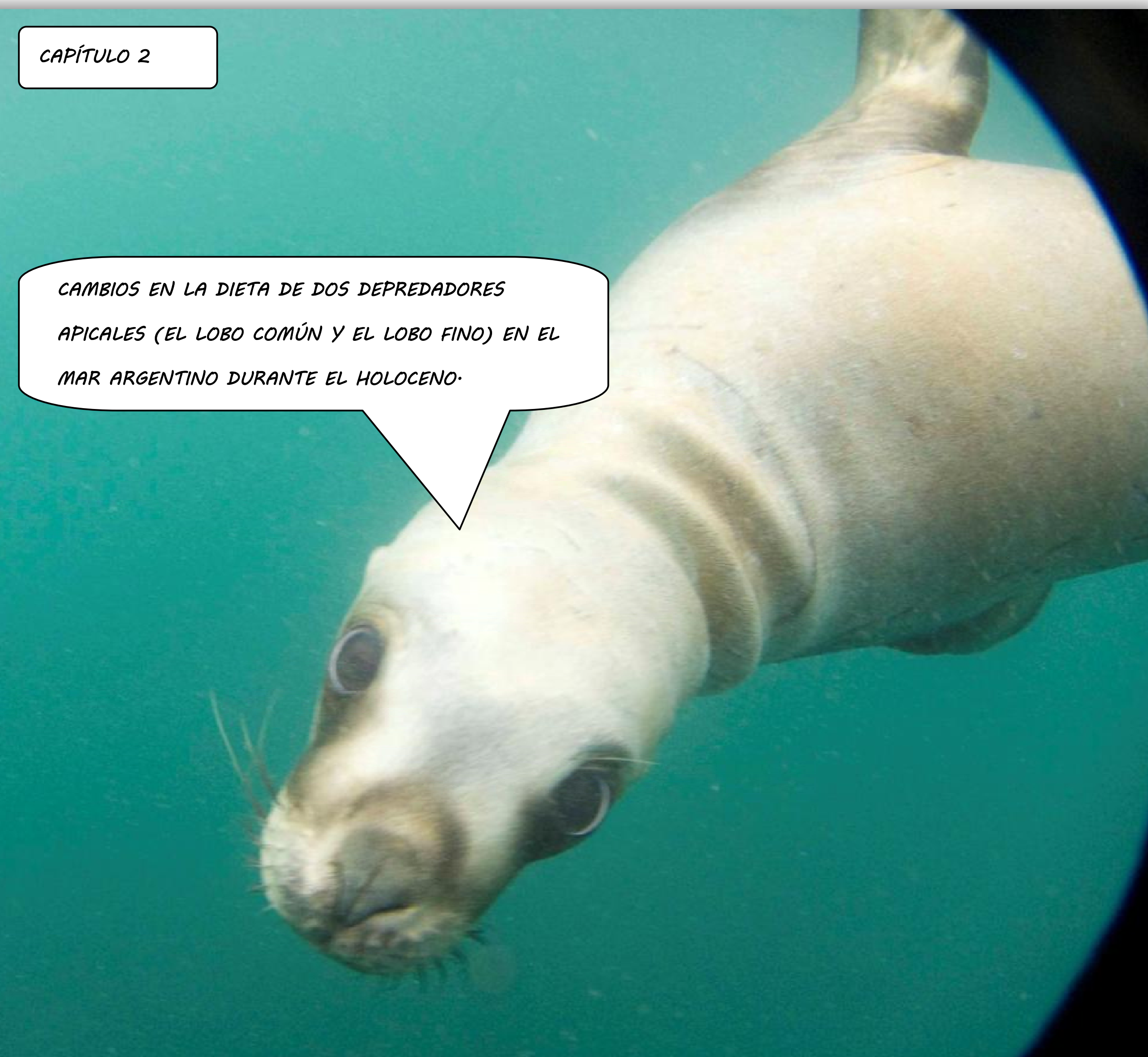

CAPÍTULO 2

CAMBIOS EN LA DIETA DE DOS DEPREDADORES APICALES (EL LOBO COMÚN Y EL LOBO FINO) EN EL MAR ARGENTINO DURANTE EL HOLOCENO.

2.1 Cambios en el nicho del lobo marino común (Otaria flavescens) en el Atlántico sud-occidental desde finales del Holoceno.

RESUMEN. Se analizaron las razones isotópicas de carbono y nitrógeno en muestras arqueológicas y modernas de hueso de lobo marino común *Otaria flavescens* para reconstruir los cambios en su dieta del desde el Holoceno tardío hasta la actualidad en el Atlántico sud-occidental. Las muestras óseas procedían de concheros situados en el centro-norte y sur de Patagonia, en Argentina, y de colecciones científicas modernas. También se analizaron las razones isotópicas de conchas de moluscos procedentes de yacimientos arqueológicos y modernos procedentes del intermareal rocoso a fin de explorar posibles cambios en la línea de base del paisaje isotópico. De este modo se pueden compara los valores isotópicos de muestras de hueso de diferentes períodos, una vez corregidos en función de la variación de la línea de base der cada época. Los resultados indican que las presas pelágicas predominaron en la dieta de los lobos marinos que vivían en la Patagonia centro-norte entre 3000 y 2000 años BP, mientras que el consumo de presas demersales se incrementó hace aproximadamente 1000 años BP. Al contrario, las proporciones de isótopos estables en hueso de lobos marinos que habitan el sur de Patagonia en diferentes momentos del Holoceno tardío indicaron una dieta relativamente estable, mientras que los lobos marinos actúales se alimentan a un nivel trófico mucho más alto que los antiguos, como también sucede en la Patagonia centro-norte. Este incremento reciente en el nivel trófico podría estar relacionado al menor tamaño de la población, causado por la caza comercial moderna, y en consecuencia a una menor competencia intraespecífica. Estos resultados confirman la plasticidad trófica del lobo marino sudamericano y subrayan las diferencias entre los nichos antiguos y actuales en especies explotadas.

PALEOBIOLOGY

Shifting niches of the South American sea lion (*Otaria flavescens*) in the southwestern Atlantic since the late Holocene

Lisette Zenteno, Florencia Borella, Julieta Gómez Otero, Ernesto Piana, Juan Bautista Belardi, Luis Alberto Borrero, Fabiana Saporiti, Luis Cardona and Enrique Crespo

Abstract.−Stable isotope ratios of carbon and nitrogen in archaeological and modern bone samples have been used to reconstruct the dietary changes of the South American sea lion *Otaria flavescens* since the late Holocene to the present in the south-western Atlantic. Bone samples were collected from archaeological sites in northern-central and southern Patagonia, Argentina, and modern scientific collections. Additionally, the stable isotope ratios in ancient and modern shells of intertidal molluscs were analysed to explore changes in the isotope baseline and allow comparison between bone samples from different periods after correction for baseline shifts. Stable isotope ratios showed that pelagic prey dominated the diet of sea lions inhabiting northern-central Patagonia 3000-2000 years BP, but the consumption of demersal prey increased approximately 1000 years BP. In contrast, stable isotope ratios from the bones of sea lions inhabiting southern Patagonia at different times during the late Holocene indicated a rather stable diet, whereas modern sea lions forage at a much higher trophic level than ancient ones, as in northern-central Patagonia. Such a recent increase in trophic level might be related to the smaller population size resulting from modern sealing and the resulting reduced intraspecific competition. These results confirm the trophic plasticity of the South American sea lion and underscore the dissimilarity between the past and modern niches of exploited species.

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Introduction

Humans have dramatically modified the ecosystems, not only due to the alteration of biogeochemical cycles (Crutzen 2002), but also because of the reduction of biodiversity (Terborgh and Estes 2010). Large species are particularly vulnerable to human impacts and many of them have declined in population size, or have become extinct before we had the opportunity to study and understand their ecological significance (Jackson et al. 2001; Martin 2005; Terborgh and Estes 2010). Thus, interpreting the biology of extant species as if they have evolved in the current, anthropogenic setting (Steadman 2006) could be misleading if anthropogenic impacts have modified their natural distribution ("e.g." Steadman 2006; Newsome et al. 2007) or have caused the functional extinction of keystone species (Jackson et al. 2001; Martin 2005; Terborgh and Estes 2010; Lotze et al. 2011). In this context, the historical perspective is essential to understand not only the evolutionary processes which operated in pristine environments, but also to provide goals for restoration and management (Jackson et al. 2001; McClenachan and Cooper 2008; Terborgh and Estes 2010; Braje and Rick 2011).

Eared seals, or Otariids, are still major components of coastal ecosystems in the temperate regions of the Southern Hemisphere, although most species were hunted to the brink of extinction throughout the 19th and 20th centuries due to commercial exploitation for their pelts and fat (Orquera 2002; Arnould 2009; Gentry 2009). The South American sea lion, *Otaria flavescens*, is widely distributed along some 10,000 km of the coast of South America, but was heavily exploited through its entire range till the first half of the 20th century (Cappozzo and Perrin 2009). In Uruguay, the population is still decreasing, although sealing ceased in 1995 (Páez 2006). The population breeding in Argentina experienced a 90% decline from the 1920s to the 1960s and currently is approximately one third of the original size (Crespo and Pedraza 1991; Reyes et al. 1999; Dans et al. 2004; Schiavini et al. 2004; Grandi et al. 2008). Numbers of sea lions declined simultaneously in the Falkland (Malvinas) Islands, where they decreased to less than 1.5% of the original population size, and the population remains small (Thompson et al. 2005).

Nevertheless, western sealers were not the first humans to exploit sea lions in the south-western Atlantic. According to the zooarchaeological record, pinnipeds were a prey also for the hunter-gatherers inhabiting the Beagle Channel during the second half of the Holocene (Schiavini 1993; Orquera and Piana 1999; Orquera et al. 2011; Tivoli and Zangrando 2011) and also for the hunter-gatherers inhabiting northern and central Patagonia during the late Holocene, although the patterns of resource use exploitation varied locally within that region (Gómez Otero, 2006, 2007; Moreno 2008; Favier Dubois et al. 2009; Favier Dubois and Kokot 2011).

Otariids were not the only marine resource used by humans in the south-western Atlantic. The Patagonian shelf is one of the most productive large marine ecosystems in the world (Longhurst 1998) and hunter-gatherer also exploited molluscs, fishes and marine birds (Schiavini 1993; Orquera and Piana 1999; Gómez Otero 2006, 2007; Moreno, 2008; Favier Dubois et al. 2009; Zangrando 2009; Zangrando et al. 2010; Orquera et al. 2011; Favier Dubois and Kokot, 2011; Tivoli and Zangrando, 2011; Borella and Cruz 2012; Favier Dubois and Scartascini 2012). Currently, the region supports important demersal fisheries targeting Argentine hake *Merluccius hubbsi*, Argentine shrimp *Pleoticus muelleri* and the squids *Ilex argentinus* and *Loligo gahi* (Bertolotti et al. 2001).

The intense exploitation of fishes, squids and crustaceans experienced during the last 40 years has deeply modified the structure of the ecosystems and caused a dramatic decrease in average fish size (Koen-Alonso and Yodzis, 2005; Dato et al. 2006). South American sea lions are generalist predators (Werner and Campagna, 1995; Thompson et al. 1998; Koen Alonso et al. 2000; Campagna et al. 2001; Riet-Sapriza et al. 2012) and have shifted diet to adapt to the new environmental conditions created by industrial fishing (Drago et al. 2009; Suarez et al. 2005; Romero et al. 2011), but at the cost of consuming less profitable prey and reducing body size (Drago et al. 2010). Nevertheless, intraspecific competition, and not competition with fisheries, has been proposed to be the major determinant of diet composition in South American sea lions (Drago et al. 2009, 2010), as they consume primarily large demersal prey when and where the population is small (Koen Alonso et al. 2000; Drago et al. 2009; Rosas et al. 1994; Oliveira et al. 2008; Riet-Sapriza et al. 2012) and shift to smaller benthic and pelagic prey when and where the population increases (Drago et al. 2009; Suarez et al. 2005; Romero et al. 2011). If this hypothesis was true, the currently trophic niche of South American sea lions would be different to that exploited in the past, when the population was much larger (Rodriguez and Bastida 1998; Dans et al. 2004; Schiavini et al. 2004).

The existence of a zooarchaeological record of South American sea lion bones dating back to the late and middle-late Holocene, combined with the existence of extensive scientific collections of modern skeletal material of South American sea lion, offers a unique opportunity to test this hypothesis. Here the stable isotope ratios of carbon and nitrogen in the bone of ancient and modern South American sea lions from Argentina were analyzed to assess the dietary changes of the species through the second half of the Holocene and determine the trophic niche of the species in ancient ecosystems. The stable isotope ratios in the shells of modern and ancient limpets and mussels have also been analyzed to reconstruct and balance for changes through time in the stable isotope baseline.

Material and Methods

Study site and sample collection.− We measured the stable isotope ratios of carbon and nitrogen of both modern and archaeological bone collagen samples of South American sea lions from two areas in Argentina (Fig. 1): northern-central Patagonia (from 39ºS to 46ºS) and southern Patagonia (from 46ºS to 55ºS). Modern samples of sea lions were collected from specimens at the scientific collections at Centro Nacional Patagónico (Puerto Madryn, Argentina) and Museo Acatushún (Ushuaia, Argentina) and the corresponding stable isotope ratios of carbon and nitrogen had been published previously elsewhere (Drago et al. 2009). Zooarchaeological bone samples were recovered from different layers of shell middens in northern-central Patagonia and southern Patagonia (Cabo Vírgenes)- Beagle Channel, (Tierra del Fuego), by researchers from CENPAT-CONICET, CADIC-CONICET and IMHICIHU-CONICET. Because the samples were dated in different laboratories and using different methods (Supplementary Table 3), the conventional, non-calibrated radiocarbon dates have been used for all sites.

Additionally, modern and zooarchaeological samples of intertidal mussels (*Aulacomya atra atra* and *Mytilus edulis)* and limpets (*Nacella magellanica)* from northern-central and southern Patagonia were collected and analyzed in order to take into account possible changes in the stable isotope baseline of the food web (Supplementary Table 4). Modern samples (N≥5 for each species and locality) of molluscs were collected from December 2009 to February 2010 at three sites along the coastline of Argentina: two in Río Negro province (northern Patagonia) and one in Tierra del Fuego province (southern Patagonia). Zooarchaeological shell samples (N=5 for each specie and site, when possible) were recovered from different layers of shell middens in northern-central Patagonia and the Beagle Channel, Tierra del Fuego (Fig. 1). While the same limpet species (*N. magellanica*) was found everywhere, only ribbed mussel (*A. atra atra*) was recovered in the shell middens of northern-central Patagonia and blue mussel (*M. edulis*) in the Beagle Channel (Terra del Fuego).

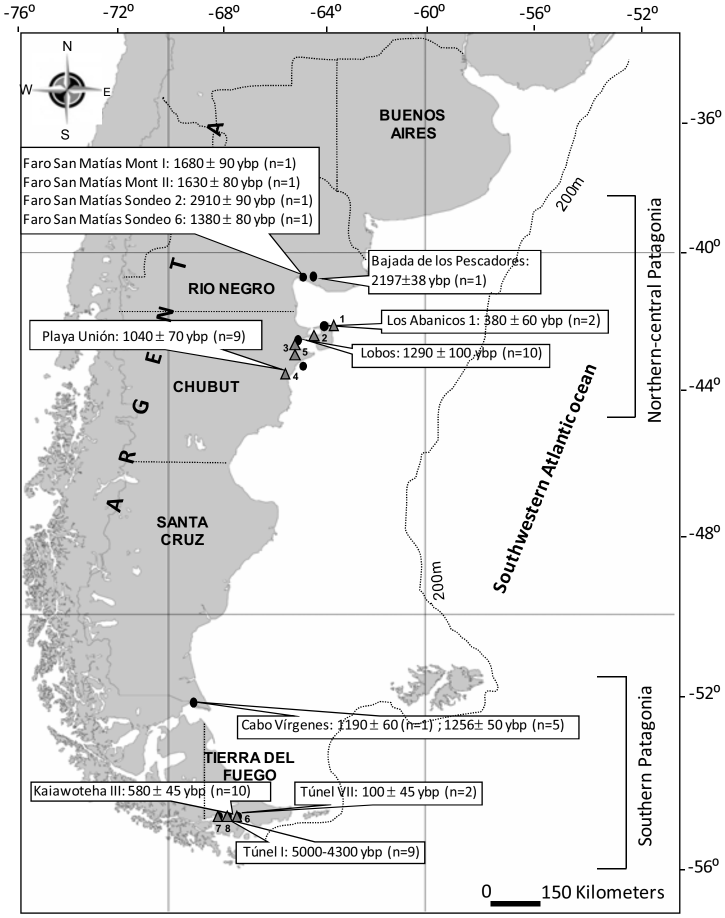

FIGURE 1. Location of archaeological sites from which sea lions and shells were sampled for stable isotope analysis. Sample sizes are listed in parentheses. The filled circles show archaeological sites for sea lions and the triangles denote sites for shells: 1= Los Abanicos 1; 2= Las Ollas Conchero 1; 3= Ecocentro Fogón 3; 4= Playa Las Lisas 2; 5= Cracker 6; Túnel VII; 7= Shamakush X; 8= Imiwaia I.

Finally, potential prey species for modern sea lions were collected for stable isotope analysis in northern-central and southern Patagonia (Table 1). Bone and shell samples were stored dry at room temperature. Samples from potential prey were stored a -20ºC until analysis.

TABLE 1. Ratios of stable isotopes of carbon and nitrogen (mean ± standard deviation) in the muscle of modern potential preys of the South American sea lion off northern-central Patagonia and southern Patagonia.

SAMPLE			***n***	**δ^{13}C (‰)** (mean ± SD)	**δ^{15}N (‰)** (mean ± SD)
NORTHERN-CENTRAL PATAGONIA					
Demersal					
Enteroctopus megalocyathus	Red Octopus	Octopodidae	4	-14.7 ± 0.6	18.5 ± 1.9
Genypterus blacodes	Pink cusk-eel	Ophidiidae	5	-14.7 ± 0.4	18.0 ± 0.3
Munida subrugosa	Squat lobster	Galatheidae	5	-15.7 ± 0.8	16.8 ± 0.4
Octopus tehuelchus	Tehuelchus	Octopodidae	5	-14.8 ± 0.2	19.9± 0.4
Paralichthys isosceles	Flounder	Paralichthyidae	5	-16.0 ± 0.4	18.0 ± 0.6
Patagonotothen cornucola	Notothenia cornucola	Nototheniidae	2	-15.6 ± 0.1	18.8 ± 0.2
Patagonotothen ramsayi	Notothenia ramsayi	Nototheniidae	2	-16.1 ± 0.2	18.6 ± 0.2
Platyxanthus patagonicus	True crabs	Platyxanthidae	5	-15.3 ± 0.2	16.3 ± 0.9
Pleoticus muelleri	Red shrimp	Solenoceridae	5	-15.9 ± 0.4	16.7 ± 0.3
Raneya brasiliensis	Banded cusk-eel	Ophidiidae	5	-15.3 ± 0.7	18.8 ± 0.5
Pelagic					
Engraulis anchoita	Argentine anchovy	Engraulidae	5	-18.0 ± 0.2	15.7 ± 0.8
Illex argentinus	Argentine short-finned squid	Ommastrephidae	5	-17.0 ± 0.6	13.7 ± 0.8
Loligo gahi	Patagonian squid	Loliginidae	5	-17.2 ± 1.0	16.2 ± 1.2
Loligo sanpaulensis	Brazilian squid	Loliginidae	5	-16.8 ± 0.2	17.2 ± 0.3
Merluccius hubbsi (≥30cm)	Argentine hake	Merlucciidae	9	-17.3 ± 0.7	16.2 ± 0.5
Merluccius hubbsi (<30cm)	Argentine hake	Merlucciidae	5	-17.0 ± 0.5	17.1 ± 0.4
Stromateus brasiliensis	Southwest Atlantic butterfish	Stromatidae	2	-17.0 ± 0.9	16.2 ± 0.4
SOUTHERN PATAGONIA					
Demersal					
Eleginops maclovinus	Patagonian blenny	Eleginopsidae	2	-16.5 ± 0.1	18.4 ± 0.4
Genypterus blacodes	Pink cusk-eel	Ophidiidae	5	-17.2 ± 0.8	18.3 ± 0.5
**Macroronus magellanicus*	Hoki	Merlucciidae	5	-18.2 ± 0.7	13.9 ± 0.7
Munida gregaria	Lobster krill	Galatheidae	5	-15.4 ± 2.6	11.9 ± 1.1
Paralichthys patagonicus	Patagonian flounder	Paralichthyidae	1	-15.8	19.0
Patagonotothen ramsayi	Rock cod	Nototheniidae	5	-18.4 ± 1.4	15.6 ± 2.2
Pleoticus muelleri	Red shrimp	Solenoceridae	5	-15.6 ± 0.4	15.7 ± 0.5
Psammobatis rudis	Smallthorn sand skate	Rajidae	3	-14.8 ± 0.8	16.7 ± 0.6
Pelagic					
Illex argentinus	Argentine short-finned squid	Ommastrephidae	5	-17.9 ± 0.4	16.4 ± 0.7
Loligo gahi	Patagonian squid	Loliginidae	5	-17.2 ± 1.0	17.3 ± 2.1
Merluccius hubbsi (≥30cm)	Argentine hake	Merlucciidae	10	-18.0 ± 0.2	17.2 ± 0.2
Merluccius hubbsi (<30cm)	Argentine hake	Merlucciidae	3	-16.8 ± 0.2	16.7 ± 0.3
*Mictophids	Lanternfish	Myctophidae	17	-21.9 ± 0.7	11.7 ± 0.9
Sprattus fuegensis	Falkland sprat	Clupeidae	5	-17.8 ± 0.3	17.2 ± 0.2
Stromateus brasiliensis	Southwest Atlantic butterfish	Stromateidae	5	-17.8 ± 0.5	15.7 ± 1.2

*Reference: Ciancio et al., 2008

Stable isotope analysis.−Bones were cleaned of sediment and dried in a stove at 50ºC. Shell samples were polished with sandpaper and with a diamond wheel drill to remove impurities and subsequently rinsed with distilled water and dried in a stove at 50ºC.White muscle from fish and mantle from squids were thawed and dried in a stove at 50°C. Once dry, all samples were ground to a fine powder with a mortar and pestle. Since shells and bone contain high concentrations of inorganic carbon, which may bias $\delta^{13}C$ values (Lorrain 2003), they were divided in two aliquots. One of them was decarbonized by soaking during in 0.5 N (bone) or 1 N (shell) hydrochloric acid (HCl) until no more CO_2 was released (Newsome et al. 2006). Since the HCl treatment adversely affects $\delta^{15}N$ values (Bunn et al. 1995), the other aliquot was not treated with HCl and used for $\delta^{15}N$ determination. Lipids were extracted from bone samples, with a chloroform/ methanol (2:1) solution (Bligh and Dyer 1959). Each vibrissa was soaked in chloroform: methanol (2:1) solution for 15 min in an ultrasonic bath. Any remaining residue on vibrissae was scrubbed off with a brush and the soaking process repeated. The samples were then dried again for 48 hr at 60ºC. Vibrissae were cut into 3 mm long consecutive sections starting from the proximal end and each section analyzed separately. Approximately 0.8 mg of bone , 0.3-mg of vibrissae, 0.4-9.9 mg of shell and 0.3 mg of white muscle from fish and mantle from cephalopods were weighed into tin cups (3.3 x 5 mm), combusted at 900ºC and analyzed in a continuous flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA; Thermo Finnigan, Bremen, Germany). Atropine was used as a system check for elemental analyses. Samples were processed at Centres Cientifics i Tecnològics de la Universitat de Barcelona, where the samples from modern sea lions in Drago et al. (2009) had been also analyzed.

The abundances of stable isotopes, expressed in delta (δ) notation, were the relative variations of stable isotope ratios expressed as permil (‰) deviations from predefined international standards as:

$$\delta X = [(R_{\text{sample}}/ R_{\text{standard}}) - 1] \times 1000 \qquad (1)$$

where X is ^{13}C or ^{15}N, and R_{sample} and R_{standard} are the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios in the sample and standard, respectively. The standards that were used were Vienna Pee Dee Belemnite (VPDB) calcium carbonate for ^{13}C and the atmospheric nitrogen (air) for ^{15}N.

Stable isotope discrimination factors.−Animals are related isotopically to their environment by means of an isotopic diet-tissue discrimination factor (Hobson, 1999). These factors vary significantly, within and between species, with the diet, physiology and tissue (Gannes et al. 1997; Olive et al. 2003; Koch 2007). Discrimination factors from diet to mammal bone have been determined experimentally only for pig (Nardoto et al. 2006), but this is unlikely to be a good animal model for South American sea lions due to different nutrient routing in omnivores and carnivores (Martínez del Rio et al. 2009). Bone is expected to integrate diet over several years (Newsome et al. 2006) and the same is true for long otariid vibrissa, with each few millimeters corresponding to several weeks (Cherel et al. 2009). As diet-to-vibrissa discrimination factors have been experimentally determined for the harp seal *Pagophilus groenlandicus* (Hobson et al. 1996) and the sea otter *Enhydra lutris nereis* (Newsome et al. 2010), much more similar to otariids, paired samples of vibrissae and bone from the same South American sea lions can be used to approximate a diet-to-bone discrimination factor by adding the average diet-to-vibrissa discrimination factor reported by Hobson et al. (1996) and Newsome et al. (2010), to the average vibrissa-to-bone offset revealed by the paired vibrissa/bone samples (equation 2).

$$\Delta_{\text{(bone-vibrissae)}} + \Delta_{\text{Means Reference (vibrissae-diet)}} = \Delta_{\text{(bone- diet)}} \quad (2)$$

Data analysis.−The $\delta^{13}C_{shell}$ and $\delta^{15}N_{shell}$ values of limpets and mussels allowed tracking changes in the stable isotope baseline through time. The $\delta^{13}C_{shell}$ and $\delta^{15}N_{shell}$ values of modern and ancient individuals of each species from the same region were compared using the non-parametric Kruskal-Wallis test for multiple comparisons, as the assumptions of normality (using Lillefors test) and homoscedasticity (using Levene test) were seldom met (Zar 1984). When statistically significant differences were found, the stable isotope baseline was considered to have changed and a correction factor was computed to allow the comparison of archaeological and modern bone samples and discriminate between baseline shifts and actual changes in trophic niche. The correction factor was computed by subtracting the average stable isotope ratio of modern shells to ancient shells from each locality and age. Secondly, the difference was added to the stable isotope ratio of ancient bones from the same locality and age, to level them with modern samples. When bones came from a stratum without associated mollusc shells, bone stable isotope ratios were corrected using the time weighted average of the correction factors computed for nearest strata below and above. A detailed description of those calculations and the resulting correction factors are shown in Table 2.

TABLE 2. Baseline correction factor for shells and sea lions to each radiocarbon year (ybp) where we obtained samples.

Age $_{shell}$ (^{14}C ybp)	Correction Factor (shell) ($\Delta = \delta^{13}C$ or $\delta^{15}N^{14}{}_{C\ age\ BP\ shell} - \delta^{13}C$ or $\delta^{15}N_{0BP}$)				Average correction factors (shell)		Age $_{bone}$ (^{14}C ybp)	Correction factors used for Baseline	
	Δ $\delta^{13}C$		Δ $\delta^{15}N$		Δ $\delta^{13}C$	Δ $\delta^{15}N$		Δ $\delta^{13}C$	Δ $\delta^{15}N$
Northern-central Patagonia									
	A. atra atra	*N. magellanica*	*A. atra atra*	*N. magellanica*					
380±60	1.5	-0.9	2.4	3.6	0.3	3.0	380±60	0.3	3.0
610±60	-0.1	-	1.6	-	-0.1	1.6	1380±80	-0.4^{*1}	1.8^{*2}
640±60							1000±70		
850±50	-	-1.6	-	1.7	-1.6	1.7	1630±80		
2140±50	1.8	-	2.2	-	1.8	2.2	1680±90		
2600±60	-	-1.7	-	3.8	-1.7	3.8	2197±38	0.1^{*3}	3.0^{*4}
5200±70	-1.8	-4.1	2.6	2.3	-2.9	2.5	2910±90	-1.7	3.8
Southern Patagonia									
	M. edulis	*N. magellanica*	*M. edulis*	*N. magellanica*					
100±45	-3.7	-6.7	1.5	1.7	-5.2	1.6	100±45	-5.2	1.6
500±100	2.1	-0.3	1.6	1.3	0.9	1.8	580±45	0.9	1.5
890	3.4	-	-	-	-3.4	1.5	1256±50-1190±60	$-3.4^{\#1}$	$1.7^{\#2}$
5940-5710	-1.5	-5.8	3.5	2.6	-3.6	3.1	5000-4300	-3.6	3.1

$*^{1,2}$ weighted value calculating by: ^{1} (0.63 * -1.6 + 0.33 * 1.8) ; ^{2} (0.63 * 1.7 + 0.33 * 2.2)
$*^{3,4}$ mean values calculating by: ^{3} 1.8 and -1.7 ; ^{4} 2.2 and 3.8
1,2 weighted value calculating by: 1 (0.90 * -3.4 + 0.10 * -3.6) ; 2 (0.9 * 1.5 + 0.10 *3.1)

Once corrected for isotope baseline shifts, stable isotope ratios in bone samples were compared with those of modern potential prey after applying the diet-to-bone discrimination factors for South-American sea lions ($\Delta\delta^{13}C = 3.5 \pm 0.8$ ‰ ; $\Delta\delta^{15}N = 4.4 \pm 0.8$ ‰) obtained in this study . Mann-Whitney U-tests were used for testing differences in the $\delta^{13}C$ and $\delta^{15}N$ signatures between demersal and pelagic modern prey.

Data are presented as mean ± standard deviation (SD) and significance was assumed at the 0.05 level. All statistical analyses were carried out with PASW Statistics (Version 17.0 for Windows, SPSS).

Results

Although the $\delta^{13}C_{shell}$ values of the mussels and limpets from northern-central Patagonia did not vary throughout the late Holocene (Fig. 2; Kruskal-Wallis test; *A. atra atra*: Chi-square = 9.418, df = 4, $p = 0.052$; *N. magellanica*: Chi-square = 5.352, df = 4, p = 0.253), those of the mollusc species collected in southern Patagonia exhibited a remarkable variability and changes run in parallel in both species (Fig. 2; Kruskal-Wallis test; *M. edulis*: Chi-square = 15.714, df = 4, p = 0.003; *N. magellanica*: Chi-square = 11.765, df = 4, p = 0.008). Likewise, differences through time in the $\delta^{15}N_{shell}$ values of mussels and limpets were statistically significant both in northern-central Patagonia (Kruskal-Wallis test; *A. atra atra*: Chi-square = 19.549, df = 4, $p < 0.001$; *N. magellanica*: Chi-square = 17.000, df = 4, p = 0.002) and in southern Patagonia (Kruskal-Wallis test; *M. edulis*: Chi-square = 15.684, df = 4, p = 0.001; *N. magellanica*: Chi-square = 14.392, df = 4, p = 0.002) and the two species from the same area exhibited the same pattern of temporal variation (Fig. 2), although each region evolved independently. These results revealed major changes in the stable isotope baseline and hence correction factors were computed for each region and period to allow the comparison of the stable isotope ratios in the bone of ancient and modern sea lions (Table 2).

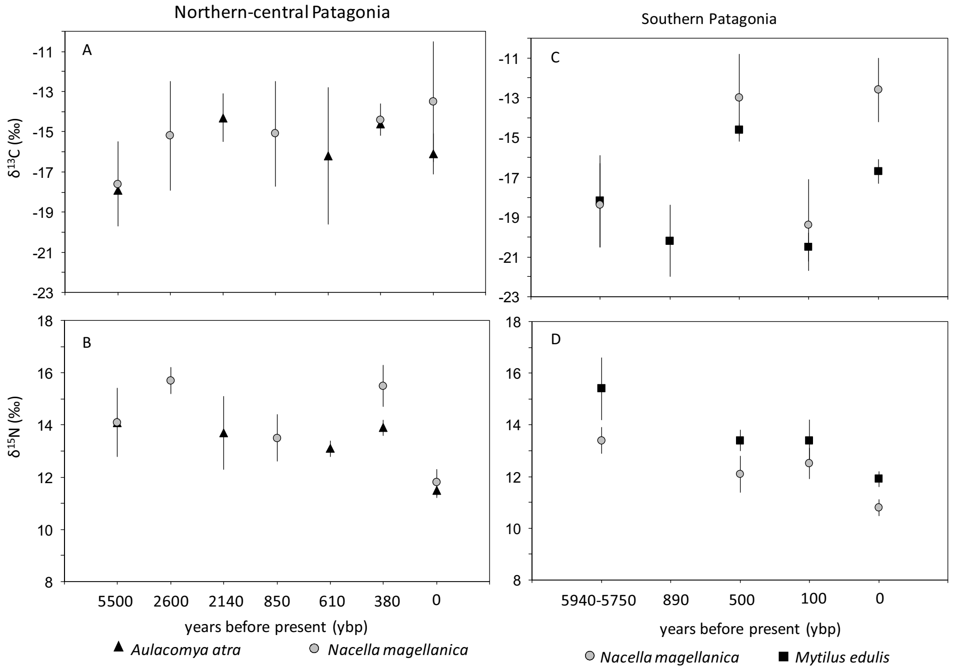

FIGURE 2. Temporal trends throughout the late Holocene of the $\delta^{13}C_{shell}$ and $\delta^{15}N_{shell}$ values is molluscs from northern-central Patagonia and southern Patagonia. Differences through time were statistically significant; except for the $\delta^{13}C_{shell}$ values of *Aulacomya atra* and *Nacella magellanica* from northern Patagonia (see the text for details about the statistical analyses).

Vibrissae were depleted both in ^{13}C and ^{15}N relative to bone (Mean $\delta^{13}C$: Vibrissae= -13.1 ± 0.8; Bone= -12.3 ± 0.8; Mean $\delta^{15}N$: Vibrissae = 21.2 ± 0.9; Bone= 22.5 ± 1.5) which resulted in an average vibrissa-to-bone discrimination factor of 0.8 ± 0.8 ‰ for δ^{13}C and 1.2 ± 1.0‰ for δ^{15}N. When combined with the diet-to-vibrissa discrimination factor (δ^{13}C = 2.7 ± 0.7‰; δ^{15}N = 3.2 ± 0.5‰) reported by Hobson et al. (1996) and Newsome et al. (2010), resulted into a diet-to-bone discrimination factor of 3.5 ± 0.8‰ for δ^{13}C and 4.4± 0.8‰ for δ^{15}N. Bone (δ^{13}C = -11.9 ± 0.4; δ^{15}N = 22.2± 0.8) was enriched relative to dentine (δ^{13}C =-12.0 ± 0.5; δ^{15}N = 21.4 ± 0.6), so the diet-to-dentine discrimination was of 3.5 ± 0.8‰ for δ^{13}C and 3.6 ± 0.8‰ for δ^{15}N.

The uncorrected $\delta^{13}C_{bone}$ and $\delta^{15}N_{bone}$ values of ancient and modern sea lions are shown in Supplementary Table 3. After correction for changes in the isotope baseline (Fig. 3), the $\delta^{13}C_{bone}$ values of modern sea lions from northern-central Patagonia were higher than those of the sea lions that inhabited the region during the second half of the Holocene (δ^{13}C *Kruskal-Wallis test*: *Chi-square* = 7.094; $df = 1$; $p < 0.05$) and the same was true for the δ^{15}N values (*Kruskal- Wallis test*: *Chi-square* = 43.628; $df = 1$; $p < 0.05$). The $\delta^{13}C_{bone}$ values of sea lions from southern Patagonia also varied through time (δ^{13}C *Kruskal-Wallis test*: *Chi-square* = 5.262; $df = 1$; $p < 0.05$), but there were no consistent differences between modern and ancient sea lions. However, the $\delta^{15}N_{bone}$ values of modern sea lions from southern Patagonia were higher than those of ancient sea lions from that area (δ^{15}N *Kruskal-Wallis test*: *Chi-square* = 44.480; $df = 1$; $p < 0.05$).

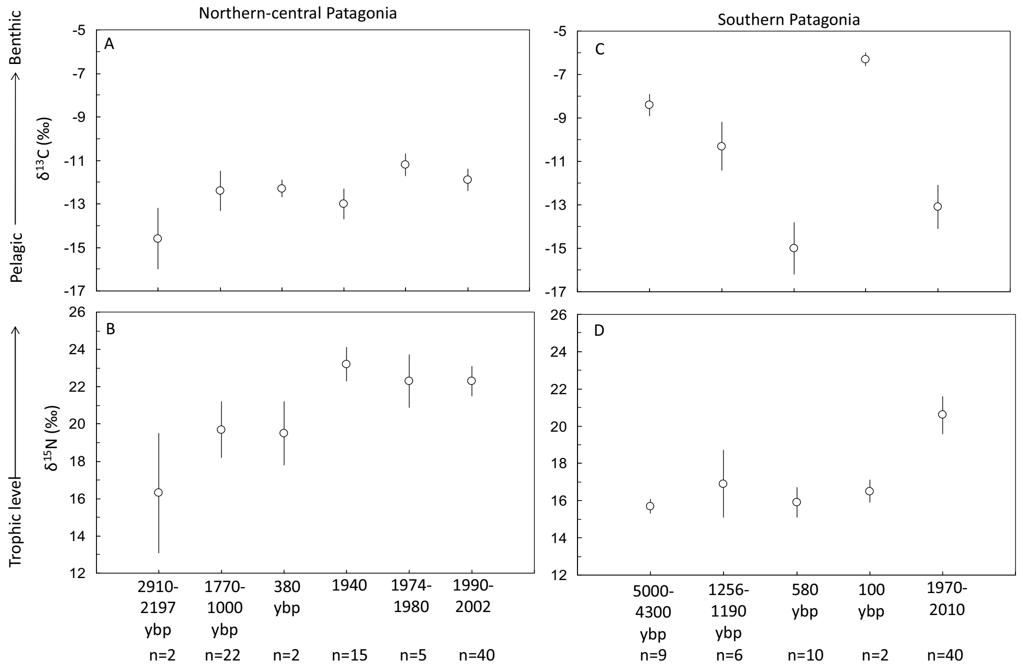

FIGURE 3. Mean (±SD) values of $\delta^{13}C_{bone}$ (a,c) and $\delta^{15}N_{bone}$ (b,d) for South American sea lions collected in northern-central Patagonia and southern Patagonia through the middle and late Holocene of Argentina, after being corrected for changes in stable isotope baseline.

The stable isotope ratios of modern potential prey from northern-central Patagonia and southern Patagonia are shown in Table 1. Demersal fishes from northern-central Patagonia were more enriched than pelagic fishes from the same region in both $\delta\ ^{13}C$ and $\delta\ ^{15}N$ and, accordingly ($\delta^{13}C$; Mann-Whitney U = 0.000, Z = -3.428, df = 17, $p < 0.000$; $\delta^{15}N$; Mann-Whitney U = 6.000, Z = -2.841, df = 17, $p < 0.003$), the simultaneous increase in the $\delta^{13}C_{bone}$ and $\delta^{15}N_{bone}$ values of the sea lions from that region throughout the Holocene indicates an increase in the consumption of demersal prey (Fig. 4). Conversely, most pelagic and demersal prey from southern Patagonia exhibit similar $\delta^{13}C$ and $\delta^{15}N$ values ($\delta^{13}C$; Mann-Whitney U = 7.500, Z = -1.934, df = 13, $p > 0.051$; $\delta^{15}N$; Mann-Whitney U = 21.000, Z = 0.000, df = 13, p = 1.000), although myctophid fishes and the squat lobster *Munida gregaria* were more depleted in ^{15}N than any other species. Accordingly, the low $\delta^{15}N_{bone}$ values typical of ancient sea lions suggest a diet dominated by low trophic level prey like the squat lobster *Munida gregaria* (Fig. 4), whereas modern sea lions consume a larger proportion of prey at a higher trophic level like the rock cod *Patagonotothen ramsayi,* the Argentine hake *Merluccius hubbsi* and the Argentine shrimp *Pleoticus muelleri*. Interestingly, the two samples from the 19th century fell outside the mixing polygon, suggesting they had a totally different diet or come from an area with a different isoscape.

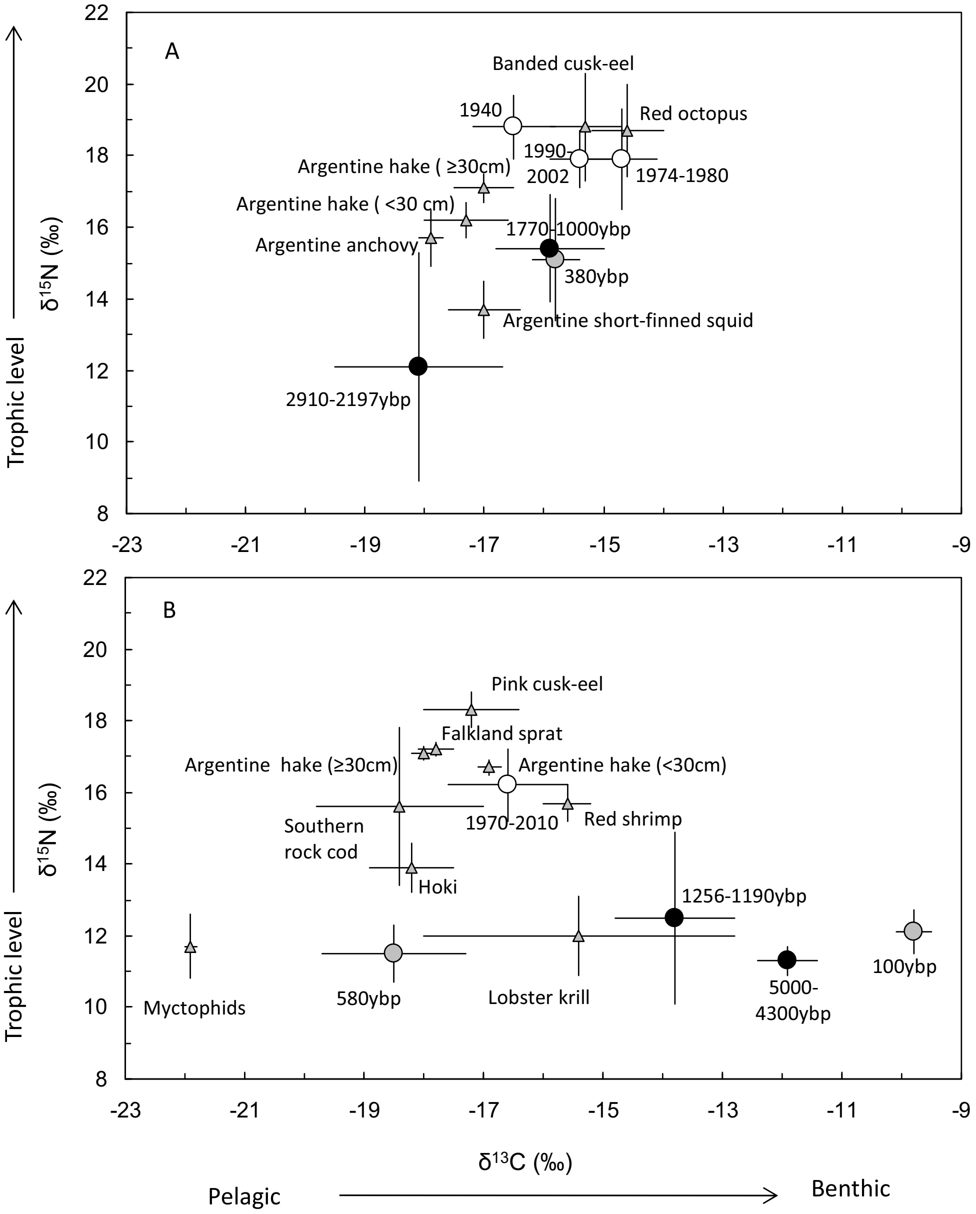

FIGURE 4. Bivariated isotopic signal of the South American sea lion from central-northern (a) and southern Patagonia (b), after correcting for differences in isotope baseline and for the diet-to-bone fractionation. Circles denote sea lions from different periods and triangles denote main preys.

Discusion

Bone collagen represents one of the best preserved proteins in fossilized animal remains (Bocherens et al. 1999) and collagen stable isotope ratios offer a valuable insight into the paleodiets and trophic levels (Ambrose and DeNiro 1989; Schwarcz, 2000; Newsome et al. 2007a). Nevertheless, historical changes in the isotopic baseline may hinder the interpretation of retrospective studies on trophic level and food web structure (Casey and Post, 2011), although most studies assume the temporal stability of the isotope baseline (Burton et al. 2001, Emslie and Patterson, 2007; Becker and Beissinger 2006; Christensen and Richardson 2008; Corbett et al. 2008; Bailey et al. 2008; Barrett et al. 2008).

Recently, Bailey et al. (2008) and Casey and Post (2011) recognized the potential of mollusc shells for the reconstruction of isotopic baseline, as filter-feeding mussels and surface-grazing snails are good proxies for the base of the pelagic and littoral food webs respectively (Post 2002) and the shell matrix proteins that make up the organic matrix of mollusc shells can become encased within mineral crystals and preserved (Crenshaw 1980). This approach has allowed the reconstruction of the temporal shifts in the isotope baseline in the marine ecosystems off Argentina during the second half of the Holocene and the calculation of correction factors that allows comparing the trophic position of sea lions at different times and with the stable isotope ratios in modern prey.

Certainly, a better reconstruction of the dietary shifts of sea lions through the second half of the Holocene would be achieved if the stable isotope ratios of ancient potential prey had been analysed. Bones of some fish species are abundant in the zooarchaeological record of both central-northern and southern Patagonia (Favier Dubois et al. 2009: Favier Dubois and Kokot 2011; Favier Dubois and Scartascini 2011; Tivoli and Zangrando 2011), but other important potential prey for sea lions, such as cephalopods, shrimps and squat lobsters (Thompson et al. 1998; Koen Alonso et al. 2000; Suárez et al. 2005; Romero et al. 2011) are missing. In this scenario, correcting for changes in the isotope baseline and latter comparison with the stable isotope ratios of modern prey seems the most convenient approach to understand the ecological significance of the changes observed in the stable isotope ratios of sea lion bone collagen.

Due to that the earliest information about the diet of sea lions dates back to a period following 3000 years in northern-central Patagonia (Favier Dubois and Scartascini 2012; Gómez Otero et al. 2013) and 1000 years in southern Patagonia (Orquera and Piana 1988, 1999; Orquera et al. 2011; Tivoli and Zangrando 2011) of exploitation of marine resource in the area, the diet of sea lions inhabiting truly pristine environment remains unknown. Nevertheless, the overall evidence indicates that modern sea lions forage currently at trophic level much higher than during the pre-contact period, both in northern-central and southern Patagonia.Nevertheless, the overall evidence indicates that modern sea lions forage currently at trophic level much higher than during the pre-contact period, both in northern-central and southern Patagonia.

Sea lions inhabiting northern-central Patagonia 3000-2000 years ago had a pelagic diet, but increased the consumption of demersal prey approximately 1000 years ago. The reason for such a change remains unknown and there is no evidence in the literature suggesting an impact of hunter-gatherers on the sea lion population of that region large enough to modify their ecology. Sea surface temperature was also rather stable off northern-central Patagonia from 2600 ^{14}C BP to the Little Ice Age (Saporiti et al. 2013) and hence cannot explain the change reported. Certainly, marine productivity declined from 2600 ^{14}C BP to 850 ^{14}C BP, but increased again during the Little Ice Age (Saporiti et al. 2014) but sea lions did not resume a pelagic diet, thus suggesting a weak causal link between marine primary productivity and the diet of sea lions.

Conversely, the stable isotope ratios in the bones of sea lions inhabiting southern Patagonia indicate a rather stable diet during most the late-Holocene. This suggests that otariid exploitation by hunter-gatherer, directed primarily to South American fur seals *Arctocephalus australis* (Schiavini 1993; Orquera and Piana 1999; Tivoli and Zangrando 2011). On the other side, it is important to note that the samples from the 19th century lay outside the mixing polygon formed by the bivariated stable isotope ratios of modern prey, even after correction for shift in the isotope baseline. Western sealing had decimated otariid populations in the region during the late 18th and the early 19th centuries and rookeries lasted only in Staten Island (Argentina) and the Falkland (Malvinas) Islands, although dwindled due to exploitation (Bridges 1949; Orquera 2002; Dickinson 2007). Only isolated otariids were sporadically recorded in the Beagle Channel during the second half of the 19th century and only a few haul-out sites were known in the Atlantic coast of Tierra del Fuego (Bridges 1949). The high $\delta^{13}C$ values of the sea lion samples from the 19th century suggest that those animals were vagrants from somewhere else. Interestingly, the $\delta^{13}C$ values of zooplankton from the Falkland (Malvinas) Islands are currently higher than those of zooplankton from southern Patagonia and those of the Southern Ocean are lower (McMahon et al. 2013). If this pattern was also true during the 19th century, the South American sea lions occurring at that time in Southern Patagonia were probably migrants from the Falkland (Malvinas) Islands.

Independently of the origin of those anomalous samples collected during the 19th century in southern Patagonia, the high $\delta^{15}N$ values observed in modern sea lions from both areas after correcting for changes in baseline indicate a recent dietary shift to higher trophic level prey, which might be linked to a smaller population size and a larger body size. We can just speculate about the changes in the body size of South American sea lions during the second half of the Holocene, because of the scarcity of well-preserved skeletal material, but Drago et al. (2010) have reported a reduction in skull dimensions as the population recovered after sealing. A smaller skull size results in a smaller mouth gape diameter, which is the ultimate determinant of prey size in aquatic vertebrates (Wainwright and Barton 1995; Karpouzi and Stergiou 2003). On the other hand, trophic level and body size are tightly linked in aquatic food webs and hence a reduction in predator body size results in a reduction in trophic level (Jennings 2005). Furthermore, air-breathing marine predators with a large body mass often exploit benthic habitats, whereas those with smaller body size typically behave as epipelagic predators (Gentry et al. 1986; Costa 1991, 1993; Costa et al. 2004), a pattern also reported for South American sea lions (Drago et al. 2009).

In any case, the overall evidence indicates that South American sea lions currently forage more benthically and at a higher trophic level than they did originally and hence occupy a totally different trophic niche. Legal protection has allowed the partial recovery of the population (Dans et al. 2004; Schiavini et al. 2004; Grandi et al. 2012) but has not restored the ecological role of the species. This is probably an unrealistic goal, considering the dramatic changes in the structure of the ecosystem caused by fishing (Koen-Alonso and Yodzis 2005), but we ignore whether the new selective pressures operating in the current anthropogenic setting will modify the evolutionary course of the South American sea lion.

Acknowledgments

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Supplementary tables

SUPPLEMENTARY TABLE 3. Ratios of stable isotopes of carbon and nitrogen in the bone tissue of South American sea lions from the archaeological sites of northern- central Patagonia (Río Negro and Chubut) and southern Patagonia (Santa Cruz and Tierra del Fuego).

ID Sample	Archaeological site	Age (^{14}C ybp)	δ^{13}C (‰)	δ^{15}N (‰)	C:N	Reference
Río Negro						
FSM-SRH	Faro San Matías Mont II	1630 ± 80	-11.4	22.4	3.3	Borrella and Cruz 2012 Favier Dubois et al., 2009
OBS 13	Faro San Matías 6	1380 ± 80	-11.2	22.4	3.1	
OBS 137	Bajada de los pescadores	2197 ± 38	-13.4	21.1	3.6	
OBS 4	Faro San Matías 2	2910 ± 90	-13.9	18.1	3.6	
FSM-SRH	Faro San Matías Mont I	1680 ± 90	-11.9	23.0	3.7	
Chubut						
36	Los Abanicos 1	380 ± 60	-12.3	21.4	4.0	Gómez Otero, 2006
82	Los Abanicos 1		-11.8	23.8	3.5	
F$_1$ 17	Playa Union	1040 ± 70	-13.7	19.9	3.3	Gómez Otero 2006
FM$_1$13	Playa Union		-13.1	19.7	4.1	
FM$_1$14	Playa Union		-13.4	21.0	3.3	
FM$_1$15	Playa Union		-12.1	20.3	3.0	
FM$_1$16	Playa Union		-12.3	18.7	3.3	
FM$_1$17	Playa Union		-12.7	18.9	3.2	
FM$_1$19	Playa Union		-12.9	22.5	3.3	
FM$_1$20	Playa Union		-12.3	21.9	3.2	
FM$_1$21	Playa Union		-12.8	20.3	3.4	
i$_1$ 61	Lobos*	1290 ± 100	-13.1	21.3	3.8	Serrán et al., 2008
i$_3$ 43	Lobos*		-13.0	22.0	3.2	
i$_4$ 44	Lobos*		-13.4	22.3	3.7	
i$_5$ 54	Lobos*		-11.0	22.2	3.4	
I$_{15}$ C1	Lobos*		-14.4	22.2	2.7	
I$_{18}$ 89	Lobos*		-13.6	25.0	3.4	
i 23	Lobos*		-12.8	21.3	3.3	
i 24	Lobos*		-14.6	23.2	3.5	
M$_1$1	Lobos*		-12.0	22.3	3.0	
M$_1$3	Lobos*		-13.0	22.4	3.8	
Santa Cruz						
CV6 4/-60-65cm	Cabo Vírgenes	1190+ 60	-13.9	20.8	3.4	L'Heureux and Franco 2002
CV20 OF1	Cabo Vírgenes	1256± 50	-14.8	15.4	3.0	Belardi et al., 2011
CV20 OF3	Cabo Vírgenes		-14.5	17.9	3.4	
CV20 OF4	Cabo Vírgenes		-12.2	19.1	3.2	
CV 20 OF6	Cabo Vírgenes		-12.3	19.6	3.9	
CV20 OF7	Cabo Vírgenes		-14.2	18.8	3.5	
Tierra del Fuego						
30459	Túnel I, Capa D	5000-4300	-11.3	19.6	3.2	Orquera and Piana, 1988
33458	Túnel I, Capa D		-12.4	18.5	3.0	
33459	Túnel I, Capa D		-11.4	18.7	3.2	
33551	Túnel I, Capa D		-11.8	18.8	3.2	
33571	Túnel I, Capa D		-12.5	19.0	3.4	
33717	Túnel I, Capa D		-12.7	18.4	2.7	
34177	Túnel I, Capa D		-12.3	18.6	3.1	
34544	Túnel I, Capa D		-12.0	18.4	3.9	
34751	Túnel I, Capa D		-11.6	18.9	3.8	
43418	Túnel VII	100±45	-11.7	18.5	2.7	Piana et al., 1992
154286	Túnel VII		-11.3	17.7	2.8	
OF 2a	Kaiawoteha III, Capa K	580 ±	-13.8	17.4	3.5	Piana et al., 2007

OF 2b	Kaiawoteha III, Capa K	45	-15.6	16.8	3.2
OF 3	Kaiawoteha III, Capa K		-15.1	16.5	2.9
OF 5	Kaiawoteha III, Capa K		-15.6	16.9	3.4
OF 7	Kaiawoteha III, Capa K		-14.2	17.6	3.7
OF 9	Kaiawoteha III, Capa K		-14.2	16.3	3.9
OF 10	Kaiawoteha III, Capa K		-12.6	17.3	4.0
OF 12	Kaiawoteha III, Capa K		-12.2	17.8	4.1
OF 14	Kaiawoteha III, Capa K		-13.2	17.8	3.3
OF 15	Kaiawoteha III, Capa K		-14.1	19.2	3.2

(*): Paleontological site

SUPPLEMENTARY TABLE 4. Ratios of stable isotopes of carbon and nitrogen in shells sampled from actual and archaeological sites of northern- central Patagonia (Chubut Province) and southern Patagonia (Tierra del Fuego Province).

Species	**Archaeological site**	**Age (^{14}C ybp)**	**δ^{13}C (‰)**	**δ^{15}N (‰)**	**Reference**
		Chubut			
Aulacomya atra atra	-------	Actual	-16.8	11.7	
Aulacomya atra atra	-------		-14.8	11.5	
Aulacomya atra atra	-------		-16.9	11.1	
Aulacomya atra atra	-------		-16.8	11.9	
Aulacomya atra atra	-------		-15.3	11.3	
Aulacomya atra atra	-------		-18.1	11.3	
Aulacomya atra atra	-------		-17.7	11.3	
Nacella magellanica	-------		-8.9	12.5	
Nacella magellanica	-------		-13.1	11.8	
Nacella magellanica	-------		-16.0	11.2	
Nacella magellanica	-------		-13.1	12.1	
Nacella magellanica	-------		-16.3	11.7	
Aulacomya atra atra	Los Abanicos 1	380 ± 60	-14.7	13.8	Gómez Otero and Suárez, 1999
Aulacomya atra atra	Los Abanicos 1		-14.3	13.7	
Aulacomya atra atra	Los Abanicos 1		-14.7	13.7	
Nacella magellanica	Los Abanicos 1		-15.7	16.2	
Nacella magellanica	Los Abanicos 1		-14.0	15.0	
Nacella magellanica	Los Abanicos 1		-14.3	16.5	
Nacella magellanica	Los Abanicos 1		-14.3	14.9	
Nacella magellanica	Los Abanicos 1		-13.8	14.8	
Aulacomya atra atra	Las Ollas conchero 1	610 ± 60 / 640 ± 60	-18.6	13.3	
Aulacomya atra atra	Las Ollas conchero 1		-13.8	13.3	
Nacella magellanica	Ecocentro Fogón 3	850 ± 150	-12.3	14.4	Gómez Otero, 2006
Nacella magellanica	Ecocentro Fogón 3		-17.2	13.3	
Nacella magellanica	Ecocentro Fogón 3		-12.1	12.1	
Nacella magellanica	Ecocentro Fogón 3		-16.3	14.4	
Nacella magellanica	Ecocentro Fogón 3		-17.4	13.6	
Aulacomya atra atra	Playas Las Lisas 2-perfil 1	2140 ± 50	-15.0	11.9	
Aulacomya atra atra	Playas Las Lisas 2-perfil 1		-13.7	13.1	
Aulacomya atra atra	Playas Las Lisas 2-perfil 1		-16.0	15.8	
Aulacomya atra atra	Playas Las Lisas 2-perfil 1		-14.0	13.8	
Aulacomya atra atra	Playas Las Lisas 2-perfil 1		-13.0	13.9	
Nacella magellanica	Playa Las Lisas 2-conchero 2	2600 ± 60	-11.4	15.3	
Nacella magellanica	Playa Las Lisas 2-conchero 2		-15.9	16.3	
Nacella magellanica	Playa Las Lisas 2-conchero 2		-17.7	15.8	
Nacella magellanica	Playa Las Lisas 2-conchero 2		-15.8	15.0	
Aulacomya atra atra	Cracker 8-Nivel 3	5200 ± 70	-17.9	14.1	
Aulacomya atra atra	Cracker 8-Nivel 3		-17.9	14.2	
Nacella magellanica	Cracker 8-Nivel 3		-17.8	13.2	
Nacella magellanica	Cracker 8-Nivel 3		-17.3	15.0	

		Tierra del Fuego			
Mytilus edulis	-------	Actual	-17.6	12.2	
Mytilus edulis	-------		-16.5	11.8	
Mytilus edulis	-------		-16.4	11.5	
Mytilus edulis	-------		-17.1	11.9	
Mytilus edulis	-------		-16.0	12.0	
Nacella magellanica	-------		-10.4	10.9	
Nacella magellanica	-------		-12.0	10.4	
Nacella magellanica	-------		-13.5	10.9	
Nacella magellanica	-------		-12.5	10.7	
Nacella magellanica	------		-14.8	11.0	
Mytilus edulis	Tunel VII	100 ± 45	-20.1	13.0	Piana et al., 1992
Mytilus edulis	Tunel VII		-19.6	13.3	
Mytilus edulis	Tunel VII		-20.3	14.3	
Mytilus edulis	Tunel VII		-21.3	14.0	
Mytilus edulis	Tunel VII		-21.1	12.2	
Nacella magellanica	Tunel VII		-16.7	13.1	
Nacella magellanica	Tunel VII		-17.4	12.0	
Nacella magellanica	Tunel VII		-21.0	13.0	
Nacella magellanica	Tunel VII		-22.0	11.7	
Nacella magellanica	Tunel VII		-19.5	12.6	
Mytilus edulis	Shamakush X, Capa E	500 ± 100	-14.3	12.9	Orquera and Piana, 1999
Mytilus edulis	Shamakush X, Capa E		-15.0	13.4	
Mytilus edulis	Shamakush X, Capa E		-14.5	13.7	
Nacella magellanica	Shamakush X, Capa E		-11.4	11.2	
Nacella magellanica	Shamakush X, Capa E		-14.5	12.7	
Mytilus edulis	Imiwaia I (M/K)	5940 ± 50 / 5750 ± 170 5840 ± 45 / 5710 ± 50	-22.3	15.1	Piana et al., 1992
Mytilus edulis	Imiwaia I (M/K)		-17.1	14.4	
Mytilus edulis	Imiwaia I (M/K)		-17.3	16.9	
Mytilus edulis	Imiwaia I (M/K)		-17.1	16.3	
Mytilus edulis	Imiwaia I (M/K)		-17.4	14.3	
Nacella magellanica	Imiwaia I (M/K)		-18.4	12.8	
Nacella magellanica	Imiwaia I (M/K)		-19.8	13.6	
Nacella magellanica	Imiwaia I (M/K)		-20.4	13.3	
Nacella magellanica	Imiwaia I (M/K)		-15.0	14.2	
Nacella magellanica	Imiwaia I (M/K)		-18.3	13.0	

2.2 Reconstrucción de la dieta de los lobos marinos finos sudamericanos en el Atlántico sudoccidental desde el Holoceno medio

RESUMEN.

Tanto en épocas históricas cómo arqueológicas, los humanos redujeron de tal manera la abundancia del lobo marino fino *Arctocephalus australis* en el Océano Atlántico sudoccidental que su papel ecológico actual podría haber cambiado drásticamente. En este artículo se han usado las razones isotópicas de nitrógeno y carbono en el colágeno óseo para reconstruir la dieta del lobo marino fino sudamericano en el Holoceno medio y tardío en la zona de Río de la Plata y zonas adyacentes, y en la Patagonia argentina. Complementariamente, se analizaron las razones isotópicas en lapas y mejillones, tanto subfósiles como actuales, para evaluar los posibles cambios en la línea de base del paisaje isotópico a través del tiempo en cada ecosistema. Los lobos marinos antiguos de Río de la Plata y zonas adyacentes mostraron valores de $\delta^{13}C$ más negativos, lo que sugiere la incorporación en la dieta de presas más pelágicas hace 7000 años que ahora. Sin embargo, las evidencias arqueológicas indican una baja explotación de los pinnípedos en la costa pampeana, con lo cual el cambio en la dieta de lobos finos se relacionaría mejor con cambios en las condiciones climáticas o ambientales. Los lobos marinos del norte y centro Patagonia mostraron una dieta constante durante los últimos 2.200 años, basada en pequeños peces pelágicos, calamares y, en menor medida, en crustáceos decápodos. Para el sur de la Patagonia, a pesar de las variaciones en la intensidad de la explotación de pinnípedos por los cazadores-recolectores durante el Holoceno medio-tardío, los lobos marinos muestran una dieta estable a lo largo de todo este período. A partir del 1835 AD, en coincidencia con la extinción virtual de los lobos marinos tras siglos de caza comercial, la dieta de los lobos marinos de la Patagonia austral se desplazó hacia presas de aguas frías y oceánicas, indicio quizás de especímenes procedentes de otros lugares. Por último, en la actualidad la dieta del lobo fino está compuesta por presas que habitan en la plataforma continental. Los resultados obtenidos no suportan la hipótesis de un impacto humano significativo por parte de los cazadores-recolectores en la ecología trófica de los lobos marinos. Al contrario la caza comercial de lobos de los siglos XVIII y XIX puede haber causado el cambio a la dieta actual de los lobos marinos en el sur de la Patagonia.

Reconstructing the diet of South American fur seals in the south-western Atlantic since the middle Holocene

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In preparation

ABSTRACT

During archaeological and historical times, humans have reduced the abundance of South American fur seals *Arctocephalus australis* from the south-western Atlantic Ocean in such a way that the current ecological role of this species may have changed dramatically. Bone collagen stable nitrogen and carbon isotopes were used to reconstruct the middle and late Holocene diet of South American fur seals from Río de la Plata and adjoining areas, and Patagonia. Complementarily, stable isotope ratios of zooarchaeological and contemporaneous limpets and mussels were analysed to assess potential changes in the isotopic baseline through time in each ecosystem. Ancient fur seals from Río de la Plata and adjoining areas showed depleted $\delta^{13}C$ values, suggesting the incorporation of more pelagic prey 7,000 years ago. However, as archaeological evidence support a low exploitation of pinniped in the Pampean coast, the shift in fur seal diet may better correlate with changes in the past climatic or environmental conditions. Fur seals from northern and central Patagonia showed a steady diet over the last 2,200 yrs based on small pelagic fish, squid, and to a lesser extent on decapod crustaceans. For southern Patagonia, despite variations in the intensity of pinniped exploitation by hunter-gatherers during the middle-late Holocene, fur seals showed a stable diet throughout all this period. By 1,835 AD, in coincidence with the virtual extinction of fur seals as consequence of fur trade, the diet of fur seals from southern Patagonia shifted towards prey from cold and oceanic waters, perhaps indicative of specimens coming from elsewhere. Finally at present, the diet of fur seals is comprised by prey inhabiting the continental shelf. Present evidence does not support a significant impact of hunter-gatherer activities on the foraging ecology of fur seals. However commercial sealing may have shaped the current diet of southern Patagonian fur seals.

INTRODUCTION

Human impacts on marine ecosystems are diverse (e.g. overfishing, pollution, habitat loss, global warming, introduction of exotic species, etc.), and not only are documented worldwide, but also appear to have originated several thousand years ago (Jackson *et al.*, 2001; Kirch, 2005; Erlandson and Rick, 2008, 2010; Harpern *et al.*, 2008; Lotze and Worm, 2009). From aboriginal and colonial exploitation to the most recent industrialized fishing and globalization, humans have had cumulative and often irreversible impacts on their environment, resulting in changes in the structure and function of coastal ecosystems (Jackson *et al.*, 2001; Kirch, 2005; Pinnegar and Engelhard, 2008; Erlandson and Rick, 2010). The south-western Atlantic coasts are not the exception to this global trend, and some environmental consequences of human activities over time have been recognized for coastal Argentina (Rodríguez and Bastida, 2002) and Falkland/Malvinas Islands (Armstrong, 1994). In this context, it becomes particularly important to understand the pre-exploitation ecological role of those species whose current ecology may have been shaped by recent exploitation and/or environmental change (Newsome *et al.*, 2007).

Pinnipeds have been exploited worldwide by humans for their meat, fat and raw material since prehistoric times. Archaeological remains along the south-western coast of southern South America evidence that hunter-gatherers exploited fur seals *Arctocephalus australis* and sea lions *Otaria flavescens* from Middle to Late Holocene (Bayón and Politis, 1996; Orquera and Piana 1999; Barbarena *et al.*, 2004; Gómez Otero, 2006; Moreno 2008; Borrero *et al.*, 2009; Favier-Dubois and Kokot, 2011; Borella *et al.*, 2011; Muñoz, 2011; Bayón *et al.*, 2012; Bonomo *et al.*, 2013). However, the degree of marine resources exploitation varied spatially and temporally along this extensive coastline. On the Pampean Atlantic coast, Middle Holocene hunter-gatherers (7,400-5,700 BP) mildly exploited marine resources, particularly pinnipeds; while during the Late Holocene (3,100-430 BP), their subsistence was basically terrestrial and exploited pinnipeds occasionally (Bayón and Politis, 1996; Bonomo, 2005; Bonomo and León, 2010; Bayón *et al.*, 2012; Bonomo *et al.*, 2013). Hunter-gatherers inhabiting the coasts of northern and central Patagonia from Middle Holocene to the beginning of the Late Holocene relied both on terrestrial and marine resources, although the relative importance of the latter varied locally and throughout time (Barbarena *et al.*, 2004; Gómez Otero, 2006; Gómez Otero *et al.*, 2007; Moreno, 2008; Favier-Dubois *et al.*, 2009; Favier-Dubois and Kokot, 2011; Moreno *et al.*, 2011). Conversely, marine resources, and particularly otariids, played a major role in the economy of hunter-gatherers inhabiting southern Patagonia since ca. 6,400 (Schiavini, 1993; Orquera and Piana, 1999; Tivoli and Zangrando, 2011; Zangrando *et al.*, 2013). Nevertheless, the relative importance of pinnipeds decreased in the economy of hunter-gatherers from 5,500-5,000 BP to the 19th century (Zangrando, 2009a, 2009b; Zangrando *et al.*, 2010; Tivoli and Zangrando, 2011), a pattern recently attributed to overexploitation (Zangrando *et al.*, 2013). By the late 19th century, most southern pinniped stocks had been drastically reduced, including Falkland/Malvinas Islands, Patagonia and Tierra del Fuego, due to the action of western sealers (Townsend, 1908; Schiavini, 1992; Bastida and Rodríguez, 1994). The implementation of conservation policies through the 20th century has allowed the partial recovery of otariid populations, although nothing is known about the recovery of their ecological role.

Currently, South American fur seals (*Arctocephalus australis*) inhabit the south-western Atlantic from southern Brazil to Cape Horn and forage mainly on small pelagic fishes, squids and crustaceans, among others (Naya *et al*., 2002; Crespo *et al*., 2008; Oliveira *et al*., 2008; Baylis *et al*., 2013). Nevertheless, current knowledge based only on recent observations may provide an incomplete picture of the true behavioural plasticity and ecological roles available to extant organisms (Burton *et al*., 2001). A historical perspective is especially relevant to understand the actual impact of human exploitation (Newsome *et al*., 2007) and the analyses of stable isotopes in specimens at museum and zooarchaeological collections offers a unique opportunity to reveal ecological responses to anthropogenic perturbation and/or environmental change over time (Hirons *et al*., 2001; Burton *et al*., 2001, 2002; Newsome *et al*., 2007, 2010; Drago *et al*., 2009; Zangrando *et al*., 2013).

These retrospectives approaches are possible because nitrogen and carbon isotopic differences at the base of marine food webs are transmitted along the food chain in a predictable way and are ultimately reflected in high trophic level predators (DeNiro and Epstein, 1978, 1981; Cherel and Hobson, 2007). While $\delta^{15}N$ values provide data on trophic level (Minagawa and Wada, 1984; Post, 2002); $\delta^{13}C$ values can reveal information on feeding locations, including the relative use of benthic and pelagic prey (France, 1995). Bone collagen can be useful for comparing the isotope ratios of many individuals over long periods of time, as it is a slow turn over tissue which in large adult mammals is expected to integrate stable isotope ratios over several years averaging the isotopic fluctuations on the long term (Schoeninger and DeNiro, 1984, Lee-Thorp et al., 1989, Hirons *et al*., 2001; Drago *et al*., 2009; Riofrío and Aurioles-Gamboa, 2013). However, when comparing among different (spatially or temporally) ecosystems, the $\delta^{15}N$ and $\delta^{13}C$ of a consumer alone provides little information about its absolute trophic position or carbon source. This is because among ecosystems it is expected a considerable variation in baseline $\delta^{15}N$ and $\delta^{13}C$ from which organisms draw their nitrogen and carbon (Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1999; Post, 2002). Therefore, without appropriate estimates of isotopic baseline in each ecosystem, there is no way to elucidate if variation in the $\delta^{15}N$ and $\delta^{13}C$ reflects changes in the foraging ecology of an organism, or merely a variation in the isotopic baseline (Post, 2002). For the estimation of isotopic baseline in aquatic food webs has been especially suggested the use of long-lived primary consumers, such as limpets and mussels, because they provide a temporal integration of the seasonal variability in the isotopic signature of primary producers. Whereas surface grazing limpets reflect the isotopic signature of the base of the littoral food web, filter-feeding mussels reflect the isotopic signature of the pelagic food web, and together they provide a good isotopic baseline for aquatic ecosystems (Post, 2002; Casey and Post, 2011). Besides, limpet and mussel are both abundant and ubiquitous in archaeological shell middens allowing the reconstruction of isotopic baselines for ancient ecosystems. Fortunately, the organic matrix of mollusc shells is preserved in subfossil and fossil samples and hence provides a way to reconstruct temporal changes in the stable isotope baseline (Casey and Post, 2011) that offer a benchmark to interpret changes in the stable isotope ratios observed in predators.

This study aims to assess whether the dietary niche of South American fur seals inhabiting the coasts of Argentina has changed since the middle-late Holocene, considering the role of human exploitation over this species. For this purpose, estimates of isotopic baseline, stable isotope ratios of zooarchaeological and contemporaneous specimens of fur seal, and its current potential prey were used to reconstruct ancient and modern isotopic landscapes in the south-western Atlantic Ocean.

MATERIALS AND METHODS

Sampling

Three major regions representative of the current distribution of South American fur seals in the south-western Atlantic Ocean were considered for this study: Río de la Plata and adjoining areas (from southern Brazil to southern Buenos Aires province), northern and central Patagonia (Río Negro, Chubut and northern Santa Cruz provinces), and southern Patagonia (southern Santa Cruz and Tierra del Fuego provinces) (Figure 1).

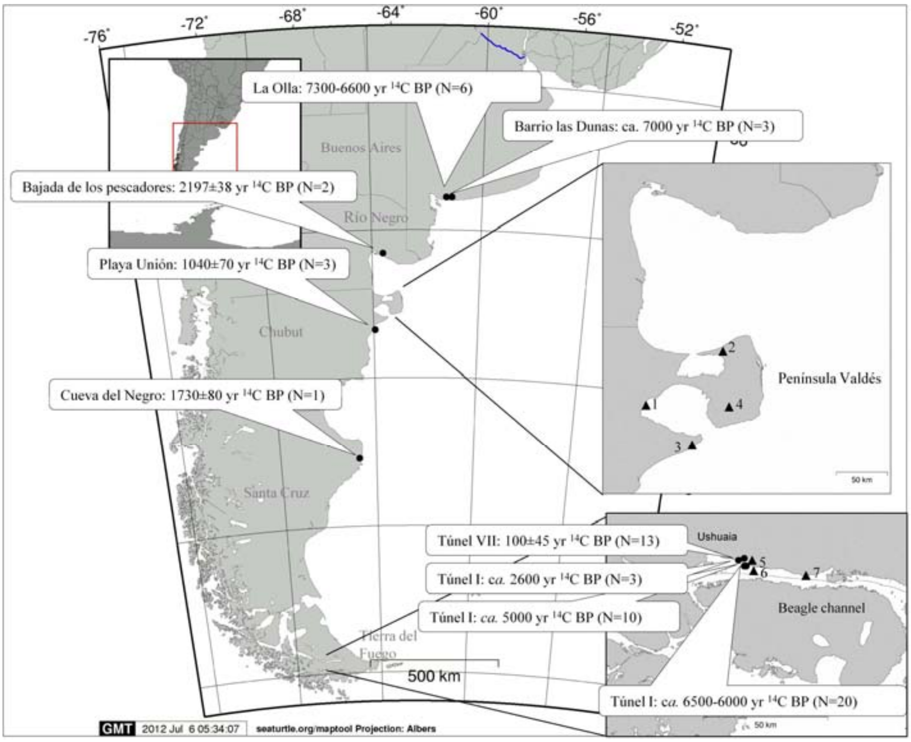

FIGURE 1. Location of archaeological sites from which fur seals and shells were sampled for stable isotope analysis. Sample sizes are listed in parentheses. The filled circles show archaeological sites for fur seals and the triangles denote sites for shells: 1= Ecocentro, hearth 3; 2= Playa Las Lisas 2, midden 2; 3= Cracker 8, level 3; 4= Las Ollas, midden 1; 5=Túnel VII; 6= Shamakush X, Capa E; 7=Imiwaia I, layer M and K.

Archaeological samples were recovered during various previous investigations at human occupation sites dated from middle to late Holocene (Table 1). Skeletal remains of fur seals come from the sites: “La Olla 1” and “Barrio Las Dunas” on the southern coast of Buenos Aires (n=9); “Bajada de los Pescadores”, “Playa Unión”, and “”Cueva del Negro”, sites scattered along the northern and central Patagonian coast (n=6); and from the stratigraphic sequence of sites “Túnel I” and “Túnel VII”, on the north coast of the Beagle Channel (n=46; Zangrando *et al*., 2013). In addition, shell remains were recovered from zooarchaeological assemblages at different layers of shell middens to estimate the baseline of the ecosystems. The ribbed mussel *Aulacomya atra atra* and the Magellanic copper limpet *Nacella magellanica* were collected from archaeological sites in Península Valdés and adjoining areas and used respectively as proxy of the base of the pelagic and littoral food web of northern and central Patagonia; in turn the blue mussel *Mytilus edulis* and the Magellanic copper limpet were collected from Túnel archaeological locality and used respectively, as indicators of the base of the pelagic and littoral food web of southern Patagonia. No archaeological shell samples were collected for Río de la Plata and adjoining areas and those proceeding from central-northern Patagonia were used in their place. Sample size of shells varied across species and localities. Minimum number of individuals (MNI) for the analysis was assessed for skeletal bone and bivalve (i.e. ribbed and blue mussels) remains.

TABLE 1. Archaeological sites where the fur seal and shell remains were recovered.

Region	**Archaeological site**	**Geographic position**	**Radiocarbon datation (yr ^{14}C BP)**	**n**	**Sampled species**	**Reference**
Río de la Plata and adjoining areas	La Olla 1	38º 57'S - 61º 22'W	from 7,300 to 6,600	6	*A. australis*	Bayón and Politis, 1996; Johnson *et al*., 2000; Blasi *et al*., 2013
	Barrio Las Dunas	38º 59'S - 61º 20'W	*ca.* 7000	3	*A. australis*	Bayón *et al*., 2012
Northern and central Patagonia	Las Ollas, midden 1	42º 38'S - 64º 05'W	610 ± 60 640 ± 40	5	*A. atra atra*	Gómez Otero, 2006
	Ecocentro, hearth 3	42º 46'S - 64º 59'W	850 ± 150	5	*N. magellanica*	Gómez Otero, 2006
	Playa Unión, Barranca Norte 1, hearth 1	43º 16'S - 65º 00'W	1,040 ± 70	3	*A. australis*	Peralta, 2001 quoted in Gómez Otero, 2006
	Cueva del Negro, grid 1, level 2	47º 54'S - 65º 46'W	1,730 ± 80	1	*A. australis*	Beretta *et al*., 2011
	Playa Las Lisas 2, profile 1	42º 10'S - 64º 02'W	2,140 ± 50	5	*A. atra atra*	Gómez Otero, 2006
	Bajada de los Pescadores	40º 55'S - 64º 23'W	2,197 ± 38	2	*A. australis*	Borella and Cruz, 2012
	Playa Las Lisas 2, midden 2	42º 10'S - 64º 02'W	2,600 ± 60	5	*N. magellanica*	Gómez Otero, 2006
	Cracker 8, level 3	42º 56'S - 64º 29'W	5,200 ± 70	5	*A. atra atra*	Gómez Otero, 2006
				2	*N. magellanica*	
Southern Patagonia	Túnel VII	54º 51'S - 67º 54'W	100 ± 45	13	*A. australis*	Orquera and Piana, 1999; Zangrando *et al*., 2013
				5	*M. edulis*	
				5	*N. magellanica*	
	Shamakush X, Capa E	54º 51'S - 67º 51'W	500 ± 100	5	*M. edulis*	Orquera and Piana, 1996, 1999
				4	*N. magellanica*	
	Túnel I, layer alfa-X	54º 51'S - 67º 54'W	2,660 ± 100 2,690 ± 80	3	*A. australis*	Orquera and Piana, 1999; Zangrando *et al*., 2013
	Túnel I, layer D (phases VI-VIII)	54º 51'S - 67º 54'W	from 4,590 ± 130 to 5,050 ± 520	10	*A. australis*	Orquera and Piana, 1999; Zangrando *et al*., 2013
	Imiwaia I, layer M and K	54º 52'S - 67º 17'W	5,940 ± 50 5,750 ± 170 5,840 ± 45 5,710 ± 50	5	*M. edulis*	Orquera and Piana, 1999, 2000
				5	*N. magellanica*	
	Túnel I, layer E and D (phases I-V)	54º 51'S - 67º 54'W	from 5,840 ± 185 to 6,470 ± 100	20	*A. australis*	Orquera and Piana, 1999; Zangrando *et al*., 2013

Contemporaneous samples of fur seals consisted of small fragments of maxillo-turbinal bones collected from skulls deposited at 3 scientific collections: (1) Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul (GEMARS) at Tramandaí, which contains skulls of individuals stranded along the coast of southern Brazil from 1994 to 2011 (n= 54 adult males; Vales *et al.*, 2013); (2) Centro Nacional Patagónico at Puerto Madryn, which contains skulls of individuals stranded along the coast of Río Negro and Chubut provinces from 1980 to 2010 (n= 32 subadult and adult males); (3) Museo Acatushún de Aves y Mamíferos Marinos Australes at Ushuaia, which contains skulls of individuals stranded along the coast of Tierra del Fuego from 1978 to 2008 (n= 6 adult males). Likewise, modern shell samples of the same species recovered in archaeological sites were collected from December 2009 to February 2010 at northern, central and southern Patagonia (n= 5 individuals per species). All these samples were stored dry until analysis.

Modern potential preys of fur seals were selected according to the literature (Schiavini, 1993; Thompson and Moss, 2001; Naya *et al.,* 2002; Szteren *et al.,* 2004; Crespo *et al.*, 2008; Oliveira *et al.,* 2008; Vallejos, 2010 quoted in Seguel *et al.*, 2013; Baylis *et al.*, 2013) and collected at southern Brazil and Buenos Aires province (see for details Vales *et al.*, 2013); off northern Patagonian coast (see for details Drago *et al.*, 2009); and off southern Santa Cruz province (from latitude 49º to 52ºS) from April 2010 to May 2011, excepting the Fuegian spratt *Sprattus fuegensis* collected on April 2000. Sampled tissues for potential prey were: white dorsal muscle for fish, mantle for squid, muscle for Argentine red shrimp *Pleoticus muelleri*, and the whole body for lobster krill *Munida gregaria*. All samples were stored in a freezer at -20°C until analysis. Additionally, stable isotope ratios of some potential prey from southern Brazil and northern Patagonia were taken from Bugoni *et al.* (2010) and Drago *et al.* (2009), respectively.

Sex and age determination of fur seals

For Túnel archaeological locality, sex and adulthood of fur seals were inferred from the shape and bone fusion of pelvis elements (King, 1983; Borella *et al.*, 2013). However, for remaining archaeological sites this information was not always known.

TABLE 2. Stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) of modern and ancient shell valves and the estimated baseline correction factors (BCFs) for archaeological fur seal bone samples from northern and central Patagonia, and southern Patagonia. Isotopic values are shown as: mean ± standard deviation (sample size).

Region	**Radiocarbon datation (yr ^{14}C BP)**	**Species**	**$\delta^{15}N$ (‰)**	**BCF for $\delta^{15}N$**	**$\delta^{13}C$ (‰)**	**BCF for $\delta^{13}C$**
Northern and Central Patagonia	present	*Aulacomya atra atra*	11.44 ± 0.28 (7)	0	-16.63 ± 1.19 (7)	0
		Nacella magellanica	11.85 ± 0.51 (5)		-13.50 ± 3.00 (5)	
	610 ± 60 / 640 ± 40	*Aulacomya atra atra*	13.08 ± 0.27 (5)	1.67	-16.19 ± 3.39 (2)	-0.56
	850 ± 150	*Nacella magellanica*	13.55 ± 0.95 (5)		-15.05 ± 2.64 (5)	
	1,040 ± 70	*Aulacomya atra atra*	No data	1.95*	No data	-0.39*
		Nacella magellanica	No data		No data	
	2,140 ± 50	*Aulacomya atra atra*	13.71 ± 1.42 (5)	3.05	-14.32 ± 1.17 (5)	0.31
	2,600 ± 60	*Nacella magellanica*	15.68 ± 0.51 (5)		-15.19 ± 2.69 (4)	
	5,200 ± 70	*Aulacomya atra atra*	14.11 ± 0.23 (5)	2.48	-17.91 ± 0.00 (2)	-2.67
		Nacella magellanica	14.14 ± 1.28 (2)		-17.55 ± 0.36 (2)	
Southern Patagonia	present	*Mytilus edulis*	11.87 ± 0.26 (5)	0	-16.73 ± 0.63 (5)	0
		Nacella magellanica	10.77 ± 0.25 (5)		-12.64 ± 1.65 (5)	
	100 ± 45	*Mytilus edulis*	13.36 ± 0.85 (5)	1.60	-20.48 ± 0.73 (5)	-5.23
		Nacella magellanica	12.49 ± 0.61 (5)		-19.35 ± 2.31 (5)	
	500 ± 100	*Mytilus edulis*	13.44 ± 0.37 (5)	1.45	-14.61 ± 0.34 (3)	0.89
		Nacella magellanica	12.10 ± 0.68 (4)		-12.98 ± 2.18 (2)	
	1,190 ± 60	*Mytilus edulis*	No data	1.65*	No data	0.33*
		Nacella magellanica	No data		No data	
	2,660 ± 100 / 2,690 ± 80	*Mytilus edulis*	No data	2.07*	No data	-0.83*
		Nacella magellanica	No data		No data	
	from 5,949 ± 50 to 5,750 ± 170	*Mytilus edulis*	15.39 ± 1.18 (5)	3.07	-18.23 ± 2.30 (5)	-3.63
		Nacella magellanica	13.39 ± 0.54 (5)		-18.40 ± 2.08 (5)	

* Baseline weighted average value computed from BCFs of adjacent periods.

For contemporaneous fur seal samples, sex was determined either by direct examination in fresh dead stranded animals, the presence of *baculum* in males or by measuring canine teeth (Molina-Schiller and Pinedo, 2004a). Individual ages were estimated from counts of growth layer groups (GLGs; Scheffer, 1950) in the dentine and/or in the cementum of different teeth. Three different techniques were used for age determination: direct counting of external rings on canine root, thin ground sections of undecalcified teeth, and decalcified and stained thin sections made with a freezing microtome. The technique employed depended on the availability of teeth from each individual (canines, incisors or post-canines) and it was assumed that one GLG is deposited per year (Schiavini *et al.,* 1992; Crespo *et al.,* 1994; Molina-Schiller and Pinedo, 2004b). Teeth were read three times by at least two readers. Subsequent readings by the same reader were spaced by at least 1 week. When readings were coincidental, that age was assigned to the individual. Whenever counting differed by less than

10% of the average of the three reads, the mean of the readings was taken as the age of the specimen (Calzada *et al.,* 1994). Where counts exceeded this arbitrary limit, teeth were re-examined or another tooth was prepared.

Stable isotope analysis

Bone, shell and prey samples were dried in a stove at 60°C for 36-48h and ground to a fine powder with a mortar and pestle. Previously, shell surfaces were polished with sandpaper and with a diamond wheel drill to eliminate impurities and then were rinsed with distilled water. Lipids were extracted with a chloroform/methanol (2:1) solution (Bligh and Dyer, 1959). Since both bone and shell samples contain high concentrations of inorganic carbon that may bias $\delta^{13}C$ values (Lorrain *et al*., 2003), they were treated by soaking for 24h in 0.5N and 1N hydrochloric acid (HCl), respectively, until no more CO_2 was released (Newsome *et al*., 2006). Since HCl treatment may alter $\delta^{15}N$ values (Bunn *et al*., 1995), each sample was split into 2 subsamples: one was used for ^{15}N analysis without decarbonising and the other one was used for ^{13}C analysis after decarbonising.

Approximately 0.60-1mg of bone, 0.15-16mg of bivalve and limpet shells, and 0.30-0.5mg of prey samples were weighed into tin cups, combusted at 900ºC, and analysed in a continuous flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA Thermo Finnigan). For shell samples, a CO_2 absorbent for elemental analysis (CaO/NaOH) was employed to avoid the saturation of the spectrometer during the analysis of the no-decarbonised samples, constituted by 90% $CaCO_2$. Stable isotope abundance is expressed in standard δ notation relative to carbonate Pee Dee Belemnite and atmospheric nitrogen. Carbon to nitrogen (C:N) mass ratio was used as proxy for data quality (e.g. an adequate lipid extraction; Newsome *et al*., 2010) . Samples were analysed at the Centres Científic i Tecnològics of the University of Barcelona. However, bone samples from Túnel archaeological locality were processed following Tykoy (2004) and were analysed at the Instituto de Geocronología y Geología Isotópica (INGEIS; Zangrando *et al*., 2013). Hence, to test whether these data sets are comparable, 4 bone samples were analysed at both laboratories.

Data analysis

For statistical analysis of the data, normality and homogeneity of variance were checked by means of modified Shapiro-Wilks and Levene tests, respectively.

To test for possible biases between the two procedures or laboratories, 4 bone samples were analysed at both laboratories and the reported isotopic values were compared through a paired *t*-test.

Changes in the isotopic baseline through time at each region were evaluated by means of ANOVA or Kruskal-Wallis tests according to their adjustment or not to parametric requirements. In case of change of the isotopic baseline and with the aim of make comparable the foraging habits of fur seals at different ecosystems and times, baseline correction factors (BCFs) for $\delta^{15}N$ and $\delta^{13}C$ were computed for each region and epoch. First, mussels and limpets were averaged; thus, integrating the two trophic pathways (pelagic and benthic) that contribute to the base of marine food webs. Then, the averaged values of modern shells were subtracted from those of archaeological shells. Second, these estimated BCFs were added to the isotopic values of archaeological fur seal bones; in this way, the stable isotope ratios in fur seal bones can be compared with those in modern preys. For those periods where the baseline could not be reconstructed by the lack of shell samples a baseline weighted average value with the nearest BCFs was computed, except for ancient fur seal samples from Río de la Plata and adjoining areas (7,000 BP) where the estimated BCFs for northern and central Patagonia area for 5,200 BP was used. For each region, comparisons of baseline-corrected isotopic ratios ($\delta^{15}N$ and $\delta^{13}C$) of ancient and modern fur seals were performed.

In order to compare the isotopic composition of fur seal bones directly to those of its prey, estimated trophic discrimination factors (TDFs) from diet to bone reported for adult males of the species were used ($\delta^{15}N = +5.14$; $\delta^{13}C = +3.63$; Vales *et al*., 2013).

RESULTS

The isotopic values of fur seal bone analysed at both laboratories were not significantly different (paired *t*-test, $p > 0.05$, n= 4); hence, samples were pooled for further analysis.

For northern and central Patagonia, $\delta^{13}C$ values of mussels and limpets revealed no significant changes during the last ca. 2,000 years (Kruskal-Wallis test *A. atra atra*: *H*= 4.8, *df*= 2, *p*= 0.0696; *N. magellanica*: *H*= 0.71, *df*= 2, *p*= 0.7001); contrary, δ^{15}N values differed significantly over this period of time (ANOVA test *A. atra atra*: $F_{2,14}$= 13.21, *p*= 0.0006; *N. magellanica*: $F_{2,12}$= 39.1, *p*< 0.0001). For southern Patagonia, δ^{15}N and δ^{13}C values varied significantly in both species of molluscs in the last ca 6,000 years (Kruskal-Wallis test *M. edulis* for δ^{15}N: *H*= 15.44, *df*= 3, *p*= 0.0015, and for δ^{13}C: *H*= 12.45, *df*= 3, *p*= 0.006; ANOVA test *N. magellanica* for δ^{15}N: $F_{3,15}$= 20.61, *p*< 0.0001, and for δ^{13}C: $F_{3,13}$= 12.59, *p*= 0.0004). These results indicate a considerable variation in the isotopic baseline of both ecosystems, highlighting the convenience of estimating an appropriate isotopic baseline for each epoch before comparing δ^{15}N and δ^{13}C values in bone samples of ancient and modern fur seals. Stable isotope ratios of mussels and limpets and the estimated BCFs for ancient isotopic landscapes from northern and central Patagonia, and southern Patagonia are shown in Table 2.

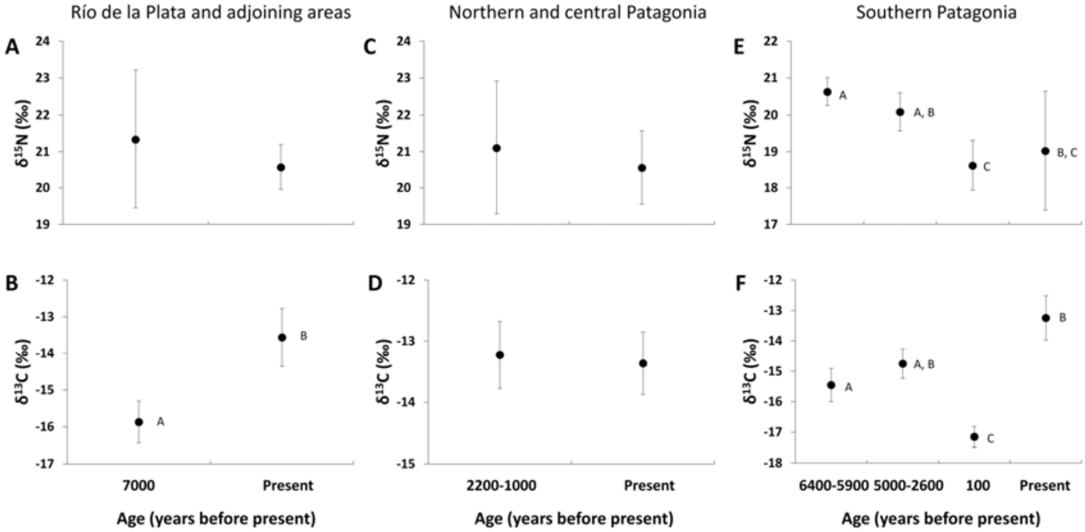

FIGURE 2 Mean and standard deviation of baseline-corrected stable isotope ratios for ancient and modern bone samples of South American fur seals *Arctocephalus australis* from the south-western Atlantic Ocean. Means with a common letter are not significantly different.

When comparing baseline-corrected isotopic ratios for bone samples of Río de la Plata and adjoining areas, ancient fur seals (*ca.* 7,000 BP) showed depleted δ^{13}C values relative to modern ones (Wilcoxon rank-sum test, *W*= 57, p< 0.0001; Figure 2B), whereas no statistically significant change were found for δ^{15}N (*t*-test, *T*= 1.20, *df*=8, *p*= 0.266; Figure 2A). For northern and central Patagonia, stable isotope ratios of ancient fur seals (*ca.* 2100-

1000 BP) were similar to those of modern ones (*t*-test; δ^{15}N: *T*= 0.70, *df*= 5, *p*= 0.513; δ^{13}C: *T*= 0.58, *df*= 32, *p*= 0.564; Figure 2C-D).

TABLE 3. Stable isotope ratios (δ^{15}N and δ^{13}C) of bone samples from modern and ancient South American fur seals *Arctocephalus australis*.

Region	Radiocarbon datation (yr ^{14}C BP)	Sample size	δ^{15}N (‰)	δ^{13}C (‰)	C/N mass ratio
Río de la Plata and adjoining areas	7,000	9	21.33 ± 1.88	-15.87 ± 0.57	3.46 ± 0.78
	present	54	20.58 ± 0.62	-13.56 ± 0.79	2.95 ± 0.16
Northern and Central Patagonia	2,200 – 1,000	6	21.10 ± 1.81	-13.22 ± 0.55	3.51 ± 0.71
	present	28	20.56 ± 1.01	-13.36 ± 0.51	2.79 ± 0.07
Southern Patagonia	6,400-5,900	20	20.64 ± 0.37	-15.46 ± 0.55	2.77±0.03
	5,000-2,600	13	20.09 ± 0.73	-14.75 ± 1.11	2.80±0.06
	100	13	18.62 ± 0.69	-17.15 ± 0.34	2.78±0.05
	present	6	19.02 ± 1.63	-13.25 ± 0.73	2.79 ± 0.09

For southern Patagonia, stable isotope ratios of bone fur seals varied through time (Kruskal-Wallis test; δ^{15}N: *H*= 28.16, *df*= 3, *p*< 0.0001; δ^{13}C: *H*= 37, *df*= 3, *p*< 0.0001). Pairwise comparison revealed that most ancient fur seals (ca. from 6,000 to 2,600 BP) were more enriched in δ^{15}N than those from 100 BP; whereas δ^{15}N of modern fur seals did not differ significantly from those of ca. 5,000-2,600 BP and 100 BP, probably due to the high variability that exist among modern samples (Figure 2E). In turn, pairwise comparison for δ^{13}C evidenced that most ancient fur seals (ca. from 6,000 to 2,600 BP) were more enriched than those from 100 BP; modern fur seal bones displayed the most enriched δ^{13}C values, although not significantly different from those of ca. 5,000-2,600 BP (Figure 2F).

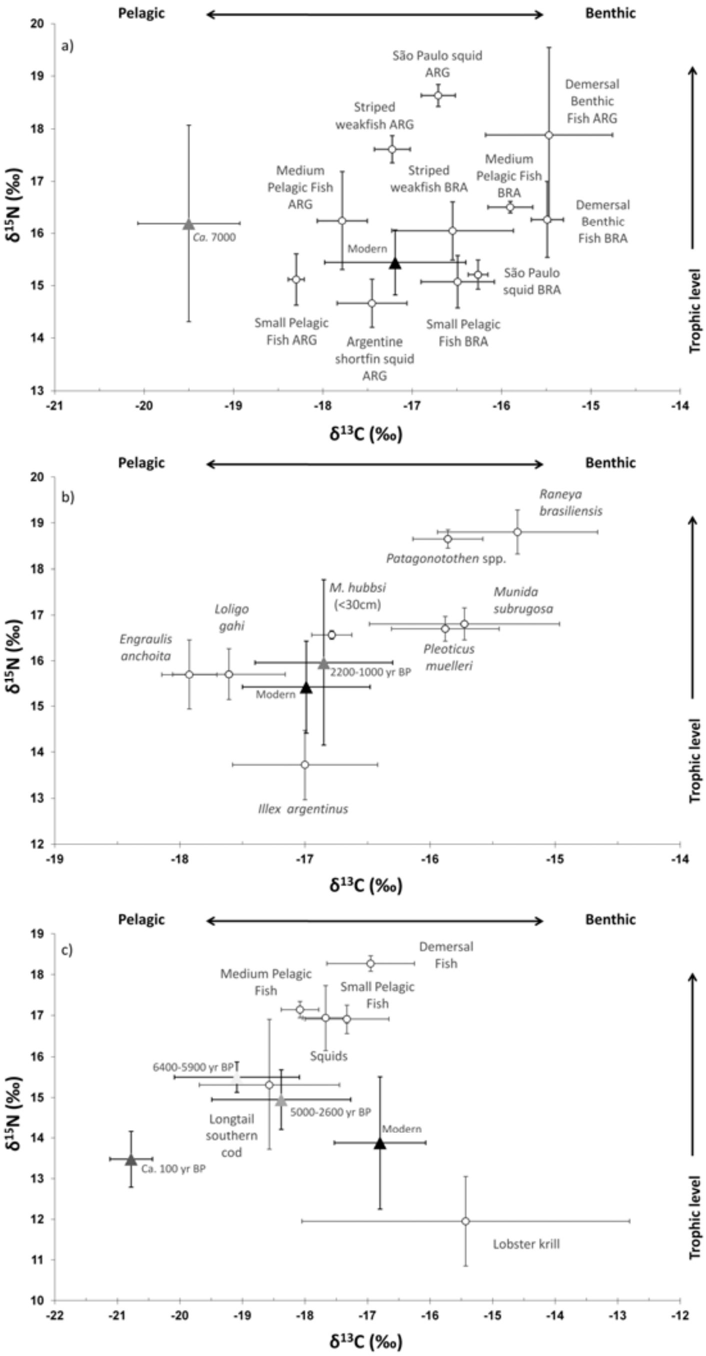

FIGURE 3. Isotopic landscape showing the stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) of modern and ancient South American fur seals (*Arctocephalus australis*) and its potential prey from the south-western Atlantic Ocean, after correcting for baseline (BCFs) and for trophic discrimination factors (TDFs). Regions: (a) Río de la Plata and adjoining areas, (b) Northern and central Patagonia, and (c) Southern Patagonia. Circles denote main prey and triangle fur seals from different periods.

Reconstructed isotopic landscapes using modern prey and fur seals corrected for trophic discrimination factor are shown in Figure 3. While the diet of modern fur seals foraging in the Río de la Plata and adjoining areas was dominated by small pelagic fish and squid, with some contribution of medium pelagic fish and demersal pelagic fish (for details see Vales *et al*., 2013), ancient fur seals (*ca*. 7,000 BP) laid outside the current isotopic landscape, showing really depleted δ^{13}C values although no changes in trophic level (similar δ^{15}N values). Fur seals from northern and central Patagonia showed a fairly stable diet over the last 2,200 years, based on small pelagic fish, squid and decapod crustaceans. At southern Patagonia, fur seals showed a steady diet from *ca*. 6,000 BP to 2,600 BP, focused mainly in the consumption of the longtail southern cod (*Patagonotothen ramsayi*); then by 100 BP shifted to a relatively low trophic level and depleted δ^{13}C values diet, escaping from the isotopic landscape proposed here; to later switch to the current diet, composed by fish, squid and lobster krill (*Munida* sp.).

DISCUSSION

Recently, Zangrando *et al*. (2013) argued that the hunting pressure by hunter-gatherers during the second half of the Holocene resulted in a change in the patterns of habitat use by fur seals in the Beagle Channel. After accounting for changes in the isotopic baseline revealed by mollusc shells, those differences vanished and only recent changes, associated to western sealing and fisheries development, stand (this study). Nevertheless, this does not dismiss the potential impact of hunter-gatherers on fur seals, supported by a reduction in the jaw size of the hunted specimens through time (Zangrando *et al*. 2013), but demonstrates the necessity for reconstructing the history of the isotope baseline when using stable isotope ratios in palaeoecological studies (Casey and Post, 2011). As such, recent claims about changes in the trophic position of some predators should be considered provisional until the appropriate ancient baselines had been reconstructed (Chamberlain *et al*., 2005; Christensen and Richardson, 2008; Esmlie and Patterson, 2007; Lorenzini *et al*., 2010; Esmlie *et al*., 2013; Wiley *et al*., 2013).

Mollusc shells are an appropriate material for that purpose, as they incorporate any variation produced at the base of the food web (e.g. changes in primary productivity, among others). Furthermore, this method overcomes the problem of the correction of δ^{13}C for the

Oceanic Suess effect (Keeling, 1979), since any effect of anthropogenic CO_2 on the $\delta^{13}C$ composition of marine phytoplankton should be integrated in the isotopic signature of primary consumers used as baseline proxies. Therefore, once the ecosystems are comparable through time, changes in $\delta^{15}N$ and $\delta^{13}C$ ratios of fur seals should respectively reflect shifts in trophic level, as well as changes in the proportion of pelagic and benthic prey in the diet, as previously described for the south-western Atlantic Ocean (Forero *et al*., 2004; Ciancio *et al*., 2008; Drago *et al*., 2009; Ricciardelli *et al*., 2010; Botto *et al*., 2011; Vales *et al*., 2013).

Off Pampean coast, ancient fur seals (*ca*. 7,000 BP) exhibited a different diet than the currently known. Whereas really depleted $\delta^{13}C$ values may be indicative of a more pelagic foraging behaviour in the past, $\delta^{15}N$ values suggest that they occupied the same trophic level than today. However, it is worth noting that this interpretation is tentative as it is based on the assumption that estimated BCFs for northern and central Patagonia (5,200 BP) is suitable for the reconstruction of the ancient isotopic landscape of Río de la Plata and adjoining areas (7,000 BP); hence, in future works it would be desirable the estimation of a more appropriate BCF.

Archaeological evidence suggests that Pampean hunter-gatherers only utilized the coastal environment during seasonal settlements (Bonomo, 2005, 2011). In addition, stable isotope analysis indicates that Middle Holocene individuals had mixed diet, based on terrestrial and marine resources, with only a moderate use of pinnipeds (Bonomo *et al*., 2013). On the other hand, palaeoceanographic conditions for the Pampean coast were different than modern ones. Coinciding with the Holocene Climatic Optimum (7,000-5,000 BP), characterized by higher temperatures and higher sea level, the Buenos Aires province coastline was placed several km westward than today (Codignotto and Aguirre, 1993). This allowed a further southward extension of the Brazilian current and warm water masses, with a slightly higher sea surface temperature (*ca*. 2ºC) than present ones (Aguirre, 1993). In addition, higher salinity gradients characterized sites which today are under the influence of the huge Río de la Plata plume and show estuarine/marginal marine conditions (Aguirre *et al*., 2011). Therefore, it is possible that the observed diet for ancient fur seals (7,000 BP) may reflect different prey availability in the past; for instance, a greater presence of typical species of warmer and more salty Brazilian Current waters, which currently distribute more northerly. However, there is no empirical evidence to support this hypothesis.

In northern and central Patagonia, fur seals showed a steady diet over the last 2,200 yrs. Like modern fur seals, the diet of ancient individuals (2,200-1,000 BP) seems to have been dominated by pelagic prey (small pelagic fish and squid) and decapod crustaceans. During the Late Holocene, different trends in the exploitation of pinniped were recorded in archaeological sites of northern and central Patagonian coasts (Gómez Otero, 2006; Gómez Otero *et al*., 2007; Moreno, 2008; Favier-Dubois *et al*., 2009; Moreno *et al*., 2011). However, in all cases were inferred mixed human diets with contributions from terrestrial and marine resources, suggesting a generalized use of resources from coastal areas in subsistence patterns of hunter-gatherers (Gómez Otero *et al*., 2007; Favier-Dubois *et al*., 2009; Moreno *et al*., 2011). Although in the Patagonian coast there was a greater use of pinniped by coastal hunter-gatherers in relation to the Pampean coast, this seems not to have affected the feeding ecology of fur seals. Notwithstanding, to get a better and deeper temporal resolution it would be desirable to increase the sample size, including samples from the Middle Holocene and from the times of fur seal trade.

For southern Patagonia, fur seals showed a stable diet from ca. 6,000 BP to at least 2,600 BP, focused mainly in the consumption of the longtail southern cod (or another prey or group of prey with a similar isotopic signature). Over this time, significant variations took place in the relations between humans and pinnipeds in the Beagle Channel region. Early assemblages (ca. 6,400-5,500 BP) were characterized by high frequencies of pinnipeds and a limited representation of other vertebrate taxa; by contrast, subsequent zooarchaeological assemblages (since 5,500-5,000 BP) showed a decrease of the relative importance of pinnipeds and an increased relevance of other resources (e.g. guanacos, birds and fish; Zangrando, 2009a, 2009b; Zangrando *et al*., 2010; Tivoli and Zangrando, 2011; Zangrando *et al*., 2013). This evidence, together with the decrease of the ages and sizes of the fur seals hunted, is thought to be a consequence of resource depression as a result of increasing or sustained predation pressure by hunter-gatherers during the Middle-Late Holocene (Zangrando *et al*., 2013). Nevertheless, beyond the variation in the intensity of pinniped exploitation, this seems not to have significantly affected the foraging behaviour of fur seals throughout this period.

One hundred yr BP, the diet of fur seals was characterized by a relatively low trophic level and the lowest mean $\delta^{13}C$ values recorded in this study. Low mean $\delta^{15}N$ and $\delta^{13}C$ values could be indicative of foraging in cold and oceanic waters of the Antarctic Convergence, as was suggested for the spectacled porpoise *Phocoena dioptrica* and the hourglass dolphin *Lagenorhynchus cruciger*, two dolphins' species that currently forage in pelagic habitats off Tierra del Fuego (Riccialdelli *et al*., 2010). Myctophid fish could have been a relevant prey over this time, as they are typical inhabitants of the continental shelf-break (Hulley, 1990), characterized by a highly ^{13}C depleted signal (Ciancio *et al*., 2008) and were previously recorded in the diet of fur seals from southern Chile and Falkland/Malvinas Islands (Vallejos, 2010 quoted in Seguel *et al*., 2013; Baylis *et al*., 2013). By this time (RC 100 ± 45 yrs BP / dendrochronologically corrected date = 1,835 AD; Orquera and Piana, 1999) zooarchaeological evidence points out a decrease consumption of otariids by hunter-gatherers from the Beagle Channel (Tivoli and Zangrando, 2011; Zangrando *et al*., 2013) due to the the virtual extinction of South American fur seals from the coasts of Argentina as consequence of commercial sealing (Schiavini, 1992). Thus, the most likely explanation to the highly ^{13}C depleted values of the fur seals from that period is that they were wanderers from somewhere else, for instance Staten Island, and usually foraged in the ^{13}C depleted waters south to it (McMahon *et al*., 2013). Contrary to the ancient diet, based primarily on longtail southern cod, modern fur seals from southern Patagonia show high δ^{13}C values and a diet that also include significant amounts of lobster krill, squid and Fuegian sprat. This matches the diet of fur seals that forage around the Falkland/Malvinas Islands (Baylis *et al*., 2013), although a better characterization of the current diet of fur seals by stomach contest or scat analyses is still needed for Southern Patagonia, as this information in conjunction with stable isotope analysis would allow a higher level of resolution in the interpretation of trophic interactions (Post, 2002).

As historical ecology is a very young discipline, any conclusion drawn at this point must be considered tentative and preliminary (Erlandson and Rick, 2011). In this sense, several issues may hinder the interpretation of the present results. Isotopic baseline needs to be accounted for within each location and each time period where archaeological samples were collected, as the use of a time averaged baseline may increase the amount of error surrounding diet and trophic position reconstructions (Casey and Post, 2011). In this sense, archaeological shell middens offer snapshots of past communities that were formed over relatively short time periods, thus avoiding the problems of long-term time averaging (Casey and Post, 2011). For this study, in some cases it was achieved a proper reconstruction of the isotopic baseline (i.e. shell valves and fur seal remains came from the same period and archaeological site); whereas in other cases, time average baselines were used because the dearth of samples. These problems could be overcome in future works by increasing the sample size. Extra limitations also come from the archaeofaunal analysis of otariid remains. Since the two most common species found in coastal sites of the region show remarkable similarities in its postcranium (especially between adult female sea lions and adult male fur seals), it is difficult for some cases to achieve specific determinations (Borella *et al.*, 2013); hence, precluding the use of a larger sample size for the analysis of stable isotopes. Moreover, for the documentation of interactions between ancient marine mammals and humans a firm grasp of the modern ecology of these organisms is required (Rick *et al.*, 2011). Nevertheless, whereas there is a good characterization of the current diet of Uruguayan fur seals (Naya *et al.*, 2002; Szteren *et al.*, 2004; Oliveira *et al.*, 2008; Franco-Trecu *et al.*, 2012, 2014; Vales *et al.*, 2013), the basic aspects of the feeding ecology of this species in Patagonia have been only recently investigated (Crespo *et al.*, 2008). A recent study based on stable isotope ratios in vibrissae of fur seals from Isla de Lobos (Uruguay) found that both sexes forage at similar trophic levels, though females had wider ranges of $\delta^{15}N$ associated with a higher consumption of prey at lower trophic levels; whereas $\delta^{13}C$ values reflected a sexual segregation in their foraging areas (Franco-Trecu *et al.*, 2014). However, certain limitations in the present work, as the lack of females in modern fur seal samples and the uncertainty of sex determination in some archaeological fur seal samples precluded us to assess for potential sex-related foraging strategies. Complementary, a better characterization of palaeoceanographic conditions during the Middle and Late Holocene for the south-western Atlantic is required to attempt inferring the availability of potential prey in the past.

As preliminary conclusions, the diet of South American fur seals seems to have changed over the last *ca*. 7,000 yrs, at least in southern Patagonia and probably in Río de la Plata and adjoining areas. Present evidence does not support a significant impact of human activities on the foraging behaviour of fur seals, except in southern Patagonia. There, commercial sealing coincided with a major dietary shift and currently fur seals consume more crustaceans that they used to do during the late Holocene.

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CAPÍTULO 3

CAMBIOS EN LAS REDES TRÓFICAS Y EN LA ECOLOGÍA TRÓFICA DE LOS DEPREDADORES APICALES DEL MAR ARGENTINO EN CONSECUENCIA AL IMPACTO HUMANO.

3.1 ¿Morfología o identidad de la especie? Un análisis de isótopos estables sobre la repartición de recursos entre los depredadores de respiración aérea.

RESUMEN. Aunque el tamaño corporal de los depredadores puede ser un factor determinante en la estructuración de las redes tróficas, existen cada vez más evidencias de que por sí solo no permite preveer bien la topología de las comunidades de depredadores y el reparto de recursos tróficos entre ellos, factores que dependen mucho de la identidad de la especies consideradas. En el presente trabajo se compara el nicho trófico de tres depredadores marinos de respiración aérea, simpátricos y sexualmente dimórficos (el lobo marino común sudamericano *Otaria flavescens*, el lobo marino fino *Arctocephalus australis* y el pingüino de Magallanes *Spheniscus magellanicus*) en tres zonas del Océano Atlántico sudoccidental (Río de la Plata y zonas adyacentes, el norte de la Patagonia y el sur de la Patagonia) para poder verificar la hipótesis según la cual la repartición de recursos se basa principalmente en el tamaño del cuerpo y la anchura de la boca, mientras que la identidad de la especie tendría un papel menor. La masa corporal y la anchura de la boca/pico se utilizaron para caracterizar la morfología de cada sexo y especie, mientras que el nicho trófico se evaluó mediante las razones de isótopos estables de carbono y nitrógeno. Se empleó el método cuantitativo SIBER para calcular el área de las elipses bayesianas y el solapamiento de los nichos isotópicos entre grupos de depredadores (especies x sexo). Los resultados mostraron que en Río de la Plata, la similitud morfológica se correlacionó significativamente con la distancia entre los grupos dentro del espacio $\delta^{13}C$-$\delta^{15}N$, pero no sucede así en el norte y el sur de la Patagonia. Por otra parte, el reparto de recursos entre grupos cambió regionalmente y algunos grupos morfológicamente muy diferentes llegaron a exhibir un gran solapamiento trófico en ciertas áreas, tales como es el caso de los machos de pingüinos y de lobo común en el sur de la Patagonia. Por el contrario, las hembras de lobo común siempre se solapan parcialmente con los machos de la misma especie, que son mucho más grandes, pero nunca lo hacen con los machos de lobos finos, morfológicamente muy similares. Estos resultados no apoyan la hipótesis de que el tamaño corporal y el diámetro de la boca son los factores más importantes en determinar la repartición de recursos dentro de ese gremio de depredadores de respiración aérea, siendo la identidad de las especies más relevante.

Morphology or species identity? A stable isotope analysis about resource partitioning between air-breathing predators.

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Summary

Although the body size of consumers may be a determinant factor in structuring food webs, recent evidence indicates that body size may fail to fully capture the topology and the resource partitioning between predators if species identity is forgotten. Here we compare the trophic niche of three sympatric and sexually dimorphic air-breathing marine predators (the South American sea lion *Otaria flavescens*, the South American fur seal *Arctocephalus australis* and the Magellanic penguin *Spheniscus magellanicus*) in three areas of the south-western Atlantic Ocean (Río de la Plata and adjoining areas, northern Patagonia and southern Patagonia) to test the hypothesis that resource partitioning is primarily based on body size and mouth diameter, with just a minor role of species identity.

Body weight and palate/bill breadth were used to characterize the morphology of each sex and species, whereas the trophic niche was assessed through the use of stable isotope ratios of carbon and nitrogen. The quantitative method SIBER was used to compute the area of the Bayesian ellipses and the overlap of the isotopic niches.

Results showed that morphological similarity was significantly correlated with distance between groups within the $\delta^{13}C$–$\delta^{15}N$ bi-plot space in Rio de la Plata area, but not in northern and southern Patagonia. Furthermore, resource partitioning between groups changed regionally and some morphologically distinct groups exhibited a large trophic overlap in certain areas, such as the case of male penguins and male sea lions did in southern Patagonia. Conversely, female sea lions always overlapped with the much larger males of the same species, but never overlapped with the morphologically similar male fur seals.

These results do not support the hypothesis that body size and mouth diameter are the single most important factors determining resource partitioning within that guild of air-breathing predators and that species identity is indeed relevant.

Key-words *Arctocephalus australis*; *Otaria flavescens*; *Spheniscus magellanicus*; body size; stable isotopes; SIBER.

Introduction

It has long been acknowledged that the body size of consumers is central to the structure and function of food webs (Elton 1927), as it is has a strong influence on energy flow, species richness, and population densities (Pimm 1982; Hairstone & Hairstone 1993; Elser *et al.* 1996). The size of morphological structures such as bills or teeth often scales with body size and thus has often been used as a morphological indicator of foraging strategies and the size of the food consumed (Diamond 1973; Grant & Grant 1982; Dayan *et al.* 1990; Karpouzi &

Stergiou 2003; Basset & Angelis 2007). Body size also imposes physiological restrictions to foraging, as in air-breathing predators where the interplay among body mass, oxygen stores and metabolic rate determine the duration and depth of dives (Boyd 1997; Schreer & Kovacs 1997; Kooyman & Ponganis 1998; Watanuki & Burger 1999; Schreer *et al.* 2001; Mori *et al.* 2005; Weise *et al.* 2010).

On that ground, size-based analysis of food webs assumes that species with a similar body size will have similar diets and hence the topology of species within the food webs will be largely determined by body size (Jennings 2005). In this way, size-based analysis offers a mechanistic, highly reductionist approach that reduces the problem of dealing with thousands of individual trophic links when analysing complex food webs. That explains why the size-based analysis of food webs has been used increasingly over the last 25 years to provide generalizations regarding food web properties (Warren & Lawton 1987; Cohen *et al.* 1993; Memmott *et al.* 2000; Williams & Martinez 2000; Kerr & Dickie 2001; Leaper & Huxham 2002; Cohen *et al.* 2003; Jennings 2005). However, some recent evidence indicates that body size may not fully capture all the relevant functional traits of vertebrate predators and that morphologically similar species may use different resources (Jeglinski *et al.* 2013). Furthermore, there is increasing evidence suggesting a poor relationship between body size and trophic level within vertebrate assemblages when species identity is ignored (Layman *et al.* 2005; Akin & Winemiller 2008; Romanuk *et al.* 2011; Madigan *et al.* 2012).

Communities of consumers, including sexually dimorphic species, offer a good opportunity to test the relative importance of body size and species identity as determinants of feeding habits. While it is true that differences in body size between males and females often result in contrasting diets (Bearhop *et al.* 2006; Drago *et al.* 2009; Weise *et al.* 2010; Silva *et al.* 2014) and that related species differing in body size often have different diets (Dellinger & Trillmich 1999; Page *et al.* 2005; Ryan *et al.* 2013; Franco-Trecu *et al.* 2014), the hypothesis that body size is more relevant than species identity to define resource use patterns has been seldom tested (Jeglinski *et al.* 2013).

The south-western Atlantic Ocean offers a good scenario to examine such relationships, as three sexually dimorphic species of air-breathing predators coexist, namely the South American sea lion *Otaria flavescens*, the South American fur seal *Arctocephalus australis* and the Magellanic penguin *Spheniscus magellanicus* (Vaz-Ferreira 1981; Vaz-Ferreira 1982; Vaz-Ferreira 1982; Scolaro *et al.* 1983; Forero *et al.* 2001). The South American sea lion is one of the largest and most dimorphic otariids (Cappozzo & Perrin 2009), with males being much larger than females (about 350 kg *vs* 150 kg); the South American fur seal is also dimorphic, with males and females reaching a body mass of 159 and 48.5 kg, respectively (Vaz-Ferreira 1982). Finally, Magellanic penguins are much less dimorphic and their body mass is much smaller than the two pinnipeds above, with females weighing about 3.7 kg and males about 4.5 kg (Scolaro *et al.* 1983; Forero *et al.* 2001). The three species coexist along 3000 kilometres of coastline, where environmental conditions range from warm temperate in Río de la Plata to cold temperate in Tierra de Fuego. The community of potential preys change accordingly (Cousseau & Perrotta 2000; Miloslavich *et al.* 2011). Body size is known to be important to explain the intraspecific variability in the diet and foraging tactics within each of the three species (Drago *et al.* 2009; Drago *et al.* 2010; Franco-Trecu *et al.* 2014; Silva *et al.* 2014), but little is known about resource partitioning among species. If the assumptions of size-based food web analysis are correct and differences in body size overwhelm species identity, the topology of the predator assemblage within the food web would be determined solely by morphology and should remain unmodified along environmental gradients.

In this paper we measure the distance and the trophic overlap between the isotopic niche of both sexes of the South American sea lion, the South American fur seal and the Magellanic penguin in three areas of south-western Atlantic Ocean. In doing so, we test the hypothesis that the resource partitioning among air-breathing predators is based primarily on body size and mouth diameter, with just a minor role for species identity, and that the topology of the community does not change regionally in the absence of morphological change. Because traditional methods for studying resource partitioning among predators are difficult to apply due to the complexity of the data required and to the impossibility of integrating uneven dietary information (Post 2002; Bearhop *et al.* 2004), we analyze the topology of food webs and the trophic niches of single species/groups, using stable isotope data (Bearhop *et al.* 2004; Layman *et al.* 2007; Schmidt *et al.* 2007). Stable isotope data are particularly useful to study trophic organization, as they provide time-averaged information that incorporate spatiotemporal scales often not considered in traditional studies (Abrantes *et al.* 2014).

Moreover, a quantitative method called SIBER has been employed to directly compare isotopic niches across different communities (Jackson *et al.* 2011)

Materials and methods

SAMPLING

The study area included the south east coast of South America, from approximately 29ºS to 55ºS (Fig. 1). The area has been divided into the following three sub-areas according to oceanographic, biogeographic and anthropogenic features (Cousseau & Perrotta 2000; Piola & Falabella 2009): Río de la Plata and adjoining areas (from southern Brazil to Buenos Aires province, Argentina), northern Patagonia (Río Negro and Chubut provinces, Argentina) and the southern Patagonia area (Santa Cruz and Tierra del Fuego provinces, Argentina).

Changes of $\delta^{13}C$ and $\delta^{15}N$ values along the food webs of the three regions have been investigated previously and everywhere demersal potential preys were found to be more enriched in ^{13}C and ^{15}N than pelagic potential preys, although in southern Patagonia the overlap between the two groups is larger (Forero *et al.* 2004; Ciancio *et al.* 2008; Drago *et al.* 2009; Riccialdelli *et al.* 2010; Botto *et al.* 2011; Vales *et al.* 2013).

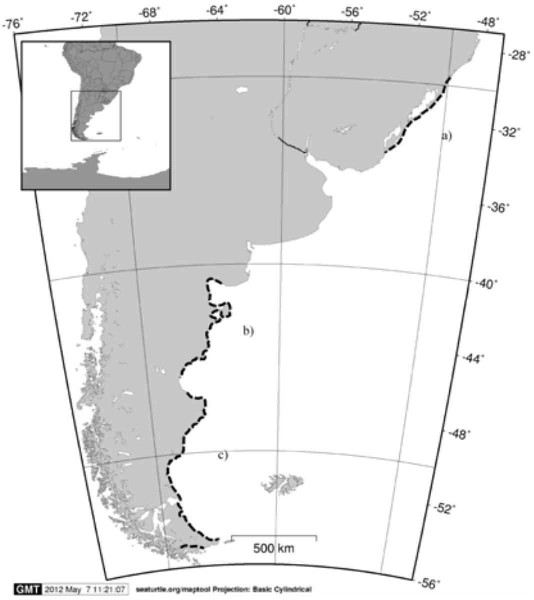

Fig. 1. Study area and zones where sampling was conducted (dashed lines). a) Río de la Plata area and adjoining areas; b) northern Patagonia area and c) southern Patagonia area.

Available evidence supports the existence of limited exchange of adult sea lions between the three areas (Zenteno *et al.* 2013) and hence stable isotope ratios in bone are expected to integrate the regional diet. Samples from the maxillo-turbinal bones of adult sea lions and fur seals of both sexes, corresponding to the periods 1981-2010 and 1978-2011 respectively, were collected from specimens preserved at the scientific collections at Museo Acatushún (Ushuaia, Argentina), Centro Nacional Patagónico (Puerto Madryn, Argentina) and Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul (Imbé, Brazil). Very distinctly from these species, Magellanic penguins are migratory (Pütz *et al.* 2000; Pütz *et al.* 2007), and bone will integrate diet across regions (Silva *et al.* 2014). For this reason, the tissue selected for the analysis was feather vane from adult males and females found dead at breeding colonies located in northern and southern Patagonia. Penguins go through a simultaneous moult replacing all feathers at the end of the reproductive period (Frere *et al.* 1996), so the isotopic signature of the feather vane informs about the location where the feather was grown (Hobson 2005), this is the breeding ground, which is the same every year (Schiavini *et al.* 2005). Since there are no penguin breeding colonies in Río de la Plata, no sampling could be conducted there. In their place, the claws of stranded juvenile penguins of both sexes found in southern Brazil were used. These samples were collected from specimens preserved at the scientific collection from Centro de Estudos Costeiros, Limnológicos e Marinhos (Imbé, Brazil). According to claw growth rates (Barquete *et al.* 2013) and time of collection, the central part of the claw is likely to be formed when the penguins were off Río de la Plata and the basal part when they were off southern Brazil, so we analyzed both sections to assess penguin foraging in the two areas. These samples were collected from specimens preserved at the scientific collection from Centro de Estudos Costeiros, Limnológicos e Marinhos (Imbé, Brazil). All samples of penguins were collected during fieldwork from 2009 to 2011 with the corresponding permissions granted by conservation agencies from the provinces of Rio Negro, Chubut, and Santa Cruz (Argentina), and of Rio Grande do Sul (Brazil). No manipulation of living animals was involved in the collection of samples as all them came from adults or juveniles found dead at the breeding colonies or migratory grounds. All samples were stored in a freezer at –20°C until analysis.

STABLE ISOTOPE ANALYSIS

Once in the laboratory, bone samples were thawed, dried in an oven at 60°C for 36-48 hours, and ground to fine powder with a mortar and pestle. Lipids were extracted from samples with a chloroform-methanol (2:1) solution (Bligh & Dyer 1959). This is because lipids are depleted in ^{13}C compared with other molecules (DeNiro & Epstein 1977) and lipid concentration in tissues may vary between and within species. Since bone samples contain high concentrations of inorganic carbon, which may cause undesirable variability in $\delta^{13}C$ (Lorrain *et al.* 2003), they were divided in two aliquots. The first was decarbonized by soaking in 0.5 M hydrochloric acid (HCl) until no more CO_2 was released (Newsome *et al.* 2006). Since HCl treatment adversely affects $\delta^{15}N$ (Bunn *et al.* 1995), the other, untreated aliquot was used for $\delta^{15}N$ analyses. Feathers and claws were washed in a chloroform-methanol (2:1) solution, rinsed thoroughly in distilled water to remove external contamination, and dried in an oven at 60°C. Then the tips (distal part) of the feathers were cut as finely as possible to allow for a precise weighing, while 2 mm long sections of the claws were sampled from base and centre of the claw. To avoid mixing the older external keratin and the recently deposited inner keratin, samples were collected along the lateral ridge of the claw.

After this preparation, approximately 0.7 mg to 1 mg of dried bone, 0.3 to 0.35 mg of feathers and 0.23-0.33 mg of claws were weighed into tin cups (3.3 × 5 mm), combusted at 900°C, and analyzed in a continuous flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA Thermo Finnigan). Stable isotope abundance is expressed in standard δ-notation in [‰] relative to carbonate Pee Dee Belemnite and atmospheric nitrogen. Analyses were performed at the Science and Technology Centres (CCiT) of the University of Barcelona.

MORPHOLOGICAL MEASUREMENTS

Mouth diameter was assessed in fur seals and sea lions by palate breadth between postcanines 3 and 4 (see Brunner 2002) and in penguins by base bill breadth. Sample size was 20 for each species (10 males and 10 females), except for female fur seals (n=7). Only adults were included. Measurements were made on skulls from the scientific collection at

Centro Nacional Patagónico (Puerto Madryn, Argentina). Body mass for each species was obtained from the following sources: Bonner 1981, Vaz-Ferreira 1981, Lima & Páez 1995, Yorio *et al.* 2001.

Table 1. Sample size and stable isotope ratio of South American fur seals, South American sea lions and Magellanic penguins in the three study areas.

			$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
Scientific name	**Tissue**	**n**	**Mean (±SD)**	**Mean (±SD)**
Río de la Plata area				
Arctocephalus australis ♀ (Brazil)	bone	5	18.8(±1.0)	-13.6 (±0.5)
Arctocephalus australis ♂ (Brazil)	bone	54	20.6 (±0.6)	-13.6 (±0.8)
Otaria flavescens ♀ (Brazil)	bone	4	20.4 (±0.3)	-12.0 (±0.3)
Otaria flavescens ♂ (Brazil)	bone	15	20.7 (±0.5)	-11.9 (±0.7)
Spheniscus magellanicus ♀ (Argentina and Brazil)	claw	18	15.1 (±1.8)	-16.8 (±0.8)
Spheniscus magellanicus ♂ (Argentina and Brazil)	claw	20	14.7 (±1.5)	-16.9 (±0.9)
Northern Patagonia				
Arctocephalus australis ♂	bone	28	20.6 (±1.0)	-13.4 (±0.5)
Otaria flavescens ♀	bone	11	22.3 (±0.5)	-12.3 (±0.6)
Otaria flavescens ♂	bone	14	22.2 (±1.0)	-11.9 (±0.6)
Spheniscus magellanicus ♀	feather	10	19.2 (±1.4)	-16.5 (±0.7)
Spheniscus magellanicus ♂	feather	7	18.8 (±2.4)	-16.2 (±1.0)
Southern Patagonia				
Arctocephalus australis ♂	bone	6	19.0 (±1.6)	-13.2 (±0.7)
Otaria flavescens ♀	bone	10	20.9 (±1.0)	-12.3 (±0.7)
Otaria flavescens ♂	bone	31	20.7 (±1.2)	-13.1 (±1.1)
Spheniscus magellanicus ♀	feather	20	18.7 (±1.2)	-16.9 (±0.8)
Spheniscus magellanicus ♂	feather	18	18.7 (±1.6)	-16.8 (±1.6)

DATA ANALYSIS

Due to the differential discrimination that occurs between different tissues in animals, stable isotopes values of carbon and nitrogen of bone, claw and feathers are not directly comparable (Hobson & Clark 1992; Todd *et al.* 2009). For this reason they were converted into those expected for muscle using correction factors (Table 2). Since discrimination factors from diet to consumer (or *viceversa*) have not been experimentally determined for none of our species and tissues, they were indirectly calculated for pinnipeds (see Vales *et al.* 2013 for details) and adapted from values of gulls fed with perch (Hobson & Clark 1992) in the case of penguins.

Table 2. Fractionation factors used in the article.

	Tissue-to-diet		
	δ^{13}C (‰)	**δ^{15}N(‰)**	**Source**
A.australis (bone)	3.6	5.1	Vales *et al.* 2013
O. flavescens (bone)	3.5	4.4	Zenteno *et al.* unpublished.
S. magellanicus (claws)	1.7	2.5	Adapted from Hobson and Clark 1992
S. magellanicus (feathers)	0.8	2.3	Adapted from Hobson and Clark 1992

Six groups (species x sex) were considered for analysis in Río de la Plata, but only five in northern and southern Patagonia due to the scarcity of suitable skeletal material from female fur seals from those areas. Once the data had been transformed into comparable units, niche similarity was assessed by computing the Euclidean distance between the centroids of groups in the δ^{13}C–δ^{15}N bi-plot space, whereas morphological similarity was assessed by computing the Euclidean distance between groups within the morphospace defined by body size and palate/bill breadth. We also applied the Bayesian method SIBER (Jackson *et al.* 2011) to compute Layman's metrics (Layman *et al.* 2007). The δ^{15}N range (NR), δ^{13}C range (CR) and the mean distance to centroid (CD) are measures of the total extent of spacing within the δ^{13}C–δ^{15}N bi-plot space. NR is the representation of the vertical amplitude of the isotopic niches, whereas CR gives an idea of the trophic diversity of resources used by predators. The mean distance to centroid provides a measure of the average degree of trophic diversity within the community. Mean nearest neighbour distance (MNND) and the standard deviation of nearest neighbour distance (SDNND) reflect the relative position of species to each other within the niche space and can be used to estimate the extent of trophic redundancy (Layman *et al.* 2007; Jackson *et al.* 2011). Finally, SIBER allowed both the calculation of the area of the frequentist standard ellipses for small sample sizes (SEA_C) and the Bayesian estimate of the standard ellipse and its area (SEA_B). The latter is a metric that, unlike the minimum convex polygon area, gives the possibility of comparing uneven or small samples, of reducing the error in calculating the isotopic niche using the ellipses, and of preserving the uncertainty of the sampling process, propagating the error along the measures. The overlap between predators SEA_C in the three areas was also calculated. All codes for SIBER analyses are contained in the package SIAR (Parnell *et al.* 2010; Parnell & Jackson 2013).

Results

Body mass and breadth of palate/bill of the three top predators are positively correlated, being females lighter and with a narrower mouth gape than males for each species (Fig.2).

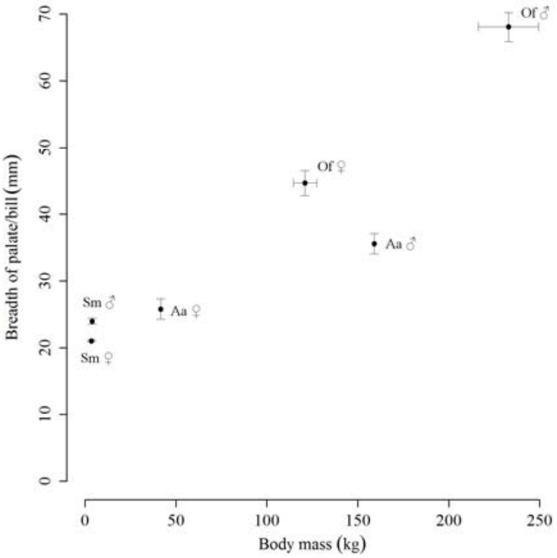

Fig. 2. Plot of the relationship between body mass and breadth of palate/bill in the three top predators split by species and sex: males and females of Magellanic penguin (Sm♂ and Sm♀), males and females of fur seal (Aa♂ and Aa♀) and males and females of sea lion (Of♂ and Of♀). The means and standard deviations (when present) of body mass for each group were obtained from Bonner 1981, Vaz-Ferreira 1981, Lima and Páez 1995, Yorio *et al.* 2001.

However, the topology of the same top predators within the δ^{13}C–δ^{15}N bi-plot space differs from morphology-based expectations in two out of three of the considered regions (Fig. 3). Indeed, morphological similarity and niche similarity were positively correlated only in Río de la Plata (r^2=0.526, p=0.002, Fig. 5). Nevertheless, the niche similarity between female sea lions and male sea lions was higher than predicted by morphology. Conversely, the niche similarity between female sea lions and penguins of either sex was lower than that predicted by morphology. As a consequence of the morphological prediction the overlap between the isotopic niches of air-breathing predators inhabiting Río de la Plata, as represented by the standard ellipses in the δ^{13}C–δ^{15}N bi-plot space, was usually low, except between the two sexes in the penguin and the sea lion (Table 3, Fig. 3a). A broad overlap between morphologically dissimilar male and female sea lions and the absence of overlap between morphologically similar male fur seal and female sea lions are observed.

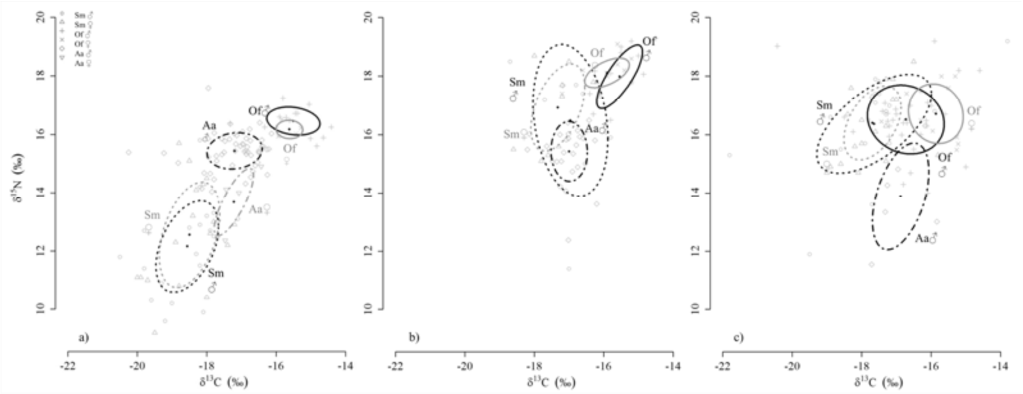

Fig. 3. Isotopic niches of the species described in the text calculated as standard ellipses area corrected for small samples (SEA_C). a) Río de la Plata area; b) northern Patagonia area; c) southern Patagonia area. Aa = *Arctocephalus australis*; Of = *Otaria flavescens*; Sm = *Spheniscus magellanicus*.

Morphological similarity and niche similarity were uncorrelated in northern Patagonia (p=0.826) because species as distinct as male penguins and male fur seals overlapped in their isotopic niches (Table 3). In fact, the ellipse of male penguins completely encompassed that of male fur seals, while only 19.75% of the male penguins' ellipse overlapped with that of male fur seals. As in Río de la Plata, the isotopic niche of female sea lions overlapped with that of male sea lions but not with that of the morphologically similar male fur seals (Table 3, Fig.3). Morphological similarity and niche similarity were also uncorrelated in southern Patagonia (p=0.820), again because the isotopic niches of morphologically dissimilar species overlapped.

Table 3. Overlap as a percentage of standard ellipses corrected for small samples (SEA_c) of the three top predators described in the text. The table should be read horizontally, as each number in the cell refers to the percentage of overlap of the area of the group indicated in row (e.g. 78.96% is the percentage of the ellipses of the females of sea lions that are overlapped with the males of the same species, while 26.46% is the percentage of the ellipses of the males of sea lions that are overlapped with the females of the same species). Aa=*Arctocephalus australis*; Of=*Otaria flavescens*; Sm=S*pheniscus magellanicus*.

Río de la Plata		**Aa**		**Of**		**Sm**	
		♀	♂	♀	♂	♀	♂
Aa	♀	1	0	0	0	6.40	4.80
	♂	0	1	0	0	0	0
Of	♀	0	0	1	78.96	0	0
	♂	0	0	26.46	1	0	0
Sm	♀	1.78	0	0	0	1	80.08
	♂	1.50	0	0	0	89.69	1

Northern Patagonia		**Aa**		**Of**		**Sm**	
		♀	♂	♀	♂	♀	♂
Aa	♀						
	♂		1	0	0	18.40	100.00
Of	♀		0	1	45.81	0	18.79
	♂		0	27.88	1	0	6.43
Sm	♀		9.74	0	0	1	95.80
	♂		19.75	1.87	1.05	35.64	1

Southern Patagonia		**Aa**		**Of**		**Sm**	
		♀	♂	♀	♂	♀	♂
Aa	♀						
	♂		1	0	4.60	0	0
Of	♀		0	1	53.11	0	25.96
	♂		4.70	32.88	1	33.87	68.97
Sm	♀		0	0	46.91	1	99.99
	♂		0	9.38	40.24	42.12	1

This was the case of male sea lions and the two sexes of the Magellanic penguin and that of female sea lions and male penguins (Table 3). As in the other areas, the sexes of the penguin and those of the sea lion overlapped widely, whereas morphologically similar male fur seals and female sea lions did not overlap.

Table 4. SIBER ellipse corrected areas of air-breathing top-predators in the three study areas.

	♀ Aa	**♂ Aa**	**♀ Of**	**♂ Of**	**♀ Sm**	**♂Sm**
Río de la Plata	2.68 (0.85-5.09)	1.62 (1.21-2.06)	1.92 (0.54-3.86)	1.49 (0.82-2.29)	4.55 (2.65-6.75)	4.07 (2.43-5.88)
Northern Patagonia	-	1.87 (1.23-2.58)	1.45 (0.72-2.34)	2.03 (1.10-3.14)	3.50 (1.65-5.79)	7.51 (2.99-13.40)
Southern Patagonia	-	4.39 (1.56-8.10)	2.73 (1.28-4.55)	4.00 (2.71-5.46)	3.07 (1.85-4.47)	6.69 (3.94-9.93)

Finally Layman's metrics indicate that the guild of air-breathing predators used a broader diversity of trophic resources in Río de la Plata than in the northern and southern Patagonia, as the carbon range (CR), the nitrogen range (NR) and the distance to the centroid (CD) were significantly larger in the former (Figs 3 and 4). However, the metrics of trophic redundancy (MNND and SDNND) did not differ between regions (Fig. 4).

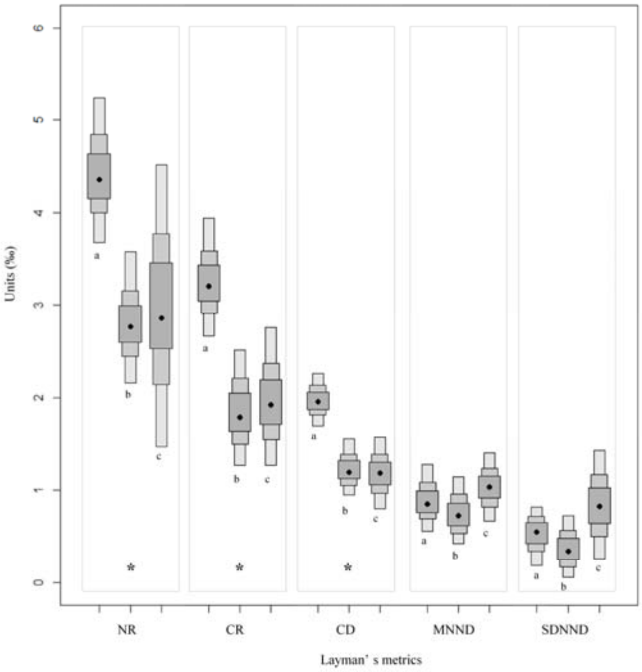

Fig. 4. Probability values of Layman's metrics in the three study areas: a) Río de la Plata area; b) northern Patagonia area and c) southern Patagonia area. The asterisks point out significant differences between regions.

Discussion

The results here reported do not support the hypothesis that mouth diameter and body size are the single most important factors determining resource partitioning at least among sea lions, fur seals and penguins in the south-western Atlantic. This is so for at least three reasons. Firstly, the distance between predators within the morphospace is correlated with the distance in the $\delta^{13}C$–$\delta^{15}N$ bi-plot space in Río de la Plata (Fig. 5), but not in northern and southern Patagonia. Secondly, morphologically dissimilar predators, as male sea lions and male penguins, broadly overlap in the $\delta^{13}C$–$\delta^{15}N$ bi-plot space in some regions, whereas morphologically close predators, as female sea lions and male fur seals, never overlap in the $\delta^{13}C$–$\delta^{15}N$ bi-plot space. Thirdly, the topology of the predators within the $\delta^{13}C$–$\delta^{15}N$ bi-plot space varies regionally, with a positive relationship between overlap and latitude (Table 3 and Fig. 3).

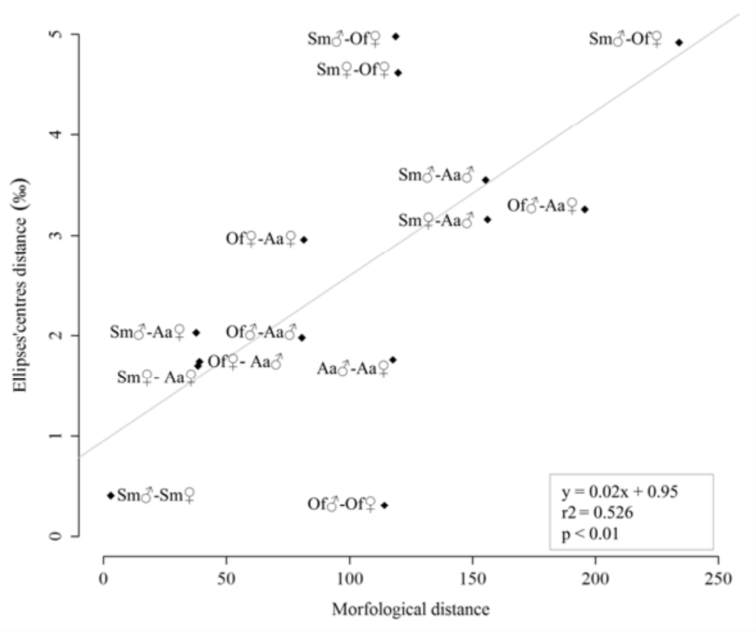

Fig. 5. Correlation in the Río de la Plata region between morphological distance and trophic distance, calculated as the distance between pairwise centroids in the $\delta^{13}C$-$\delta^{15}N$ bi-plot space. Aa = *Arctocephalus australis*; Of = *Otaria flavescens*; Sm = *Spheniscus magellanicus*.

According to the optimal foraging theory, predators should maximize the energy intake for time unit spent foraging (Stephens & Krebs 1986). In pinnipeds this is often achieved by selecting the largest available prey (MacLeod *et al.* 2006). Although studies on this respect in pinnipeds and penguins are lacking, in fishes the optimal prey diameter is 40-70 % of the predator's mouth diameter (Wainwright & Barton 1995). Whatever the case, we would expect that the gradient in mouth size would correlate with that of prey size and therefore sea lion males would consume the largest prey, followed by female sea lions and male fur seals, and ending with female fur seals and Magellanic penguins of both sexes (Fig. 2). The distribution of the predator assemblage within the δ^{13}C–δ^{15}N bi-plot space of Río de la Plata fits that observed within the morphospace and agrees with published dietary information indicating that in Río de la Plata and adjoining regions sea lions consume larger prey than fur seals, which in turn consume larger prey than penguins (Naya *et al.* 2000; Fonseca *et al.* 2001; Naya *et al.* 2002; Szteren *et al.* 2004; Pinto *et al.* 2007; Franco-Trecu *et al.* 2012; Vales *et al.* 2013; Franco-Trecu *et al.* 2014). The dietary differences between female sea lions and male fur seals of similar body size can also be explained by the narrower palate of the latter, which may restrict the consumption of deep-bodied demersal species enriched in ^{15}N (Botto *et al.* 2011; Vales *et al.* 2013). However, morphology cannot explain the dietary overlap between male and female sea lions, even less considering that the sexual dimorphism of this species increases at high latitude (Sepúlveda *et al.* 2013). This result indicates that species identity might be more important than body size as a determinant of patterns in resource use by certain groups of organisms, as previously reported for other pinnipeds (Jeglinski *et al.* 2013).

However, the matching between morphology and trophic niche vanishes definitively in northern and southern Patagonia, where the distance between penguins and sea lions in the δ^{13}C -δ^{15}N bi-plot space is strongly reduced despite significant differences in body size and mouth diameter. Furthermore, the isotopic niche of male fur seals in northern Patagonia is totally embraced by that of male penguins (Fig. 3b), whereas that of male sea lions in southern Patagonia largely overlaps with that of male penguins (Fig. 3c). Penguins forage on small pelagic fishes and squids in northern and southern Patagonia (Scolaro *et al.* 1999; Forero *et al.* 2002; Wilson *et al.* 2005) and hence the close proximity between the ellipses of penguins and those of male fur seals and male sea lions, respectively, suggests a higher consumption of pelagic prey by pinnipeds at higher latitudes. This interpretation is supported by the available data from stomach contents and scat analysis from sea lions in Río de la

Plata and northern Patagonia (Koen Alonso *et al.* 2000; Suarez *et al.* 2005). Unfortunately, there is no published information about the diet of fur seals in northern Patagonia and of sea lions in southern Patagonia. In any case, SIBER confirms a reduction in the range of resources used by the predator assemblage in northern and southern Patagonia when compared with Río de la Plata, which may explain the increasing overlap between species at higher latitudes and the consequent departure from predictions based on morphology.

The poleward decrease of diversity characteristic of the Patagonian shelf (Cousseau & Perrotta 2000; Miloslavich *et al.* 2011) may explain that pattern. For instance, deep-bodied sciaenids represent a common prey of sea lions in Río de la Plata (Riet-Sapriza *et al.* 2013; Zenteno *et al.* unpublished), but they are present only up to the northernmost part of Patagonia (Cousseau & Perrotta 2000; Balech & Ehrlich 2008). Likewise small, streamlined anchovies (*Engraulis anchoita*), which abound in Río de la Plata and northern Patagonia, where they are distributed all over the continental shelf, are an important prey for penguins and fur seals (Scolaro *et al.* 1999; Naya *et al.* 2002), but in southern Patagonia their ecological role is replaced by the Patagonian sprat (*Sprattus fuegensis*), a much scarcer and coastal species (Cousseau & Perrotta 2000). There is no dietary information about sea lions and fur seals in southern Patagonia, but in nearby Falkland (Malvinas) islands, most air-breathing predators converge in the use of lobster krill, *Munida gregaria* (Thompson *et al.* 1998; Pütz *et al.* 2001; Laptikhovsky 2009), also an important prey for fur seals in southern Chile (Hernández 2012) despite its low energy density (Ciancio *et al.* 2007). Lobster krill is very abundant in waters of the south-western Atlantic (Tapella *et al.* 2002; Clausen *et al.* 2005; Romero *et al.* 2006; Vinuesa & Varisco 2007) and, although not very energetic prey, are the favourite food of many predators because of their small size, composition rich in protein and fat, and their ability to form large clusters (Vinuesa & Varisco 2007). Thus, a low diversity of potential prey and the high abundance of lobster krill may explain why morphology fails to predict resource partitioning off northern and southern Patagonia.

It should be noted, however, that intensive exploitation of fish, seal and whale populations has dramatically changed the structure of marine ecosystems worldwide (Caddy 1998; Pauly *et al.* 1998; Devine *et al.* 2006) and hence the results here reported may not reveal the natural partitioning of resources among the considered species. During the 20th century the South American sea lion (*Otaria flavescens*) was intensely exploited, mostly in

Península Valdés (northern Patagonia) and Tierra del Fuego (Crespo & Pedraza 1991; Cappozzo & Perrin 2009). Although no commercial harvest was carried out in northern Argentina, the sea lion colonies known to have existed there since at least 1581 have vanished as a result of human activities (Rodriguez & Bastida 1998). The sea lion population has increased recently in most of their distribution range, except in Uruguay (Páez 2006), but the current population is still only one third of its original size (Crespo & Pedraza 1991; Reyes *et al.* 1999; Dans *et al.* 2004; Schiavini *et al.* 2004). The population of fur seal of Uruguay was exploited intensively from the end of the XVIII century and, after reaching the nadir in 1940, it increased steadily once management measures were implemented, even though commercial sealing continued until 1991 (Vaz-Ferreira 1982). Currently, the largest world rookeries of the South America fur seal are found in Uruguay (Naya *et al.* 2002), but the populations are still below pre 20th century numbers throughout its range (Páez 2006; Túnez *et al.* 2008). On the contrary, the Magellanic penguin has expanded its geographical range northwards (Schiavini *et al.* 2005). The expansion is the likely result of the decline experienced by its competitors although there is no agreement on the trend of the global population because, while in the new colonies of northern Patagonia the number of individuals is increasing, in the historical core of the species, located in central Patagonia, colonies show the opposite trend (Gandini *et al.* 1996). Finally, the development of bottom trawling has lead to a major decrease in the abundance of large, demersal predatory fishes both in Río de la Plata and northern Patagonia (Bertolotti *et al.* 2001; Vasconcellos & Csirke 2011; Milessi & Jaureguizar 2013).

In conclusion, the results reported here reveal that differences in body size and mouth diameter may fail to predict resource partitioning between air-breathing predators in the south-western Atlantic and that dimorphic individuals of the same species have more similar diets than individuals from different species with a similar body size and mouth diameter.

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3.2 Cambios latitudinales en la estructura de las redes tróficas marinas en el Océano Atlántico sur-oeste.

RESUMEN. A pesar de enormes esfuerzos, todavía no se conocen bien los factores que determinan la estructura de las redes tróficas. En el presente trabajo se utilizan los isótopos estables de carbono y nitrógeno para determinar la posición trófica de más de 40 especies marinas de la plataforma continental de tres regiones del sudooeste del Atlántico (la zona subtropical del Río de la Plata, la zona templada del norte de la Patagonia y la zona fría del sur de la Patagonia) y el método SIBER (Stable Isotope Bayesian Ellipses in R) para analizar la longitud y la topología de las redes alimentarias resultantes. Los resultados indican que la longitud de la cadena disminuye y que le redundancia trófica aumenta al aumentar de la latitud, cualquiera que sea el compartimiento de la red trófica considerado. Este patrón no se puede explicar por los cambios en la productividad primaria ni por la variabilidad estacional de la temperatura superficial de mar en el Atlántico sudoccidental, ya que se observa una relación inversa entre esta y la longitud de la red trófica, al contrario de lo que indicado en la bibliografía para otras regiones. En realidad, la reducción latitudinal en la diversidad de las especies registrada en el Atlántico sudoccidental podría ser la razón principal para el patrón observado, aunque la zona ha sido profundamente modificada por la explotación de los mamíferos marinos y la pesca. Esta hipótesis está suportada por la reciente reconstrucción de la red trófica marina de la misma región durante el Holoceno, donde se observó que también en el pasado la longitud de la cadena disminuía y su redundancia aumentaba con la latitud.

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Latitudinal changes in the structure of marine food webs in the south-western Atlantic Ocean

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ABSTRACT: Despite huge efforts, there is still limited understanding of the factors determining the structure of food webs. Here we use stable isotopes of carbon and nitrogen to ascertain the trophic position of more than 40 marine species from the continental shelf of three regions in the South-western Atlantic (subtropical Río de la Plata, temperate northern Patagonia and cold southern Patagonia) and use SIBER (Stable Isotope Bayesian Ellipses in R) to analyse the length and the topology of the resulting food webs. The results indicate that food web length decreases and that trophic redundancy increases as latitude increases, whatever the compartment of the food web considered. This pattern cannot be explained by changes in primary productivity and there is an inverse relationship between the length of the food web and the seasonal variability in the sea surface temperature in the South-western Atlantic, opposite to the pattern reported elsewhere. Actually, the latitudinal reduction of species diversity reported for the South-western Atlantic may be the primary reason for the observed pattern, although the area has been profoundly modified by marine mammal exploitation and fishing. This hypothesis is supported by the recent reconstructions of marine food web during the late Holocene in the same regions, when food web length decreased and redundancy increased with latitude.

KEYWORDS: ^{13}C; ^{15}N; pinniped; species diversity; trophic structure; Patagonian shelf.

INTRODUCTION

Food web structure can be described by the trophic links between the different community components, including information on overall food chain length, connectivity and movement of carbon and nutrients through the different food chains (Polis & Strong 1996, Pimm 2002). Understanding the structure of food webs is a central topic in ecology (Elton 1927, Lawton 1989, Pimm et al. 1991, Post 2002) and its relevance has increased even more after the popularisation of the ecosystem approach for the management of marine fisheries (Botsford et al. 1997, Pikitch et al. 2004).

The structure and the length of the food webs are influenced by both natural factors, like resource availability, animal body size, ecosystem size and history (Cohen et al. 1993, Post 2002, Jennings 2005), and human disturbance (Post 2002, Koen-Alonso & Yodzis 2005). Although many studies have investigated different food web patterns (Pimm et al. 1991, Dunne 2006) and the mechanisms which regulate them, only limited progress has been made in understanding what ultimately determines the length of the food webs (Post 2002, Post & Takimoto 2007, Takimoto & Post 2013), probably because multiple factors control food chain length (Post 2002, Thompson & Townsend 2005). The role of human disturbance has proven to be particularly elusive and the intuitively appealing negative effect on food web length (Post 2002) has not been clearly demonstrated (Takimoto & Post 2013, Warfe et al. 2013), with recent results pointing in the opposite direction (Saporiti et al. in press).

Until recently, the main problem in this kind of studies was that the traditional methods to assess the structure of food webs were difficult to apply for the complexity of the data required or for the impossibility of integrating uneven dietary information (Post 2002, Bearhop et al. 2004). The new quantitative methods developed during the last decade to analyse the topology of food webs using stable isotope data offer a good opportunity to gain a further insight (Bearhop et al. 2004, Layman et al. 2007, Schmidt et al. 2007), although very few studies have used this approach to study food web structure (Jackson et al. 2012, Abrantes et al. 2014) due to its novelty.

The South-western Atlantic Ocean supports some of the most important fishing grounds world-wide (Bertolotti et al. 2001, Vasconcellos & Csirke 2011), along over 28 latitude degrees and gradients of temperature, productivity and biodiversity (Rivas et al. 2006, Piola & Falabella 2009, Rivas 2010, Miloslavich et al. 2011). The region has a long record of human exploitation of coastal resources, as hunter-gatherers settled in coastal areas some 6000 years ago (Orquera & Gómez Otero 2008, Favier Dubois et al. 2009, Orquera et al. 2011). Western exploitation began in the 17th century, with the commercial hunting of southern right whales (*Eubalaena australis*), followed by the South American fur seals (*Arctocephalus australis*), both decimated during the 18th and the 19th century (Ellis 1969, Tønnessen & Johnsen 1982, Reeves et al. 1992, Bastida & Rodríguez 2003). Latter followed the exploitation of the South American sea lion (*Otaria flavescens*), whose population was reduced drastically during the first half of the 20th century (Godoy 1963, Crespo & Pedraza 1991, Dans et al. 2004), followed by the elephant seal (*Mirounga leonina*) and several species of cetaceans (Clark 1887, Bastida & Rodríguez 2003, Trathan & Reid 2009). Finally industrial fishing, mainly for hake (*Merluccius hubbsi*) and other demersal species, developed in the 1960s, with landings increased significantly in the decade 1970-1980, then back down in the '90s when protection measures became necessary (Bertolotti et al. 2001). All this, together with the arrival of some species of invasive weeds that now dominate the community in large areas (Casas et al. 2004), has led to a reorganisation of the ecosystem, with a strong anthropogenic pressure on the apex predators.

Here we use stable isotope analysis and SIBER (Stable Isotope Bayesian Ellipses in R) (Jackson et al. 2011), to measure and compare the structure of the marine food web of three regions in the South-western Atlantic differing in their natural and anthropogenic characteristics, to detect potential patterns related to them.

MATERIAL AND METHODS

Sampling

The study area included the South-western Atlantic Ocean, from approximately 29ºS to 55ºS (Fig. 1). The area has been divided into the following three sub-areas according to oceanographic, biogeographic and anthropogenic features (Cousseau & Perrotta 2000, Acha et al. 2004, Piola & Falabella 2009): Río de la Plata and adjoining areas (from southern Brazil to Buenos Aires province, Argentina), northern Patagonia (Río Negro and Chubut provinces, Argentina) and the southern Patagonia area (Santa Cruz and Tierra del Fuego provinces, Argentina). Samples of particulate organic matter (POM), benthic macroalgae, benthic molluscs (grazers and suspension feeders), small pelagic fishes and squids, medium pelagic fishes, demersal fishes, South American sea lions, South American fur seals and Magellanic penguins (*Spheniscus magellanicus*) were collected from the three areas using a variety of techniques. Note that most of the species for the Río de la Plata area were collected both along the Argentine and southern Brazilian coastline, as previous evidence indicated differences in stable isotope ratios for the two areas (Bugoni et al. 2010, Silva et al. 2014) (Fig. 1). Most samples were collected between October 2009 and December 2011, except those of sea lions and fur seals, which come for the period 1981-2010 and 1978-2011 respectively and some prey samples from Chubut and from Brazil which were collected between 2006 and 2007. Sample number was 5 for each species if possible (see Supplementary Data).

POM samples were collected on the continental shelf in front of Mar del Plata (Buenos Aires province), Golfo Nuevo (Chubut province) and Puerto Deseado (Santa Cruz province) (Fig. 1) using a plankton net (20 µm mesh size) and were separated from the zooplankton in the lab. POM was filtered using a precombusted GF/C filter and whole filter contents were analysed. Macroalgae and benthic molluscs were collected by hand in Mar del Plata, Punta Mejillón and Playas Doradas (Río Negro province), Punta Quilla and Bahía Laura (Santa

Cruz province) whereas fishes and cephalopods were provided by local fishermen in each sub-sampling area. A fragment of thallus was analysed for macroalgae, whereas mantle and white dorsal muscle were analysed for cephalopods and fishes respectively. Additional, stable isotope data for anchovy from southern Brazil were taken from Bugoni et al. (2010).

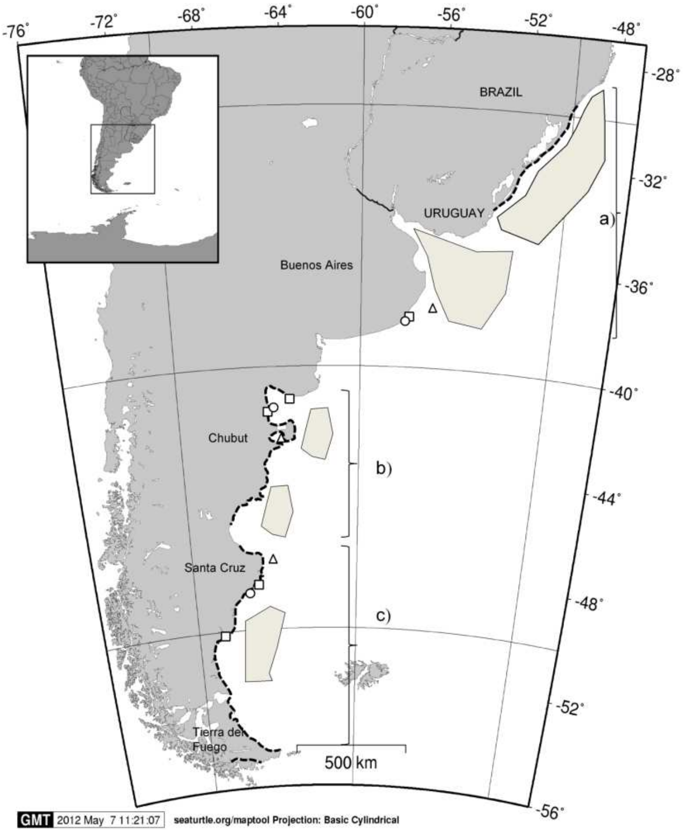

Fig. 1. Study area, regions and sampling zones. a) Río de la Plata and adjoining areas; b) northern Patagonia and c) southern Patagonia. The grey shapes represent the sampling areas for invertebrates and fishes, while the dashed lines represent the sampling areas of pinnipeds and penguins. Empty circles=algae; empty squares=herbivores; empty triangles=POM.

Available evidence supports the existence of limited exchange of adult sea lions between the three areas (Zenteno et al. 2013) and hence stable isotope ratios in bone are expected to integrate the regional diet. Turbinated bone samples of adult sea lions and fur seals of both sexes, corresponding to the periods 1981-2010 and 1978-2011 respectively, were collected from specimens preserved at the scientific collections at Museo Acatushún (Ushuaia, Argentina), Centro Nacional Patagónico (Puerto Madryn, Argentina) and Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul (Imbé, Brazil). Very distinctly from these species, Magellanic penguins are migratory (Pütz et al. 2000, Pütz et al. 2007) and bone will integrate diet across regions (Silva et al. 2014). For this reason, the tissue selected for the analysis was feather vane from adult males and females found dead at breeding colonies located in northern and southern Patagonia. Penguins go through a simultaneous moult replacing all feathers at the end of the reproductive period (Frere et al. 1996), so the isotopic signature of the feather vane informs about the location where the feather was grown (Hobson 2005), this is, the breeding ground, which is the same every year (Schiavini et al. 2005). Since there are no penguin breeding colonies in Río de la Plata, no sampling could be conducted there. In their place, the claws of stranded juvenile penguins of both sexes found in southern Brazil were used. These samples were collected from specimens preserved at the scientific collection from Centro de Estudos Costeiros, Limnológicos e Marinhos (Imbé, Brazil). According to claw growth rates (Barquete et al. 2013) and time of collection, the central part of the claw is likely to be formed when the penguins were off Río de la Plata and the basal part when they were off southern Brazil, so we analysed both sections to assess penguin foraging in the two areas. No manipulation of living animals was involved in the collection of samples as fur seal, sea lions and penguins came from adults or juveniles found dead at the breeding colonies or migratory grounds.

All soft tissue samples were stored in a freezer at –20°C until analysis.

Stable isotope analysis

Once in the laboratory, samples were thawed, dried in an oven at 60°C for 36-48 hours, and ground to a fine powder with a mortar and pestle. Lipids were extracted from all samples with a chloroform/ methanol (2:1) solution (Bligh & Dyer 1959). This is because lipids are depleted in ^{13}C compared with other molecules (DeNiro & Epstein 1977) and lipid concentration in tissues may vary between species and also within species. This variation results in an artefactually variation of the overall tissue $\delta^{13}C$ value. Since bone, POM and macroalgae samples contain high concentrations of inorganic carbon, which may cause undesirable variability to $\delta^{13}C$ (Lorrain et al. 2003), they were divided in two aliquots. The first was decarbonised by soaking in 0.5 M hydrochloric acid (HCl) until no more CO_2 was released (Newsome et al. 2006). Since HCl treatment adversely affects $\delta^{15}N$ (Bunn et al.

1995), the other aliquot remained untreated and used for δ^{15}N analyses. Feathers and claws were washed in a chloroform-methanol (2:1) solution, rinsed thoroughly in distilled water to remove external contamination, and dried in an oven at 60°C after which they were cut in little pieces.

Approximately 10-15 mg of POM with filter, 0.8-1.0 mg of algae, 0.3 mg of mollusc mantle and fish muscle , 0.3-0.5 mg of crustaceans and 0.6-1.0 mg of dried bone were weighed into tin cups (3.3 × 5 mm), combusted at 900°C, and analysed in a continuous flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA Thermo Finnigan). Stable isotope abundance is expressed in standard δ notation relative to carbonate Pee Dee Belemnite and atmospheric nitrogen. International secondary isotope standards of known C^{13}/C^{12} and N^{15}/N^{14} ratios, as given by the IAEA (International Atomic Energy Agency), namely: polyethylene (IAEA CH7, δ^{13}C =−31.8‰), sucrose (IAEA CH6, δ^{13}C = –10.4 ‰), ammonium sulphate (IAEA N1; δ^{15}N=+0.4% and IAEA N2; δ^{15}N=+20.3%), potassium nitrate (USGS 34; δ^{15}N=21.7%), L-glutamic acid (USGS 40; δ^{15}N=24.6 %; δ^{13}C=22.6,2%), and caffeine (IAEA 600; δ^{15}N=1.0%; δ^{13}C=27.7%) were used for calibration of δ^{13}C and δ^{15}N. The precision for nitrogen was 0.2 ‰ and for carbon 0.3‰. Analyses were performed at the Science and Technology Centres (CCiT) of the University of Barcelona.

Data analysis

Species were grouped into functional guilds. POM and algae was grouped together, representing the primary producers. Limpets and mussels were joined into an herbivores guild. The three guilds of secondary and tertiary consumers (small pelagic fish and squids, medium pelagic fish and demersal fish and crustaceans) were created following the biological and ecological features of different species of fish, cephalopods and crustaceans (Cousseau & Perrotta 2000, Froese & Pauly 2011, WoRMS 2014). Finally sea lions, fur seals and Magellanic penguins were considered separately for species and sex.

Due to the differential discrimination that occurs between different tissues in animals, stable isotopes values of carbon and nitrogen of bone, claw, muscle, mantle and entire animal are not directly comparable (Hobson & Clark 1992, Todd et al. 2009). For this reason the stable isotope ratios of top predator tissues (bones, claws and feathers) were converted into those expected for muscle using different correction factors (Table 1).

Table 1. Fractionation factors used in the article.

	Tissue-to-diet			**Diet-to-muscle**		
	$\delta^{13}C$ (‰)	**$\delta^{15}N$(‰)**	**Source**	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**	**Source**
A.australis (bone)	3.6	5.1	Vales et al. 2013	1.2	2.2	Adapted from Hobson & Clark (1992) and Ben-David, (1996)
O. flavescens (bone)	3.6	4.2	L. Zenteno (unpublished data)			
S. magellanicus (claws)	1.7	2.5	Adapted from Hobson & Clark 1992	0.3	1.4	Gulls fed with perch (Hobson & Clark 1992)
S. magellanicus (feathers)	0.8	2.3	Adapted from Hobson & Clark 1992			

Once all the data were transformed into comparable units, we applied a Bayesian version of Layman's metrics (Layman et al. 2007) called SIBER (Jackson et al. 2011). The $\delta^{15}N$ range (NR), $\delta^{13}C$ range (CR) and the mean distance to centroid (CD) are measures of the total extent of spacing within the $\delta^{13}C$–$\delta^{15}N$ bi-plot space. NR is the representation of the vertical structure of the web, whereas CR gives us an idea of the trophic diversity at the base of the web and the mean distance to centroid provides a measure of the average degree of trophic diversity within a food web. Mean nearest neighbour distance (MNND) and the standard deviation of nearest neighbour distance (SDNND) reflect the relative position of species to each other within the niche space and can be used to estimate the extent of trophic redundancy (Layman et al. 2007). Finally standard ellipses, corrected for small sample size (SEA_C), were calculated for each species/functional guild described above as a measure of the mean core population isotopic niche/resource use area, instead of the total area of the convex polygon (TA). The standard ellipse is to bivariate data as standard deviation is to univariate data and so is expected to be insensitive to sample size, in contrast to the convex polygon, which generally increases with sample size even if the underlying population has remained the same (Jackson et al. 2011). Finally Bayesian estimate of the standard ellipse and its area (SEA_B) for each species/functional guild were calculated. SEA_B is a metric that gives the possibility of comparing uneven or small samples, of reducing the error in calculating the isotopic niche using the ellipses, and of preserving the uncertainty of the sampling process, propagating the error along the measures.

All codes for SIBER analyses are contained in the package SIAR (Parnell et al. 2010, Parnell & Jackson 2013).

RESULTS

The structure of the three food webs described above with standard ellipses corrected for small sample size (SEA$_{C}$) is shown in Fig 2. The nitrogen range (NR) of the whole food web, indicative of food chain length, was wider in Río de la Plata and northern Patagonia than in southern Patagonia (Fig 3) and the same was true for the demersal compartment. Such a latitudinal decrease was observed in all the compartments, but the NR of northern Patagonia was sometimes closer to that or Río de la Plata or to that of southern Patagonia, depending on the compartment considered (Table 2). Conversely, the horizontal breadth of the food web (CR) did not vary between the three areas, thus revealing a similar relative importance of phytoplankton and macroalgae to the carbon pool fuelling the food web along the coast.

Table 2. Probability values of Layman's metrics in the three geographical areas analyzed. Values are indicated as the mean and the 95% of credibility interval in parentheses. Metrics that present differences from area to area are indicated by superscripts. Groups sharing the same superscript number (1, 2) are not significantly different

NR (‰)	**Air-breathing top predators only**	**Without air-breathing top predators**	**Pelagic food web**	**Demersal food web**
Río de la Plata	9.64 (8.87-10.40)^{1}	8.16 (7.49-8.84)^{1}	6.51 (5.71-7.73)^{1}	8.14 (7.45-8.82)^{1}
Northern Patagonia	9.21 (7.81-10.60)^{1,2}	6.80 (5.71-7.99)^{1,2}	4.87 (3.51-6.27)^{1,2}	6.74 (5.35-8.09)^{1}
Southern Patagonia	6.85 (5.93-7.81)^{2}	4.82 (3.95-5.73)^{2}	4.57 (3.68-5.47)^{2}	3.82 (2.58-5.07)^{2}
CR (‰)				
Río de la Plata	4.65 (3.48-6.41)	3.36 (1.43-5.50)	2.85 (0.18-5.22)	1.79 (-0.12-3.92)
Northern Patagonia	2.83 (2.11-3.62)	2.16 (1.45-3.21)	0.72 (-0.06-1.70)	1.27 (0.01-2.41)
Southern Patagonia	3.09 (2.15-4.22)	3.33 (2.28-4.39)	0.75 (-0.09-1.88)	1.08 (-0.09-2.44)
CD (‰)				
Río de la Plata	3.19 (2.92-3.47)^{1}	2.91 (2.61-3.22)^{1}	3.61 (2.99-4.27)^{1}	4.21 (3.78-4.68)^{1}
Northern Patagonia	2.54 (2.20-2.89)^{2}	2.70 (2.36-3.07)^{1,2}	2.48 (1.83-3.14)^{1,2}	3.44 (2.71-4.16)^{1,2}
Southern Patagonia	2.24 (1.93-2.57)^{2}	2.24 (1.92-2.57)^{2}	2.34 (1.92-2.77)^{2}	2.02 (1.34-2.71)^{2}
MNND (‰)				
Río de la Plata	1.68 (1.28-2.11)	2.28 (1.87-2.69)	7.21 (5.98-8.54)^{1}	8.41 (7.55-9.35)^{1}
Northern Patagonia	1.70 (1.33-2.10)	1.40 (0.77-2.11)	4.96 (3.65-6.29)^{1,2}	6.88 (5.41-8.31)^{1,2}
Southern Patagonia	1.59 (1.23-1.98)	1.66 (0.91-2.37)	4.67 (3.83-5.54)^{2}	4.03 (2.68-5.42)^{2}
SNND (‰)				
Río de la Plata	1.99 (1.35-2.67)	1.42 (0.95-1.92)	-	-
Northern Patagonia	2.25 (1.52-2.93)	0.60 (0.08-1.12)	-	-
Southern Patagonia	1.51 (0.91-2.15)	0.90 (0.12-1.69)	-	-

The trophic diversity (CD) decreased clearly from Río de la Plata to southern Patagonia (Fig 3 and Table 2), thus revealing increased trophic overlap and redundancy at higher latitude, mainly because of the decrease in the NR above reported. Finally, the overall density of species packing (MNND) and the evenness of species packing (SDNND) did not statistically differ between areas when the whole food web was considered (Fig 3), although MNND decreased with latitude when the pelagic and demersal food compartments were analysed independently (Table 2).

Bayesian estimate of the standard ellipse and its area (SEA_B) for each species/functional guild was calculated to allow comparison between uneven samples. Dramatic differences in SEA_C between geographic areas (Fig. 2) were not reflected in differences in the SEA_B, since primary producers, herbivores, small pelagic fishes and squids, medium pelagic fishes, males of fur seals, females of sea lions and both sexes of penguins did not vary significantly between the three areas (Table 3). This is because SEA_B captures all the same properties as SEAc, but is unbiased with respect to sample size. However, the SEA_B of both demersal fish and males of sea lions was larger in southern Patagonia than anywhere else (Table 3). These results indicate that the width of the resources use areas of most guilds did not vary from area to area, with the exception of males of sea lions and demersal fishes which widened southward.

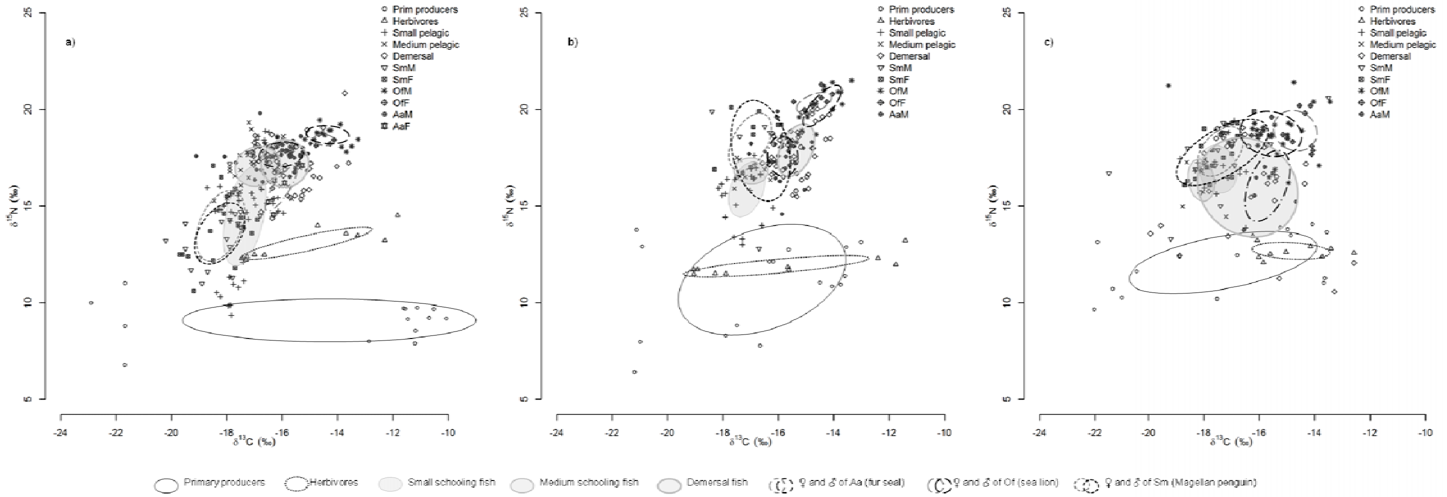

Fig. 2. Isotopic niches/resources use areas of the species/functional guilds described in the text calculated with standard ellipses area corrected for small sample size ($\mathrm{SEA_C}$). Stable isotope values of top predators' tissues were converted into those expected for muscle using different correction factors (see Table 1). a) Río de la Plata; b) northern Patagonia; c) southern Patagonia.

Table 3. Bayesian ellipses areas of functional guilds of the food web along the latitude. Functional groups/species that present differences from area to area are indicated by superscripts. Groups sharing the same superscript number (1, 2) are not significantly different. Aa=*Arctocephalus australis*; Of=*Otaria flavescens*; Sm=*Spheniscus magellanicus*.

	Primary producers	**Herbivores**	**Small pelagic fish and squids**	**Medium pelagic fish**	**Demersal fish and crustaceans**	**♂ Aa**	**♀ Of**	**♂ Of**	**♀ Sm**	**♂Sm**
Río de la Plata	16.7 (9.0-25.6)	4.3 (2.0-7.1)	5.6 (4.0-7.4)	2.7 (1.8-3.6)	3.3 (2.4-4.2) ^{1}	1.6 (1.2-2.1)	2.0 (0.5-4.0)	1.5 (0.8-2.3) ^{1}	4.5 (2.6-6.7)	4.1 (2.4-6.0)
Northern Patagonia	22.1 (12.7-33.0)	5.3 (2.5-8.9)	2.9 (1.8-4.0)	1.9 (0.7-3.4)	2.7 (1.9-3.5) ^{1}	1.9 (1.2-2.6)	1.5 (0.7-2.4)	2.0 (1.1-3.2) ^{1,2}	3.5 (1.7-5.8)	7.4 (3.0-13.1)
Southern Patagonia	13.3 (7.26-20.0)	2.5 (1.2-4.1)	2.8 (1.7-4.2)	2.1 (1.0-3.5)	13.5 (8.7-19.0) ^{2}	4.4 (1.6-8.2)	2.7 (1.3-4.6)	4.0 (2.7-5.5) ^{2}	3.1 (1.9-4.5)	6.7 (3.9-9.9)

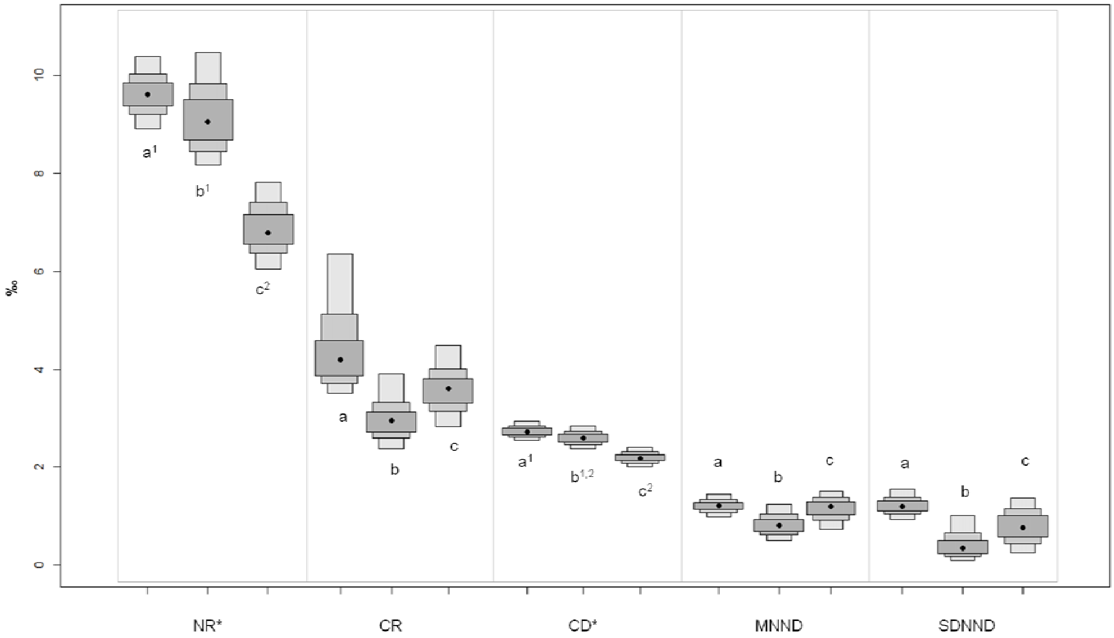

Fig. 3. Probability values of Layman's metrics of the marine food webs of the south-western Atlantic. Metrics that present differences from area to area are indicated by an asterisk. Geographical areas sharing the same superscript number (1,2) are not significantly different. a) Río de la Plata; b) northern Patagonia; c) southern Patagonia.

DISCUSSION

Examining food webs structure involves analysing and comparing the relative position of species, populations, or individuals within a niche space (Layman et al. 2007). Stable isotope analysis and Bayesian mixing models are emerging as one of the most important tools for examining the structure and dynamics of food webs. Here we characterised the topology of the South-west Atlantic Ocean food web along a latitudinal gradient using stable isotope analysis and SIBER on different tissues of approximately 40 taxa, from phytoplankton to marine mammals. The main shortcoming of this study is the fact that different tissues were analysed, integrating different spans of time. This is because of the difficulties of sampling muscle marine mammals and penguins, the tissue used for all the other animal species. We tried to overcome this problem was to use fractionation factors to transform the data of the consumers into diet data, although this method adds noise to the analysis and represents a source of error in the interpretation.

Another significant problem is that the samples used in the study of pinnipeds belong to a period of more than three decades. Our interpretations assume no change in the isotopic baseline of the region over that time, a hypothesis that remains untested as we are not aware of any study reconstructing the regional isotopic baseline during that period, although the regional isotopic baseline has certainly during the late Holocene (Saporiti et al. in press).

Bayesian Layman's measures calculated using SIBER indicates that the food web of southern Patagonia is the shortest and the most redundant one, whereas the food web of Río de la Plata and adjoining areas is the longest and the most diverse (Figs.2, 3 and Table 2). A clear latitudinal gradient is observed in the range of nitrogen, which is wider in the Río de la Plata and adjoining area and narrower in southern Patagonia. The nitrogen range of northern Patagonia does not differ from that of Río de la Plata if we consider the whole food web and the demersal compartment, while it is lower in all other cases (Table 2).

It is worth noting that there is an inverse relationship between the length of the food web and the seasonal variability in the sea surface temperature in the South-western Atlantic (Rivas 2010), a pattern opposite to that reported by Jennings & Warr (2003) for the North Sea, where the regions with the smallest annual variation of temperature had the longest food webs. Nevertheless, the region here considered spans over a much larger area. The relationship between food web length and primary productivity is also unclear, because the lowest productivity is recorded off northern Patagonia (Piola & Falabella 2009), but the length of the food web there is intermediate between those of Río de la Plata and southern Patagonia.

The trophic diversity, measured by the mean distance to centroid in the isotopic space (CD), also decreases southward, both considering the entire food web and each single compartment (Table 2). This reveals increased trophic overlap and redundancy at higher latitude, a result that agrees with previous research on the neighbouring Scotia Sea, where trophic overlap and redundancy is even higher, although species identity changes completely (Stowasser et al. 2012). It is worth to note that such shortening of the food web and increased redundancy was true also for the three species of air-breathing predators considered, although they differed dramatically in body size (Bonner 1981, Vaz-Ferreira 1981, Lima & Páez 1995, Yorio et al. 2001) and were expected to differ in they access to resources.

As some authors pointed out, the change in the trophic level of top predators or intermediate consumers can change the food chain length (Post & Takimoto 2007) and in this case it seems that top predators change their diet along the latitude, according with the biogeographic changes in the prey assemblages (Balech & Ehrlich 2008). For example, deep-bodied sciaenids represent a common prey of sea lions in Río de la Plata (Riet-Sapriza et al. 2013), but they do not exist in most of Patagonia (Cousseau & Perrotta 2000). Likewise small, streamlined anchovies (*Engraulis anchoita*) are an important prey for penguins and fur seals (Scolaro et al. 1999, Naya et al. 2002), but they only abound on the shelf off Río de la Plata and northern Patagonia. Conversely, the much scarcer and coastal Patagonian sprat (*Sprattus fuegensis*) replaces them in southern Patagonia (Cousseau & Perrotta 2000).

Human impact could be another important factor to take into account in the analysis of the South-western Atlantic Ocean food web. All the populations of the South American sea lion in the region were intensely exploited during the 20th century but the species survived and numbers are currently increasing in most areas, except Uruguay (Godoy 1963, Dans et al. 2004, Schiavini et al. 2004, Páez 2006). When demographic (Reyes et al. 1999, Dans et al. 2004, Schiavini et al. 2004, Páez 2006) and dietary information (Koen Alonso et al. 2000, Naya et al. 2000, Szteren et al. 2004, Oliveira et al. 2008, Drago et al. 2009, Romero et al. 2011, Riet-Sapriza et al. 2013) are combined, there is strong evidence indicating that average prey size and sea lion population size are inversely related, thus indicating a potential shortening of the web length when and where sea lions are abundant. Recent reconstructions of the structure of the marine food webs of northern and southern Patagonia during the second half of the Holocene support that interpretation, as ancient food webs were shorter than modern ones (Saporiti et al. in press). Nevertheless, the same study shows that during the late Holocene the food webs from southern Patagonia were also shorter than those from central-northern Patagonia (Saporiti et al. in press), indicating that the latitudinal gradient here reported has a natural cause.

In conclusion, the length of the food web decreases and the redundancy increases southward over the continental shelf of the South-western Atlantic. That pattern may be caused by the lower species diversity at higher latitudes, even though all the coastal ecosystems in the region have been profoundly modified by human exploitation and the structure of the modern food webs here reported differ significantly from that of the original, pristine ecosystems (Saporiti et al. in press).

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3.3 Redes tróficas más largas y menos solapadas en los ecosistemas marinos alterados por el hombre: confirmaciones del pasado.

RESUMEN. La explotación humana de los recursos marinos se caracteriza por la eliminación preferencial de las especies de mayor tamaño. Aunque se espera que esto modifique la estructura de las redes tróficas, no se conocen bien las posibles consecuencias de tal alteración. En el presente trabajo utilizamos el análisis de isótopos estables y el programa SIBER para evaluar los cambios en la estructura de las redes tróficas marinas costeras en el Atlántico sudoccidental durante la segunda mitad del Holoceno, como resultado de la explotación secuencial de los recursos marinos por los cazadores- recolectores aborígenes, los cazadores de focas y los pescadores modernos. Se recogieron muestras tanto en concheros aborígenes como en museos. Las valvas de moluscos herbívoros del intermareal rocoso, tanto arqueológicas como actuales, fueron empleadas para reconstruir los cambios en la línea de base del paisaje isotópico, mientras que se utilizaron los huesos modernos y arqueológicos de los lobos marinos *Otaria flavescens* y *Arctocephalus australis* y pingüino de Magallanes *Spheniscus magellanicus* para analizar los cambios en la estructura de la comunidad de los principales depredadores del ecosistema. En contra de lo esperado, las redes tróficas antiguas son más cortas, más redundante y presentan mayor solapamiento que las actuales, tanto en el centro-norte de la Patagonia como en el sur. Estos sorprendentes resultados pueden explicarse por la enorme repercusión de la caza sobre las poblaciones de los pinnípedos, más que debido a la pesca industrial. Al final de la época de explotación peletera, las poblaciones de pinnípedos se hallaban con toda seguridad muy por debajo de la capacidad de carga del ecosistema, lo que liberó a los supervivientes de la competencia intraespecífica y les permitió incrementar el consumo de presas de mayor talla y de mayor nivel trófico, lo que a su vez condujo a las cadenas tróficas más largas y menos solapadas que observamos en la actualidad.

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Longer and less overlapping food webs in anthropogenically disturbed marine ecosystems: confirmations from the past.

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Abstract

The human exploitation of marine resources is characterised by the preferential removal of the largest species. Although this is expected to modify the structure of food webs, we have a relatively poor understanding of the potential consequences of such alteration. Here, we take advantage of a collection of ancient consumer tissues, using stable isotope analysis and SIBER to assess changes in the structure of coastal marine food webs in the South-western Atlantic through the second half of the Holocene as a result of the sequential exploitation of marine resources by hunter-gatherers, western sealers and modern fishermen. Samples were collected from shell middens and museums. Shells of both modern and archaeological intertidal herbivorous molluscs were used to reconstruct changes in the stable isotopic baseline, while modern and archaeological bones of the South American sea lion *Otaria flavescens*, South American fur seal *Arctocephalus australis* and Magellanic penguin *Spheniscus magellanicus* were used to analyse changes in the structure of the community of top predators. We found that ancient food webs were shorter, more redundant and more overlapping than current ones, both in northern-central Patagonia and southern Patagonia. These surprising results may be best explained by the huge impact of western sealing on pinnipeds during the fur trade period, rather than the impact of fishing on fish populations. As a consequence, the populations of pinnipeds at the end of the sealing period were likely well below the ecosystem's carrying capacity, which resulted in a release of intraspecific competition and a shift towards larger and higher trophic level prey. This in turn led to longer and less overlapping food webs.

Introduction

Human activities have altered most of the coastal marine ecosystems of the world over many centuries, causing reductions in population sizes, shifts in geographic ranges, and losses of diversity, biomass, and ecosystem functioning [1,2,3,4,5,6]. Both aboriginal and industrial exploitation of marine resources are characterised by the preferential removal of the largest species [3,7,8,9,10], a process thought to shorten size-structured marine food webs [4,11,12]. However, so far, megafaunal exploitation has generally resulted in population collapse and top predator rarity, rather than in true extinctions [13,14,15]. The difference between rarity and extinction is relevant, because the extinct species no longer belong to the local food web, whereas the scarce ones remain, although it has been argued that these can be considered functionally extinct [10,16].

To understand the actual relevance of both extinction and scarcity of formerly abundant megafauna species, we need to assess their role in the pristine ecosystems in which they have evolved. This can be achieved by studying marine protected areas (e.g. [17]) but the influence of the human disturbed matrix in which they are embedded is difficult to control. Furthermore, marine reserves are often too small to support viable populations of large top predators or encompass entire foraging ranges [18] and have not been protected for long enough to guarantee full recovery [19]. A second approach is through ecosystem modelling (e.g. [20,21]), but this can be hampered by the limited perspective of contemporary data [3], the difficulties of model parameterisation [22] and unknown changes in the diet and foraging behaviour of predators through time (e.g. [23,24]). A third approach consists of using ancient biological material, such as bones and shells, to reconstruct trophic relationships in a time span prior to the anthropogenic alteration of marine ecosystems [3].

The mechanisms and underlying causes of a number of cases of population collapses or extinctions have been clarified by analysing the fossil and zooarchaeological records (e.g. [25]). However, this method brings little information about past diets, trophic levels and food-web structure. The development of stable isotope analyses and quantitative methods for analysing the food-web topology [26,27,28] allows the reconstruction of past trophic relationships based on ancient biological material [29], since the stable isotope ratios in consumer tissues represent those of their diet in a predictable manner [30,31]. The marine ecosystems off Argentina have suffered major anthropogenic changes during the past two centuries. Firstly, European sealers locally extirpated the South American fur seal (*Arctocephalus australis*) during the 19th century and were at least in part responsible for a decline in South American sea lion populations (*Otaria flavescens*) during the first half of the 20th century [32,33,34,35,36]. When exploitation ceased most populations of this species had been reduced to <10% of the pre-exploitation numbers and their recovery did not begin until the early 1990s in Argentina, after several decades of stagnation [34,37,38]. As a result, the current populations of both species are still well below pre-exploitation numbers [34,39,40,41,42]. Furthermore, fisheries targeting large demersal fishes were established in Río de la Plata and northern Patagonia in the 1970s, causing a population decline in several large benthic predatory fish species [43,44,45,46]. Finally, the Argentine population of the Magellanic penguin (*Spheniscus magellanicus*) increased during the 20th century, both in number of individuals and geographic range [47], perhaps due to the decline of competitors and predators because of the exploitation of pinnipeds [48].

However, the European sealers and fishermen were not the first humans to exploit the marine resources off Argentina. Aboriginal hunter-gatherers began to exploit the local populations of fur seals, sea lions and other marine species during the middle Holocene [49,50,51,52,53,54]. Even though the general opinion is that the impact on the populations of pinnipeds was minimal [49,55]. More recently, Zangrando and colleagues [56] argued that human pressures on fur seals in the Beagle Channel during the late Holocene might have resulted in demographic and ecological changes, based on evidence from stable isotope analyses and the decreasing age and size of hunted individuals. However, these results remain inconclusive because potential variations of the stable isotope baseline through time were not accounted for [57]. The zooarchaeological record preserved in the hunter-gatherers middens offers an excellent opportunity to reconstruct the structure of ancient marine food webs (while accounting for potential changes in stable isotopic baselines) in the South-western Atlantic and compare it with that of modern food webs.

In this paper, we use the stable isotopes of carbon and nitrogen from the shells of mollusc shells to set the stable isotopic baseline and from bones of marine mammals and penguins to reconstruct the changes in the topology of coastal food webs from central-northern Patagonia and southern Patagonia through the second half of the Holocene. Through this, we aim to assess whether the structure of the food web has changed as a consequence of human exploitation during the studied period.

Material and Methods

Ethics Statement

Permits to collect modern samples (Table 1 and S1) were issued by the “Dirección de Fauna y Flora Silvestre”, and the “Dirección de Areas Protegidas”, both from the Province of Chubut. The zooarchaeological samples come from previous fieldwork carried out by Julieta Gómez Otero, Florencia Borrella, Martín Serrán and Lorena Peralta in Golfo San Matías and Península Valdés (central-northern Patagonia), Eduardo Moreno in Santa Cruz (southern

Patagonia) and Ernesto Piana, Luis Orquera, Angie Tivoli and Francisco Zangrando in the Beagle Channel (Tierra del Fuego). All the samples used for this study come from stranded animals, died naturally (except for mussels and limpets), or from archaeological remains (shell middens). All specimen numbers and repository information are shown in Tables 2 and 3, and in Supporting Information (Tables S2 and S3). Due to the low proportion of organic matter present in the archaeological shells, the entire valve was used to undertake isotopic analyses. However, samples of the same ages are available to allow the work to be reproducible.

Study site and sample collection

Bones and shells are commonly used in paleontological and archaeological isotopic studies because they contain organic remains and they are often abundant in archaeological deposits as well as in historic museum collections [24,58,59,60]. Furthermore, the proteins they contain integrate the diet over several years [61,62,63]. Accordingly, we determined the ratios of stable isotopes of carbon and nitrogen in the organic matrix from the shell of modern and archaeological intertidal mussels (*Aulacomya atra atra* and *Mytilus edulis)* and limpets (*Nacella magellanica),* and in modern and archaeological bone tissue from South American sea lions, South American fur seals and Magellanic penguins. Mussels and limpets were used to characterise the trophic level 1 (herbivores), which allows us to interpret whether shifts in the predators are more likely linked to prey switching or a change in the isotopic baseline. Both modern and archaeological samples were collected in two areas of the South-east coast of South America (Figure 1): central-northern Patagonia (Río Negro and Chubut provinces) and southern Patagonia (Santa Cruz and Tierra del Fuego provinces). These two areas differ in oceanographic, biogeographic and anthropogenic features, with central-northern Patagonia being less productive and more affected by anthropogenic impacts (industrial fishing) than southern Patagonia [64,65].

Nasal turbinates from modern marine mammal were sampled from specimens at the scientific collections of the *Centro Nacional Patagonico* (Puerto Madryn, Argentina) and *Museo Acatushún* (Ushuaia, Argentina) and analysed. Modern penguin bones from adult penguins found dead at breeding colonies distributed along central-northern Patagonia and southern Patagonia were also analysed. Modern mollusc samples were collected from

December 2009 to February 2010 at three sites along the coastline of Argentina: two in the Río Negro province (central-northern Patagonia) and one in the Tierra del Fuego province (southern Patagonia) (Figure 1, Table 1).

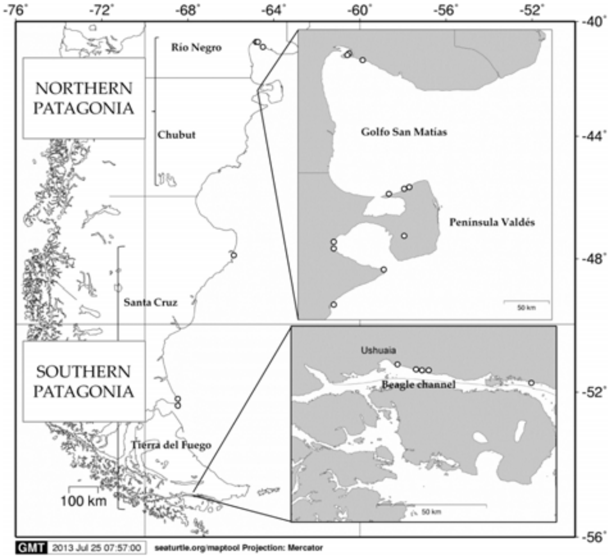

Figure 1. Study areas (central-northern Patagonia and southern Patagonia) and sampling approximate zones. Empty dots represent archaeological sites.

Sex is often difficult to assess when only fragmented individuals are recovered from the zooarchaelogical record, despite being a major determiner in the foraging habits of fur seals, sea lions and penguins [47,66,67,68,69]. Accordingly, a sensitivity analysis was run using modern samples from the Río de la Plata region (between southern Brazil and Buenos Aires province) to assess the sensitivity of food web reconstruction using SIBER (see Data analysis). Blue mussels (*Mytilus edulis*) were collected in the Río de la Plata region to represent ribbed mussel (*Aulacomya atra atra*), and the limpet *Siphonaria lessoni* to represent *Nacella magellanica* (Table 1).

Zooarchaeological bones (generally humeri, mandibles, coxal bones, ribs and femurs) and shell samples recovered from shell middens come from previous fieldwork carried out by Julieta Gómez Otero, Florencia Borrella, Martín Serrán and Lorena Peralta in Golfo de San Matías and Península Valdés (central-northern Patagonia), Eduardo Moreno in Santa Cruz (southern Patagonia) and Ernesto Piana, Luis Orquera, Angie Tivoli and Francisco Zangrando in the Beagle Channel (Tierra del Fuego) (Figure 1, Tables 2 and 3). The samples were dated in different laboratories and using different methods; in particular, in central-northern Patagonia, almost all dated samples were marine shells instead of charcoal. As CO_2 diffuses slowly from the atmosphere to the ocean, changes in the abundance of ^{14}C in sea water are delayed in comparison to changes in the atmosphere [70]. Such a lag is known as the reservoir effect and is the responsible for the difference between the radiocarbonic age of coal and shells from the same archaeological level. Reservoir effect data for the central-northern Patagonia region are emerging only recently [71], and they suggest a relatively small difference between marine and terrestrial ages on the basis of a few samples. Although the use of a correction for reservoir effect would be preferable [52], we refer to the conventional, uncalibrated radiocarbon dates for all the sites. This shortcoming should not be of great importance in these types of studies for which precise dates are not required, but large time intervals should suffice.

All samples were stored in a freezer at –20°C until analysis.

Table 1. Samples used to reconstruct the modern food webs

Species	**Area**	**N**
Herbivores		
Mytilus edulis	Río de la Plata	5
Aulacomya atra atra	Northern Patagonia	7
Aulacomya atra atra	Southern Patagonia	5
Siphonaria lessoni	Río de la Plata	5
Nacella magellanica	Northern Patagonia	5
Nacella magellanica	Southern Patagonia	5
Top Predators		
Arctocephalus australis	Río de la Plata	60
Arctocephalus australis	Northern Patagonia	29
Arctocephalus australis	Southern Patagonia	7
Otaria flavescens	Río de la Plata	19
Otaria flavescens	Northern Patagonia	36
Otaria flavescens	Southern Patagonia	41
Spheniscus magellanicus	Río de la Plata	20
Spheniscus magellanicus	Northern Patagonia	20
Spheniscus magellanicus	Southern Patagonia	40

Stable isotope analysis

Once in the laboratory, bone and shell samples were thawed and dried in an oven at 50°C, and ground to a fine powder with a mortar and pestle. Shell samples were pre-polished with sandpaper and with a diamond wheel drill to remove impurities. They were subsequently rinsed with distilled water and lipids were extracted in all samples with a chloroform/ methanol (2:1) solution [72].

Since both bone and shell contain high concentrations of inorganic carbon, which may bias δ13C values [73], they were divided into two aliquots. The first was decarbonised by soaking in 0.5 N (bone) or 1 N (shell) hydrochloric acid (HCl) until no more CO_2 was released [74]. Since the HCl treatment adversely affects $\delta^{15}N$ values [75], the second aliquot was not treated with HCl and used for $\delta^{15}N$ determination.

Dried powdered samples and secondary reference standards were combusted at 900°C, and analysed in a continuous flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA Thermo Finnigan). For the shell samples, a CO_2 absorbent for elemental analyses (CaO/NaOH) was employed to avoid the saturation of the spectrometer during the analysis of the non-acid washed samples, constituted by 90% $CaCO_3$. Stable isotope abundance is expressed in standard δ notation relative to carbonate Pee Dee Belemnite and atmospheric nitrogen. Analyses were performed at the Science and Technology Centre (CCiT) of the University of Barcelona.

Data analysis

Limpets and mussels were analysed together under the "herbivore" category, representing, in the same functional group, both benthic (limpets) and pelagic (mussels) compartments [76]. Each top predator species was analysed separately. Archaeological data were grouped into broad time intervals to enable quantitative reconstruction of food webs. Consequently in central-northern Patagonia all the archaeological samples were pooled together under a single time interval, from 5200±70 yr ^{14}C BP until 380±60 yr ^{14}C BP. This period is entitled the "Pre-contact period" since it predates the arrival of European settlers, opposed to the term post-contact used in archaeology [51,53,77]. Ancient samples from southern Patagonia were split in two different periods. The early aboriginal period (EAP) ranging from 6000 to 1100 years ago was characterised by very high oceanic primary productivity [78] and the prevalence of pinnipeds in the economy of hunter-gatherers [50].

Table 2. Archaeological samples from northern-central Patagonia.*Lobos is a paleontological site, since here sea lions died naturally and massively due to a land slide.

Species	N	Laboratory ID	Archaeological site	Age (^{14}C yr BP)	Reference	Repository information
Herbivores						
Aulacomya atra atra	3	A7-cC1, C4, C5	Los Abanicos 1	380±60	[105]	CENPAT, Puerto Madryn (Argentina)
Aulacomya atra atra	2	A8-cC2, C4	Las Ollas conchero 1	610±60 640±60	[52]	CENPAT, Puerto Madryn (Argentina)
Aulacomya atra atra	5	A5-cC1, C2, C3, C4, C5	Playas Las Lisas 2-perfil 1	2140±50	[52]	CENPAT, Puerto Madryn (Argentina)
Aulacomya atra atra	2	A11-cC3, C4	Cracker 8-Nivel 3	5200±70	[52]	CENPAT, Puerto Madryn (Argentina)
Nacella magellanica	5	A7-cL1, L2, L3 L4, L5.	Los Abanicos 1	380±60	[105]	CENPAT, Puerto Madryn (Argentina)
Nacella magellanica	5	A10-cL1, L2, L3, L4, L5.	Ecocentro Fogón 3	850±150	[52]	CENPAT, Puerto Madryn (Argentina)
Nacella magellanica	4	A4- cL1, L3, L4	Playa Las Lisas 2-conchero 2	2600±60	[52]	CENPAT, Puerto Madryn (Argentina)
Nacella magellanica	2	A11-cL1, L2	Cracker 8-Nivel 3	5200±70	[52]	CENPAT, Puerto Madryn (Argentina)
Predators						
Arctocephalus australis	3	F1 18, F1 19, FM1 11	Playa Unión-Barranca Norte	1040±70	Peralta, 2001 quoted in [52]	CENPAT, Puerto Madryn (Argentina)
Arctocephalus australis	2	90, 91	Bajada de los pescadores	2197±38	[51]	INCUAPA-UNCPBA, Buenos Aires F.D. (Argentina)
Otaria flavescens	2	36, 82	Los Abanicos 1	380±60	[105]	CENPAT, Puerto Madryn (Argentina)
Otaria flavescens	9	F1 17, FM1 13-17, FM1 19-21	Playa Unión-Barranca Norte	1040±70	Peralta, 2001 quoted in [52]	CENPAT, Puerto Madryn (Argentina)
Otaria flavescens	10	i1(61), i3(43), i4(44), i5(54), i15(C1), i18(89), i23, i24, M11, M13	Lobos*	1290±100	[106]	CENPAT, Puerto Madryn (Argentina)
Otaria flavescens	2	FSM - SRH Mont II OF costilla, OBS 13	Faro San Matías- Sondeo 6	1380±80	[51]	INCUAPA-UNCPBA, Buenos Aires F.D. (Argentina)

Otaria flavescens	1	OBS 137	Bajada de los pescadores	2197±38	[51]	INCUAPA-UNCPBA, Buenos Aires F.D. (Argentina)
Otaria flavescens	2	FSM - SRH Mont I OF cost px med, OBS 4	Faro San Matías, Sondeo 2	2910±90	[51]	INCUAPA-UNCPBA, Buenos Aires F.D. (Argentina)
Spheniscus magellanicus	4	7,72, 80, 82	Bajada de los pescadores	2197±38	[51]	INCUAPA-UNCPBA, Buenos Aires F.D. (Argentina)
Spheniscus magellanicus	3	OBS 26, FSM-S2N2 Obs 21, FSM-S2N3 Obs26-tibia derecha.	Faro San Matías, Sondeo 2	2910±90	[51]	INCUAPA-UNCPBA, Buenos Aires F.D. (Argentina)

Table 3. Archaeological samples from southern Patagonia.

Species	**N**	**Laboratory ID**	**Archaeological site**	**Age (^{14}C yr BP)**	**Reference**	**Repository information**
Herbivores						
Mytilus edulis	5	A17-cM1, M2, M3, M4, M5	Tunel VII	100±45	Piana et al., 1992 quoted in [107]	CENPAT, Puerto Madryn (Argentina)
Mytilus edulis	3	A15-cM1, M2, M3	Shamakush X, Capa E	500±100	Orquera and Piana, 1999 quoted in [50]	CENPAT, Puerto Madryn (Argentina)
Mytilus edulis	5	A19-cM1, M2, M3, M4, M5	Imiwaia I (M/K)	5940 ± 50 5750 ± 170 5840 ± 45 5710 ± 50	Piana et al., 1992 quoted in [107]	CENPAT, Puerto Madryn (Argentina)
Nacella magellanica	5	A17-cL1, L2, L3, L4, L5	Tunel VII	100±45	Piana et al., 1992 quoted in [107]	CENPAT, Puerto Madryn (Argentina)
Nacella magellanica	2	A15-cL2, L4	Shamakush X, Capa E	500±100	Orquera and Piana, 1999 quoted in [50]	CENPAT, Puerto Madryn (Argentina)
Nacella magellanica	5	A19-cL1, L2, L3, L4, L5	Imiwaia I (M/K)	5940 ± 50 5750 ± 170 5840 ± 45 5710 ± 50	Piana et al., 1992 quoted in [107]	CENPAT, Puerto Madryn (Argentina)
Top predators						

Arctocephalus australis	13	44331, 155288, 150329, 152253, 152439, 151607, 154656, 151575, 151912, 154284, 153887, 55456, 155447	Tunel VII, layer B	100±45	Piana et al., 1992 quoted in [107]	CADIC, Ushuaia (Argentina)
Arctocephalus australis	1	CV6 4/-45-50cm	CV6 4/-45-50 cm	1190±60	[108]	INCUAPA-UNCPBA / IMHICIHU, Buenos Aires F. D. (Argentina)
Arctocephalus australis	1	CdN2-0072	Cueva del Negro-cuadrícula 1 Nivel 2	1730±80	[109]	CENPAT, Puerto Madryn (Argentina)
Arctocephalus australis	3	37295, 37456, 37340	Tunel I, Capa X/α	2660±100 2690±80 3030±90	[110]	CADIC, Ushuaia (Argentina)
Arctocephalus australis	10	194047, 43247, 174498, 193261, 67319, 66397, 202083, 186854, 65989, 202401	Tunel I, Capa D	5000-4300	[110]	CADIC, Ushuaia (Argentina)
Arctocephalus australis	20	217933, 215241, 223614, 215940/215933, 53580, 68445, 64460, 213370, 215074, 58630, 190846, 63330, 213732, 52463, 226119, 69639, 189603, 216713, 212616/212653, 224151	Tunel I, Capa D/E	6400-5900	[110]	CADIC, Ushuaia (Argentina)
Otaria flavescens	2	43418, 154286	Tunel VII	100±45	Piana et al., 1992 quoted in [107]	CADIC, Ushuaia (Argentina)
Otaria flavescens	10	OF 2a, OF 2b, OF 3, OF 9, OF 12, OF 14, OF 15, OF 5, OF 7, OF 10	Kaiyawoteha III, Capa K	580±45	[111]	CADIC, Ushuaia (Argentina)
Otaria flavescens	1	CV6 4/-60-65cm	CV6 4/-60-65 cm	1190±60	[108]	INCUAPA-UNCPBA / IMHICIHU, Buenos Aires F. D. (Argentina)

Otaria flavescens	5	CV20 OF1, CV20 OF3, CV20 OF4, CV20 OF6, CV20 OF7	CV20	1256±50	[112]	CONICET, Río Gallegos/CONICET-IMHICIHU, Buenos Aires (Argentina)
Otaria flavescens	9	30459, 33459, 33551, 33571, 33717, 34177, 34544, 34751, 33458	Tunel I, Capa D	5000-4300	[110]	CADIC, Ushuaia (Argentina)
Spheniscus magellanus	2	10030, 10100	Shamakush X, Capa E	500±100	Orquera and Piana, 1999 quoted in [50]	CADIC, Ushuaia (Argentina)
Spheniscus magellanus	3	pingüino 4a, pingüino 4b, pingüino 6,	Kaiyawoteha III, Capa K	580±45	[111]	CADIC, Ushuaia (Argentina)
Spheniscus magellanus	4	12433, 12268, 10116, 10115	Mischiuen I, Capa C sup	890±90	Piana et al., 2004 quoted in [113]	CADIC, Ushuaia (Argentina)
Spheniscus magellanus	1	9255	Mischiuen I, Capa C inf	1060±85	Piana et al., 2004 quoted in [113]	CADIC, Ushuaia (Argentina)
Spheniscus magellanus	2	19098, 19264	Shamakush I, Capa D	1220 ± 110 940 ± 110	[114]	CADIC, Ushuaia (Argentina)
Spheniscus magellanus	1	10122	Shamakush I, Capa C	1000 (ca.)	[114]	CADIC, Ushuaia (Argentina)
Spheniscus magellanus	4	3761, 4179, 3522, 3641	Mischiuen I, Capa F	4890±210 4430±180	Piana et al., 2004 quoted in [113]	CADIC, Ushuaia (Argentina)
Spheniscus magellanus	3	1925, 26006, 27597	Imiwaia I (M/K)	5940 ± 50 5750 ± 170 5840 ± 45	Piana et al., 1992 quoted in [107]	CADIC, Ushuaia (Argentina)

Conversely, the late aboriginal period (LAP), ranging from 1000 to 100 years ago, was characterised by a much lower oceanic primary productivity [78] and a lower reliance of the hunter-gatherers economy on pinnipeds. Modern data were analysed separately, so five different food webs were analysed: two in central-northern Patagonia (one archaeological and one modern) and three in southern Patagonia (two archaeological and one modern).

SIBER (Stable Isotope Bayesian Ellipses in R) [79] was used to compute Bayesian Layman's metrics that summarised food web structures in each region and epoch. Only five of the six measures proposed by Layman et al. (2007) [27] were calculated. The $\delta^{15}N$, $\delta^{13}C$ ranges (NR and CR, respectively) and the mean distance to centroid (CD) are measures of the total extent of spacing within the $\delta^{13}C$–$\delta^{15}N$ bi-plot space and gives a measure of community niche width that is not particularly sensitive to sample size. Nitrogen range (NR) is the representation of the vertical structure of the web; carbon range (CR) gives us an idea of the trophic diversity at the base of the web, while the mean distance to centroid provides a measure of the average degree of trophic diversity within a food web [27]. Mean nearest neighbour distance (MNND) and the standard deviation of nearest neighbour distance (SDNND) reflect the relative position of species to each other within the niche space and can be used to estimate the extent of trophic redundancy.

Furthermore, the overlap (‰) among top predators' standard ellipses corrected for small sample size (SEA_C) was calculated in order to analyse resource partitioning among them over time. Comparison of metrics was based on 95% credibility intervals. All codes for SIBER analyses are contained in the package SIAR [80,81]. Finally, SIBER Bayesian ellipse areas (SEA_B) were calculated for the three top predators to measure their isotopic niche width. This approach is similar to a bootstrap, assigning measures of uncertainty, based on Markov-Chain Monte Carlo (MCMC) simulation to construct parameters of ellipses.

In addition, a simulation was performed to test the sensitivity of SIBER metrics to biases in the sex ratio of the top predators. A similar data set from Río de la Plata was used for this analysis (see Supporting Information, Table S1). Three different scenarios were simulated: one where only females were included, one where only males were included and a third situation with a balanced sex ratio. These three simulated food webs should represent the three hypothetical and extreme situations emerging from the analysis of the zooarchaeological record, where the sex of the top predators was usually unknown.

Results

The structures of the five food webs analysed are shown in Figure 2. The $\delta^{15}N$ values of herbivores decreased from past to present (Table 4) both in central-northern Patagonia (Wilcoxon-Mann-Whitney test: W=3, $p<0.001$) and in southern Patagonia (ANOVA: $F_{2,32}=24.7$, $p<0.01$). Likewise the $\delta^{13}C$ values of ancient herbivores from southern Patagonia differed from the modern ones (ANOVA: $F_{2,32}=5.42$, $p<0.01$) but changes were not statistically significant in central-northern Patagonia (t-test: t=-0.09, df=16.777, p=0.93). These results demonstrate that the isotopic baseline may change dramatically throughout time and allow us to properly interpret the structure of the ancient food webs.

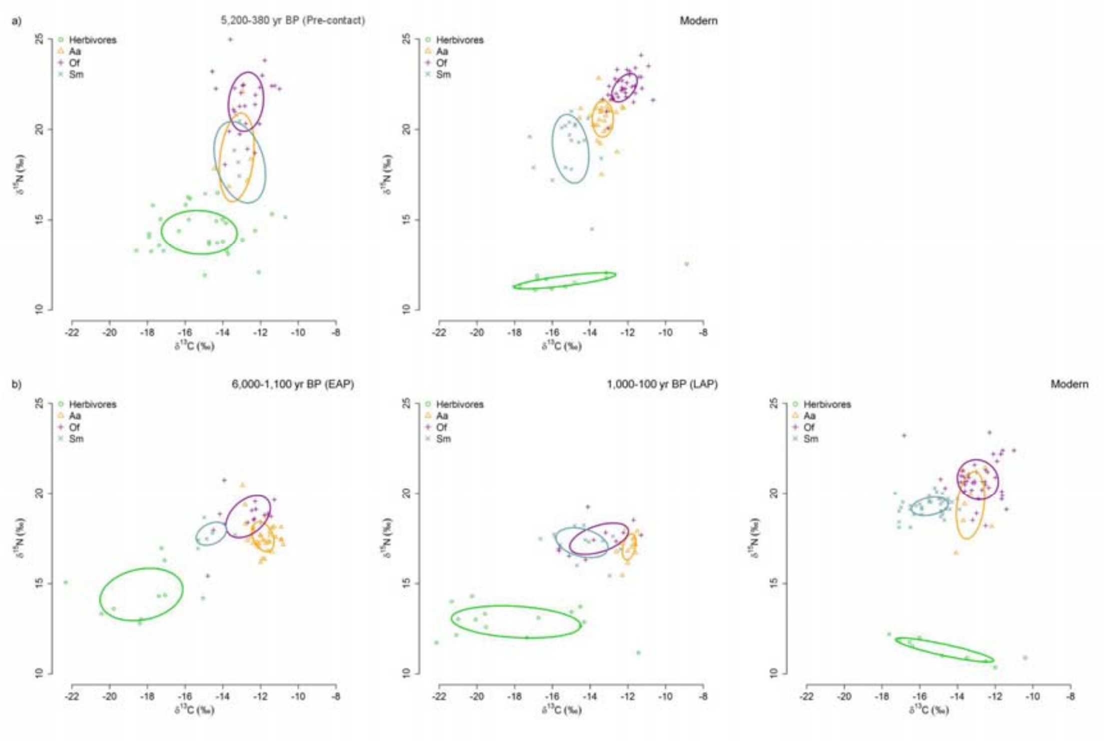

Figure 2. Isotopic niches/resource use areas of the species/functional groups described in the text and calculated with the standard ellipse areas corrected for small sample size (SEA_C) over time in the two geographical areas. a) Central-northern Patagonia and b) Southern Patagonia. Herbivores=mussels and limpets; Aa=South American fur seals; Of=South American sea lions; Sm=Magellanic penguins.

Table 4. Mean and standard deviation of nitrogen and carbon stable-isotope in central-northern and southern Patagonia.

Central-northern Patagonia				**$\delta^{15}N$ (‰)**		**$\delta^{13}C$ (‰)**	
Group	**Tissue**	**N**		**Mean (±SD)**		**Mean (±SD)**	
		Pre-contact	**Modern**	**Pre-contact**	**Modern**	**Pre-contact**	**Modern**
Herbivores	Shell	28	12	14.30 (±1.19)	11.61 (±0.42)	-15.25 (±1.97)	-15.32 (±2.57)
Top Predators							
Arctocephalus australis	Bone	5	29	18.45 (±2.12)	20.59 (±0.99)	-13.26 (±0.80)	-13.32 (±0.54)
Otaria flavescens	Bone	26	36	21.52 (±1.60)	22.30 (±0.78)	-12.77 (±0.91)	-12.17 (±0.66)
Spheniscus magellanicus	Bone	7	20	18.19 (±2.05)	18.93 (±1.85)	-13.10 (±1.25)	-15.03 (±0.94)

Southern Patagonia					**$\delta^{15}N$ (‰)**			**$\delta^{13}C$ (‰)**		
Group	**Tissue**	**N**			**Mean (±SD)**			**Mean (±SD)**		
		EAP	**LAP**	**Modern**	**EAP**	**LAP**	**Modern**	**EAP**	**LAP**	**Modern**
Herbivores	Shell	10	15	10	14.39 (±1.36)	12.87 (±0.86)	11.32 (±0.62)	-18.32 (±2.07)	-17.93 (±3.31)	-14.69 (±2.46)
Top Predators										
Arctocephalus australis	Bone	35	13	7	17.58 (±0.81)	17.02 (±0.69)	19.34 (±1.72)	-11.86 (±0.58)	-11.92 (±0.34)	-13.31 (±0.69)
Otaria flavescens	Bone	15	12	41	18.70 (±1.13)	17.47 (±0.82)	20.76 (±1.10)	-12.66 (±1.13)	-13.52 (±1.48)	-12.92 (±1.07)
Spheniscus magellanicus	Bone	7	13	40	17.75 (±0.58)	17.25 (±0.79)	19.27 (±0.51)	-14.61 (±0.74)	-14.43 (±1.33)	-15.46 (±0.96)

The three food webs simulated for the sensitivity analysis did not differ in any of the Layman's metrics (Table 5). The areas of the Bayesian ellipses (SEA_B) estimated for the top predators did not either differ among scenarios either, except for fur seals, whose area was maximised when sex ratio was balanced. However, large differences were observed in the overlap between the standard ellipses corrected for small sample size (SEA_C) of fur seals and penguins: it ranged from zero when only male fur seals were considered, to 43.73% (fur seals) and 21.34% (penguins) when only females were included. This indicates that the lack of information on the actual sex ratio of ancient data sets is unlikely to bias the overall structure of the food web. Nonetheless caution is needed when interpreting patterns of niche overlap, as they may be sensitive to the sex ratio of the sample.

The horizontal structure of the food web (CR) did not vary throughout time in central-northern Patagonia but in southern Patagonia the carbon range is currently smaller than in the two past periods considered (Figure 3 and 4). The nitrogen range (NR), indicative of food chain length, increased from past to present in both regions, and did not differ between ancient food webs from southern Patagonia (Figure 3 and 4). Finally, the food webs from southern Patagonia were shorter than those from central-northern Patagonia during the late Holocene as well as in the present.

Table 5. Probability values of Layman's metrics in three simulated model food webs for Río de la Plata region, including only females, males or both sexes in the samples of predators. NR = nitrogen range; CR = carbon range; CD = mean distance to centroid; MNND = mean nearest neighbour distance; SDNND = standard deviation of nearest neighbour distance. For more details see *Data analysis* in Material and Methods.

	NR	CR	CD	MNND	SDNND
♀♀	8.01 (7.00-9.04)	6.03 (4.46-7.64)	3.14 (2.77-3.51)	2.95 (2.50-3.41)	2.43 (1.55-3.35)
♂♂	8.32 (7.82-8.82)	6.16 (4.75-7.55)	3.44 (3.13-3.76)	3.23 (2.90-3.55)	2.50 (1.80-3.22)
♀♂	8.22 (7.55-8.87)	6.03 (4.57-7.42)	3.25 (2.93-3.57)	3.14 (2.75-3.55)	2.39 (1.69-3.10)

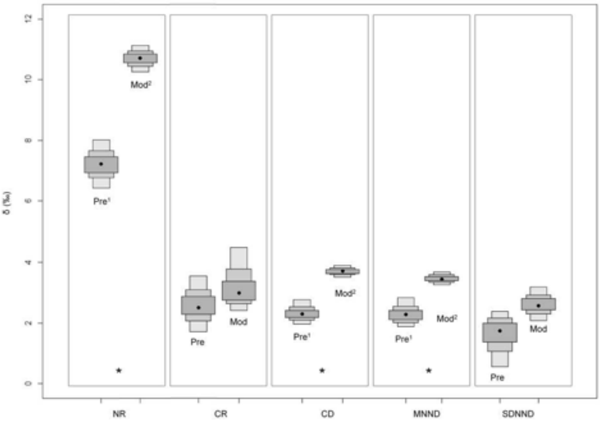

Figure 3. Probability values of Layman's metrics over the time in the central-northern Patagonia. Metrics that present differences over the time are indicated by an asterisk and superscripts. Pre=pre-contact period; Mod= modern period.

CD and MNND also changed throughout time in both regions, being smaller in the past. This indicates an increase in the trophic diversity and a decrease in the trophic redundancy in modern food webs. Regarding the three species of air predators the areas of the standard ellipses did not overlap in the modern $\delta^{13}C$–$\delta^{15}N$ bi-plot space of central-northern Patagonia (Table 6 and Figure 2). Conversely, the topology of the three species within the Pre-contact $\delta^{13}C$–$\delta^{15}N$ bi-plot space of the same region departed dramatically from expectations, as the standard ellipses of all the species overlapped one another, especially those of Magellanic penguins and fur seals, in sharp contrast with the low overlap currently observed (Table 6).

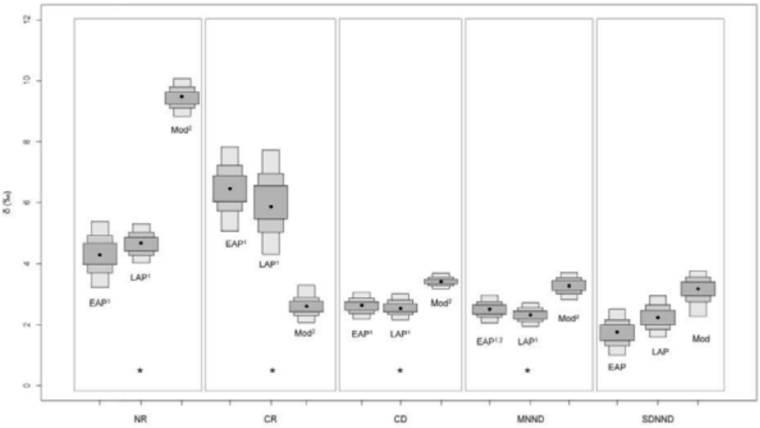

Figure 4. Probability values of Layman's metrics over the time in the southern Patagonia. Metrics that present differences over the time are indicated by an asterisk ad superscripts. Groups sharing the same superscript number (1, 2) are not significantly different. EAP=early aboriginal period; LAP=late aboriginal period; Mod=modern period.

The topology of the three species in the δ^{13}C–δ^{15}N bi-plot space of southern Patagonia also changed over time, as the overlap among the ellipses of the three species was almost zero in the EAP period (except between sea lions and fur seals where it was 15.38%), increased between penguins and sea lions in the LAP period and is currently about 34% between fur seals and sea lions. Interestingly, the SIBER ellipse areas (SEA_B) calculated for each species (Table 7) exhibited a decreasing trend throughout time in central-northern Patagonia, although it was statistically significant only for sea lions. Conversely in southern Patagonia, the sea lions' ellipse area has been constant over time, whereas that of fur seals showed a trend to increase through time and that of penguins slightly increased from the EAP period to the LAP period to then slightly decreased in the present food web (Table 7).

Table 6. Areas of the estimated Bayesian ellipses of the species/functional groups over the time in central-northern and southern Patagonia. Values are indicated as the mean and the 95% of credibility interval in parentheses. Metrics that present differences between ages are indicated by superscripts. Aa=*Arctocephalus australis*; Of=*Otaria flavescens*; Sm=S*pheniscus magellanicus*.

Central-northern Patagonia	**Herbivores**	**Aa**	**Of**	**Sm**
Pre-contact	7.4 (4.9-10.3)	6.1 (1.9-11.7)	4.7 (3.0-6.6)^1	7.7 (3.1-13.6)
Modern	3.9 (2.0-6.3)	1.9 (1.3-2.6)	1.6 (1.1-2.1)^2	5.5 (3.3-8.1)
Southern Patagonia				
EAP	8.6 (4.1-14.2)	1.6 (1.1-2.1)	4.0 (2.1-6.1)	2.2 (0.9-3.8)
LAP	9.0 (5.0-13.9)	1.3 (0.7-2.0)	3.9 (2.0-6.2)	3.5 (1.8-5.5)
Modern	4.1 (1.9-6.7)	4.4 (1.8-7.8)	3.8 (2.7-5.0)	1.7 (1.2-2.2)

Table 7. Overlap as a percentage of standard ellipses corrected for small samples (SEA_c) of the three top predators described in the text. The tables should be read horizontally, as each number in the cell refers to the percentage of overlap of the area of the group indicated in each row (e.g. 11.37% is the percentage of the ellipses of fur seals that are overlapped with the ellipses of the sea lions, while 16.42% is the percentage of the ellipses of the sea lions that are overlapped with the fur seals). Aa=*Arctocephalus australis*; Of=*Otaria flavescens*; Sm=S*pheniscus magellanicus*.

Central-northern Patagonia											
PRE-CONTACT	**Aa**	**Of**	**Sm**	**MODERN**	**Aa**	**Of**	**Sm**				
Aa	**1**	11.37	86.30	**Aa**	**1**	0.00	0.00				
Of	16.42	**1**	5.05	**Of**	0.00	**1**	0.00				
Sm	64.56	2.62	**1**	**Sm**	0.00	0.00	**1**				
Southern Patagonia											
EAP	**Aa**	**Of**	**Sm**	**LAP**	**Aa**	**Of**	**Sm**	**MODERN**	**Aa**	**Of**	**Sm**
Aa	**1**	15.38	0.00	**Aa**	**1**	0.00	0.00	**Aa**	**1**	34.19	0.00
Of	5.60	**1**	0.05	**Of**	0.00	**1**	53.24	**Of**	38.42	**1**	0.00
Sm	0.00	0.13	**1**	**Sm**	0.00	58.28	**1**	**Sm**	0.00	0.00	**1**

All the results of the stable isotopes analyses described in the above are publicly available in the Supporting Information (Table S1-S3).

Discussion

The study of the zooarchaeological record using stable isotope analysis certainly offers a window to explore the structure of ancient food webs, but it is not free from problems. Historical changes in the isotopic baseline are a major shortcoming in retrospective studies using stable isotope analysis to assess changes in trophic level and food web structure [57]. Although widely recognised as a confusing factor, previous studies often assumed the temporal stability of the isotopic baseline [82,83,84,85,86,87,88,89], but the results reported here demostrate that changes can be dramatic. Post [76] suggested the use of filter feeding mussels and surface-grazing snails as proxies for the baselines of pelagic and littoral aquatic food webs respectively and Bailey and colleagues [88] and Casey and Post [57] recognised the potential of mollusc shells to reconstruct the isotopic baseline in retrospective studies, since their organic matrix is encased within mineral crystals and hence, preserved [90]. The present study demonstrates the potential of the method and offers new perspectives using material that is widely available in paleontological and archaeological collections.

Another drawback from retrospective studies is the uneven distribution of specimens across space and time, which forced us to pool samples of disparate radiocarbon age to reconstruct ancient communities. Uncertainty about the gender of most specimens is another setback of the zooarchaeological record, as sexual secondary characters can seldom be observed. The sensitivity analysis conducted here confirmed the robustness of Layman's metrics to changes in sex ratios of penguins, sea lions and fur seals. Conversely, the overlap between the Bayesian ellipses was highly sensitive to the sex ratio of those species and hence caution is needed when interpreting those results.

The overall evidence reported here indicates that modern marine food webs of central-northern and southern Patagonia are longer (NR) than the ancient ones (Figs 2-4). Such a conclusion is in sharp contrast with the idea that human exploitation has shortened food webs because of the preferential removal of top predators [4]. Certainly, increased scarcity of large, marine species may have forced fisheries to target smaller species, but there is no reason why surviving top predators had to experience a similar shift. Marine predators are limited by the size of the prey they can consume and draw their energy from a very limited range of trophic levels, in contrast with fisheries [91]. Furthermore, it should be noted that the impact of sealing on the populations of fur seals and sea lions was much larger [39,40] than that of fishing on the populations of hake, squid and anchovies [20].

Surviving sea lions and fur seals off Argentina have certainly been under carrying capacity during the second half of the 20th century, when the population was less than 10% of the original numbers [39]. This reduced intraspecific competition and led to a major dietary shift in favour of benthic, larger prey with a higher trophic level [24]. Only recently, as the population of sea lions is rebuilding and approaching carrying capacity, sea lions experience resource limitation again and intraspecific competition forces them to increase the consumption of smaller and less profitable prey [92]. Information about the historical dietary changes of South American fur seals is restricted to the last three decades in Río de la Plata and reveals no major dietary changes [93]. However, the population was dramatically reduced during the first half of the 20th century and evidence from other fur seal species in the South-western Atlantic Ocean [94] suggest that this group of smaller and more pelagic pinnipeds also forage at a higher trophic level after severe population declines.

Trophic diversity, measured as the mean distance to the centroid in the isotopic space (CD) also increases in the present food webs, while redundancy (MNND) decreases thus revealing a higher trophic overlap in the past (Figs 2-4). This was confirmed by the isotopic niche overlap of the three air-breathing top predators, although they differed dramatically in body size and mouth diameter (Table 6). A similar scenario has been reported for waters off Peru, where sea lions, fur seals and penguins primarily rely on the large population of anchoveta *Engraulis ringens,* supported by intense oceanic productivity [95,96,97]. Similarly, a high trophic overlap has often been reported for other wasp-waisted ecosystems in upwelling regions [98]. Currently, a wasp-waist ecosystem supported by amphipods exists off southern Patagonia [99], but amphipods are not consumed directly by fur seals and sea lions. Perhaps a similar wasp-waisted ecosystem supported by small schooling fish might have existed off Patagonia during the Holocene, where primary productivity was usually higher than now [78] and hence it could have supported a larger population of small schooling fish and squids.

However, there are at least two reasons to believe that this is not the explanation for the high levels of overlap and redundancy of the ancient food webs reported here. Firstly, the large population of fur seals inhabiting the highly productive Río de la Plata rely heavily on anchovies and squids [93], but the much smaller sea lion population consumes primarily demersal fishes [100]. Secondly, marine productivity during the late aboriginal period off southern Patagonia was much lower than during the early aboriginal period and closer to actual productivity levels [78], but the structure of the trophic web was indistinguishable from that observed in the same region during the early aboriginal period. Thus, a direct link between productivity, predator diet and the structure of trophic overlap is probably unclear.

Empirical evidence has indicated that marine environments with lower annual temperature variability have smaller predator-prey mass ratios and, consequently, longer food chains [101]. It can be argued that changes in sea water temperature throughout the second half of the Holocene may explain the difference observed between the ancient and modern marine food webs in the South-western Atlantic. However, available evidence rules out major changes in sea surface temperature during the considered time span [51,55,102]. Furthermore, there is an inverse relationship between the length of the current food webs and the seasonal variability in the sea surface temperature in the South-western Atlantic [103], a pattern opposite to that reported by Jennings and Warr (2003)[101]. Finally, the difference in the length of the food chain observed between the two areas in both periods is smaller than the difference between periods in both areas.

Thus, human disturbance stands as the most likely reason for the differences in the structure of the food web reported here. Even so, human disturbance is not the only factor explaining the length of marine food webs, as those from southern Patagonia were always shorter and more overlapping than the central-northern Patagonia ones. This might be a consequence of the latitudinal decrease in species diversity reported in the South-western Atlantic [64,104] and was also probably the reason in the late Holocene, since it is unlikely that the impact of the hunter-gatherers inhabiting central-northern Patagonia on marine resources was larger than that of the hunter-gatherers inhabiting southern Patagonia [51,52,53].

In conclusion, this study strongly support the hypothesis that selective exploitation of marine ecosystems, targeting primarily top predators, leads to longer and less overlapping food webs, if top predators are not extinct but survive well below carrying capacity. The situation might be different if human exploitation targeted primarily intermediate trophic levels as a result of the legal protection of top predators.

Furthermore, this study demonstrates the necessity to reconstruct the isotopic baseline in retrospective studies and how this can be achieved by analysing the organic matter encased into the shell of molluscs.

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Supporting Information

Table S1. Modern nitrogen and carbon stable-isotope ratios in Río de la Plata and adjoining areas. These data have been used to perform the sensitivity test for the method.

Sample	Specie/Group	Sex	$\delta^{13}C$	$\delta^{15}N$
RP-H1	Herbivore	NA	-17,79	12,31
RP-H2	Herbivore	NA	-16,15	11,99
RP-H3	Herbivore	NA	-17,00	11,85
RP-H4	Herbivore	NA	-16,73	12,05
RP-H5	Herbivore	NA	-17,16	11,91
RP-H6	Herbivore	NA	-17,76	12,43
RP-H7	Herbivore	NA	-17,46	13,62
RP-H8	Herbivore	NA	-22,50	12,29
RP-H9	Herbivore	NA	-16,78	12,92
RP-H10	Herbivore	NA	-21,17	12,32
RP-Aa1	*A. australis*	female	-13,81	19,26
RP-Aa2	*A. australis*	female	-12,80	20,05
RP-Aa3	*A. australis*	female	-13,84	17,50
RP-Aa4	*A. australis*	female	-14,04	18,15
RP-Aa5	*A. australis*	female	-13,44	19,14
RP-Aa6	*A. australis*	male	-16,62	20,53
RP-Aa7	*A. australis*	male	-15,60	20,50
RP-Aa8	*A. australis*	male	-12,87	20,52
RP-Aa9	*A. australis*	male	-13,31	20,80
RP-Aa10	*A. australis*	male	-13,09	20,43
RP-Aa11	*A. australis*	male	-13,11	20,93
RP-Aa12	*A. australis*	male	-13,87	20,53
RP-Aa13	*A. australis*	male	-13,34	20,81
RP-Aa14	*A. australis*	male	-12,97	20,07
RP-Aa15	*A. australis*	male	-14,51	19,29
RP-Aa16	*A. australis*	male	-14,22	19,18
RP-Aa17	*A. australis*	male	-13,34	21,23
RP-Aa18	*A. australis*	male	-14,32	22,73
RP-Aa19	*A. australis*	male	-13,40	20,74
RP-Aa20	*A. australis*	male	-12,58	20,64
RP-Aa21	*A. australis*	male	-12,78	20,95
RP-Aa22	*A. australis*	male	-12,64	20,63
RP-Aa23	*A. australis*	male	-13,25	19,46
RP-Aa24	*A. australis*	male	-13,69	21,50
RP-Aa25	*A. australis*	male	-12,74	20,73
RP-Aa26	*A. australis*	male	-13,04	19,88

RP-Aa27	*A. australis*	male	-12,62	19,76
RP-Aa28	*A. australis*	male	-13,50	21,11
RP-Aa29	*A. australis*	male	-13,19	20,55
RP-Aa30	*A. australis*	male	-14,15	21,19
RP-Aa31	*A. australis*	male	-14,33	21,00
RP-Aa32	*A. australis*	male	-14,44	19,82
RP-Aa33	*A. australis*	male	-12,90	20,18
RP-Aa34	*A. australis*	male	-15,19	20,17
RP-Aa35	*A. australis*	male	-14,08	20,23
RP-Aa36	*A. australis*	male	-14,27	19,80
RP-Aa37	*A. australis*	male	-13,63	20,08
RP-Aa38	*A. australis*	male	-13,55	20,58
RP-Aa39	*A. australis*	male	-14,09	20,41
RP-Aa40	*A. australis*	male	-13,93	20,46
RP-Aa41	*A. australis*	male	-12,78	20,72
RP-Aa42	*A. australis*	male	-13,84	20,91
RP-Aa43	*A. australis*	male	-13,71	20,98
RP-Aa44	*A. australis*	male	-14,32	20,37
RP-Aa45	*A. australis*	male	-12,87	20,57
RP-Aa46	*A. australis*	male	-13,10	19,68
RP-Aa47	*A. australis*	male	-13,57	21,16
RP-Aa48	*A. australis*	male	-13,94	21,00
RP-Aa49	*A. australis*	male	-12,84	21,54
RP-Aa50	*A. australis*	male	-13,24	20,59
RP-Aa51	*A. australis*	male	-12,84	20,53
RP-Aa52	*A. australis*	male	-13,23	21,00
RP-Aa53	*A. australis*	male	-13,53	20,81
RP-Aa54	*A. australis*	male	-12,50	21,17
RP-Aa55	*A. australis*	male	-13,13	21,32
RP-Aa56	*A. australis*	male	-14,16	19,60
RP-Aa57	*A. australis*	male	-13,28	20,56
RP-Aa58	*A. australis*	male	-13,23	20,47
RP-Aa59	*A. australis*	male	-13,20	20,72
RP-Of1	*O. flavescens*	female	-12,23	20,71
RP-Of2	*O. flavescens*	female	-11,68	20,42
RP-Of3	*O. flavescens*	female	-11,82	20,22
RP-Of4	*O. flavescens*	female	-12,33	20,13
RP-Of5	*O. flavescens*	male	-12,01	20,67
RP-Of6	*O. flavescens*	male	-12,30	20,80
RP-Of7	*O. flavescens*	male	-11,45	21,23
RP-Of8	*O. flavescens*	male	-12,40	20,44

RP-Of9	*O. flavescens*	male	-12,20	21,44
RP-Of10	*O. flavescens*	male	-11,04	20,09
RP-Of11	*O. flavescens*	male	-13,73	20,58
RP-Of12	*O. flavescens*	male	-11,85	20,92
RP-Of13	*O. flavescens*	male	-11,45	21,23
RP-Of14	*O. flavescens*	male	-12,73	20,45
RP-Of15	*O. flavescens*	male	-11,79	20,92
RP-Of16	*O. flavescens*	male	-11,41	20,06
RP-Of17	*O. flavescens*	male	-10,81	20,45
RP-Of18	*O. flavescens*	male	-12,11	20,78
RP-Of19	*O. flavescens*	male	-11,23	19,80
RP-Sm1	*S. magellanicus*	female	-14,30	19,70
RP-Sm2	*S. magellanicus*	female	-13,00	17,00
RP-Sm3	*S. magellanicus*	female	-14,90	15,00
RP-Sm4	*S. magellanicus*	female	-14,10	20,10
RP-Sm5	*S. magellanicus*	female	-13,10	17,00
RP-Sm6	*S. magellanicus*	female	-15,90	17,40
RP-Sm7	*S. magellanicus*	female	-14,90	17,30
RP-Sm8	*S. magellanicus*	female	-15,20	17,10
RP-Sm9	*S. magellanicus*	female	-15,40	17,30
RP-Sm10	*S. magellanicus*	female	-14,50	20,00
RP-Sm11	*S. magellanicus*	male	-14,10	16,00
RP-Sm12	*S. magellanicus*	male	-13,90	20,50
RP-Sm13	*S. magellanicus*	male	-11,30	14,50
RP-Sm14	*S. magellanicus*	male	-14,20	18,30
RP-Sm15	*S. magellanicus*	male	-14,00	20,20
RP-Sm16	*S. magellanicus*	male	-15,30	17,40
RP-Sm17	*S. magellanicus*	male	-15,80	17,20
RP-Sm18	*S. magellanicus*	male	-14,80	17,40
RP-Sm19	*S. magellanicus*	male	-14,60	19,20
RP-Sm20	*S. magellanicus*	male	-14,10	19,40

Table S2. Modern and archaeological nitrogen and carbon stable-isotope ratios in central-northern Patagonia. Table shows the list of samples, grouped according to their historical period (modern and pre-contact), and δ^{13}C and δ^{15}N values.

Sample	**Species/Group**	**Period**	**δ^{13}C**	**δ^{15}N**
NP-H1	Herbivore	modern	-16,80	11,70
NP-H2	Herbivore	modern	-14,80	11,50
NP-H3	Herbivore	modern	-16,90	11,10
NP-H4	Herbivore	modern	-16,80	11,90
NP-H5	Herbivore	modern	-15,30	11,30

NP-H6	Herbivore	modern	-18,05	11,30
NP-H7	Herbivore	modern	-17,72	11,30
NP-H8	Herbivore	modern	-8,88	12,54
NP-H9	Herbivore	modern	-13,13	11,76
NP-H10	Herbivore	modern	-16,03	11,16
NP-H11	Herbivore	modern	-13,14	12,06
NP-H12	Herbivore	modern	-16,33	11,71
NP-Aa1	*A. australis*	modern	-13,55	22,83
NP-Aa2	*A. australis*	modern	-12,30	21,24
NP-Aa3	*A. australis*	modern	-13,12	21,28
NP-Aa4	*A. australis*	modern	-13,40	21,55
NP-Aa5	*A. australis*	modern	-13,25	20,49
NP-Aa6	*A. australis*	modern	-13,46	19,21
NP-Aa7	*A. australis*	modern	-13,12	20,03
NP-Aa8	*A. australis*	modern	-13,45	20,97
NP-Aa9	*A. australis*	modern	-13,63	21,14
NP-Aa10	*A. australis*	modern	-12,57	18,76
NP-Aa11	*A. australis*	modern	-14,01	20,75
NP-Aa12	*A. australis*	modern	-13,85	20,25
NP-Aa13	*A. australis*	modern	-13,72	20,22
NP-Aa14	*A. australis*	modern	-13,39	17,52
NP-Aa15	*A. australis*	modern	-13,39	21,01
NP-Aa16	*A. australis*	modern	-13,27	19,88
NP-Aa17	*A. australis*	modern	-13,06	21,07
NP-Aa18	*A. australis*	modern	-13,59	20,23
NP-Aa19	*A. australis*	modern	-12,90	20,15
NP-Aa20	*A. australis*	modern	-12,62	20,94
NP-Aa21	*A. australis*	modern	-14,57	20,63
NP-Aa22	*A. australis*	modern	-14,51	21,16
NP-Aa23	*A. australis*	modern	-12,79	21,63
NP-Aa24	*A. australis*	modern	-13,38	21,17
NP-Aa25	*A. australis*	modern	-13,62	19,37
NP-Aa26	*A. australis*	modern	-13,52	20,53
NP-Aa27	*A. australis*	modern	-13,16	20,78
NP-Aa28	*A. australis*	modern	-12,96	21,02
NP-Aa29	*A. australis*	modern	-12,23	21,17
NP-Of1	*O. flavescens*	modern	-12,79	21,69
NP-Of2	*O. flavescens*	modern	-11,90	23,00
NP-Of3	*O. flavescens*	modern	-11,60	22,00
NP-Of4	*O. flavescens*	modern	-11,30	24,10
NP-Of5	*O. flavescens*	modern	-12,10	21,80

NP-Of6	*O. flavescens*	modern	-11,90	23,20
NP-Of7	*O. flavescens*	modern	-11,60	23,40
NP-Of8	*O. flavescens*	modern	-12,51	22,68
NP-Of9	*O. flavescens*	modern	-11,29	22,90
NP-Of10	*O. flavescens*	modern	-11,25	22,27
NP-Of11	*O. flavescens*	modern	-12,85	21,86
NP-Of12	*O. flavescens*	modern	-12,30	22,70
NP-Of13	*O. flavescens*	modern	-11,40	22,90
NP-Of14	*O. flavescens*	modern	-11,70	21,50
NP-Of15	*O. flavescens*	modern	-12,13	22,03
NP-Of16	*O. flavescens*	modern	-10,66	21,62
NP-Of17	*O. flavescens*	modern	-10,90	23,50
NP-Of18	*O. flavescens*	modern	-12,75	21,69
NP-Of19	*O. flavescens*	modern	-12,26	22,21
NP-Of20	*O. flavescens*	modern	-11,64	22,42
NP-Of21	*O. flavescens*	modern	-12,35	22,15
NP-Of22	*O. flavescens*	modern	-13,04	21,91
NP-Of23	*O. flavescens*	modern	-12,57	23,31
NP-Of24	*O. flavescens*	modern	-12,68	22,79
NP-Of25	*O. flavescens*	modern	-12,04	23,31
NP-Of26	*O. flavescens*	modern	-12,92	21,65
NP-Of27	*O. flavescens*	modern	-12,05	22,57
NP-Of28	*O. flavescens*	modern	-12,32	22,32
NP-Of29	*O. flavescens*	modern	-12,14	22,25
NP-Of30	*O. flavescens*	modern	-11,78	22,36
NP-Of31	*O. flavescens*	modern	-12,51	21,79
NP-Of32	*O. flavescens*	modern	-13,33	21,66
NP-Of33	*O. flavescens*	modern	-12,62	21,98
NP-Of34	*O. flavescens*	modern	-13,03	20,07
NP-Of35	*O. flavescens*	modern	-12,99	22,39
NP-Of36	*O. flavescens*	modern	-13,13	21,00
NP-Sm1	*S. magellanicus*	modern	-15,00	19,40
NP-Sm2	*S. magellanicus*	modern	-15,00	17,80
NP-Sm3	*S. magellanicus*	modern	-15,30	17,90
NP-Sm4	*S. magellanicus*	modern	-17,00	17,90
NP-Sm5	*S. magellanicus*	modern	-16,00	17,20
NP-Sm6	*S. magellanicus*	modern	-14,80	20,20
NP-Sm7	*S. magellanicus*	modern	-14,80	20,30
NP-Sm8	*S. magellanicus*	modern	-15,10	20,40
NP-Sm9	*S. magellanicus*	modern	-14,60	19,30
NP-Sm10	*S. magellanicus*	modern	-13,40	18,40

NP-Sm11	*S. magellanicus*	modern	-15,10	19,70
NP-Sm12	*S. magellanicus*	modern	-15,30	20,20
NP-Sm13	*S. magellanicus*	modern	-13,90	14,50
NP-Sm14	*S. magellanicus*	modern	-15,50	20,10
NP-Sm15	*S. magellanicus*	modern	-14,30	19,40
NP-Sm16	*S. magellanicus*	modern	-15,00	21,00
NP-Sm17	*S. magellanicus*	modern	-17,20	19,60
NP-Sm18	*S. magellanicus*	modern	-14,10	20,60
NP-Sm19	*S. magellanicus*	modern	-15,30	20,20
NP-Sm20	*S. magellanicus*	modern	-13,90	14,50
A7-cC1	Herbivore	pre-contact	-14,74	13,79
A7-cC4	Herbivore	pre-contact	-14,31	13,71
A7-cC5	Herbivore	pre-contact	-14,74	13,67
A8-cC2	Herbivore	pre-contact	-18,59	13,29
A8-cC4	Herbivore	pre-contact	-13,79	13,30
A5-cC1	Herbivore	pre-contact	-14,96	11,93
A5-cC2	Herbivore	pre-contact	-13,73	13,11
A5-cC3	Herbivore	pre-contact	-15,97	15,83
A5-cC4	Herbivore	pre-contact	-14,00	13,79
A5-cC5	Herbivore	pre-contact	-12,95	13,88
A11-cC3	Herbivore	pre-contact	-17,91	14,06
A11-cC4	Herbivore	pre-contact	-17,91	14,21
A7-cL1	Herbivore	pre-contact	-15,74	16,19
A7-cL2	Herbivore	pre-contact	-14,01	15,03
A7-cL3	Herbivore	pre-contact	-14,28	16,49
A7-cL4	Herbivore	pre-contact	-14,35	14,94
A7-cL5	Herbivore	pre-contact	-13,84	14,83
A10-cL1	Herbivore	pre-contact	-12,28	14,40
A10-cL2	Herbivore	pre-contact	-17,16	13,28
A10-cL3	Herbivore	pre-contact	-12,10	12,10
A10-cL4	Herbivore	pre-contact	-16,33	14,39
A10-cL5	Herbivore	pre-contact	-17,39	13,58
A4-cL1	Herbivore	pre-contact	-11,39	15,31
A4-cL3	Herbivore	pre-contact	-15,85	16,27
A4-cL4	Herbivore	pre-contact	-17,72	15,81
A4-cL5	Herbivore	pre-contact	-15,80	15,02
A11-cL1	Herbivore	pre-contact	-17,81	13,24
A11-cL2	Herbivore	pre-contact	-17,30	15,05
N° 90	*A. australis*	pre-contact	-13,68	16,83
N° 91	*A. australis*	pre-contact	-14,45	17,83
F1 18	*A. australis*	pre-contact	-12,96	22,09

F1 19	*A. australis*	pre-contact	-12,69	17,16
FM1 11	*A. australis*	pre-contact	-12,52	18,36
36	*O. flavescens*	pre-contact	-12,29	21,38
82	*O. flavescens*	pre-contact	-11,78	23,82
i 1 (61)	*O. flavescens*	pre-contact	-13,11	21,27
i 3 (43)	*O. flavescens*	pre-contact	-13,04	22,01
i 4 (44)	*O. flavescens*	pre-contact	-13,37	22,28
i 5 (54)	*O. flavescens*	pre-contact	-10,99	22,24
i 15 (C1)	*O. flavescens*	pre-contact	-14,37	22,25
i 18 (89)	*O. flavescens*	pre-contact	-13,60	24,97
i 23	*O. flavescens*	pre-contact	-12,83	21,29
i 24	*O. flavescens*	pre-contact	-14,56	23,20
M1 1	*O. flavescens*	pre-contact	-12,04	22,32
M1 3	*O. flavescens*	pre-contact	-12,96	22,41
FSM-SRH-Mont II OF (costilla)	*O. flavescens*	pre-contact	-11,41	22,40
OBS 13	*O. flavescens*	pre-contact	-11,25	22,41
FSM-SRH-Mont I OF (cost px med)	*O. flavescens*	pre-contact	-11,91	22,98
OBS 4	*O. flavescens*	pre-contact	-13,89	18,06
OBS 137	*O. flavescens*	pre-contact	-13,45	21,10
F1 17	*O. flavescens*	pre-contact	-13,67	19,89
FM1 13	*O. flavescens*	pre-contact	-13,10	19,74
FM1 14	*O. flavescens*	pre-contact	-13,37	20,98
FM1 15	*O. flavescens*	pre-contact	-12,06	20,31
FM1 16	*O. flavescens*	pre-contact	-12,31	18,70
FM1 17	*O. flavescens*	pre-contact	-12,70	18,92
FM1 19	*O. flavescens*	pre-contact	-12,90	22,47
FM1 20	*O. flavescens*	pre-contact	-12,27	21,90
FM1 21	*O. flavescens*	pre-contact	-12,78	20,32
OBS 26	*S. magellanicus*	pre-contact	-13,13	17,43
7	*S. magellanicus*	pre-contact	-14,93	16,44
72	*S. magellanicus*	pre-contact	-10,68	15,14
80	*S. magellanicus*	pre-contact	-13,27	20,79
82	*S. magellanicus*	pre-contact	-13,10	20,46
FSM-S2N3-Obs26 (tibia derecha)	*S. magellanicus*	pre-contact	-13,18	18,19
FSM-S2N2-Obs21 (cráneo)	*S. magellanicus*	pre-contact	-13,39	18,85

Table S3. Modern and archaeological nitrogen and carbon stable-isotope ratios in southern Patagonia. Table shows the list of samples, grouped according to their historical period (modern, LAP and EAP), and $\delta^{13}C$ and $\delta^{15}N$ values.

Sample	**Species/Group**	**Period**	**$\delta^{13}C$**	**$\delta^{15}N$**
SP-H1	Herbivore	Modern	-17,62	12,20

SP-H2	Herbivore	Modern	-16,54	11,76
SP-H3	Herbivore	Modern	-16,40	11,52
SP-H4	Herbivore	Modern	-17,10	11,85
SP-H5	Herbivore	Modern	-16,01	12,01
SP-H6	Herbivore	Modern	-10,40	10,90
SP-H7	Herbivore	Modern	-12,00	10,37
SP-H8	Herbivore	Modern	-13,50	10,90
SP-H9	Herbivore	Modern	-12,50	10,70
SP-H10	Herbivore	Modern	-14,80	11,00
SP-Aa1	*A. australis*	Modern	-13,70	21,27
SP-Aa2	*A. australis*	Modern	-13,69	18,48
SP-Aa3	*A. australis*	Modern	-14,08	16,69
SP-Aa4	*A. australis*	Modern	-12,20	18,15
SP-Aa5	*A. australis*	Modern	-12,54	21,44
SP-Aa6	*A. australis*	Modern	-13,63	19,41
SP-Aa7	*A. australis*	Modern	-13,32	19,96
SP-Of1	*O.flavescens*	Modern	-12,10	22,20
SP-Of2	*O.flavescens*	Modern	-11,90	21,80
SP-Of3	*O.flavescens*	Modern	-13,10	21,60
SP-Of4	*O.flavescens*	Modern	-11,70	22,20
SP-Of5	*O.flavescens*	Modern	-11,65	20,11
SP-Of6	*O.flavescens*	Modern	-11,66	19,68
SP-Of7	*O.flavescens*	Modern	-11,62	19,88
SP-Of8	*O.flavescens*	Modern	-12,69	20,69
SP-Of9	*O.flavescens*	Modern	-13,83	20,65
SP-Of10	*O.flavescens*	Modern	-12,35	20,33
SP-Of11	*O.flavescens*	Modern	-11,40	19,10
SP-Of12	*O.flavescens*	Modern	-11,00	22,40
SP-Of13	*O.flavescens*	Modern	-13,73	21,28
SP-Of14	*O.flavescens*	Modern	-13,20	18,50
SP-Of15	*O.flavescens*	Modern	-12,50	18,20
SP-Of16	*O.flavescens*	Modern	-12,90	19,70
SP-Of17	*O.flavescens*	Modern	-11,60	22,40
SP-Of18	*O.flavescens*	Modern	-14,90	20,80
SP-Of19	*O.flavescens*	Modern	-12,99	18,89
SP-Of20	*O.flavescens*	Modern	-12,54	20,68
SP-Of21	*O.flavescens*	Modern	-12,70	20,20
SP-Of22	*O.flavescens*	Modern	-14,65	20,30
SP-Of23	*O.flavescens*	Modern	-12,50	21,30
SP-Of24	*O.flavescens*	Modern	-13,80	21,00
SP-Of25	*O.flavescens*	Modern	-13,40	20,90

SP-Of26	*O.flavescens*	Modern	-12,40	21,20
SP-Of27	*O.flavescens*	Modern	-12,00	20,90
SP-Of28	*O.flavescens*	Modern	-13,60	20,50
SP-Of29	*O.flavescens*	Modern	-13,00	21,20
SP-Of30	*O.flavescens*	Modern	-13,20	20,60
SP-Of31	*O.flavescens*	Modern	-13,25	20,19
SP-Of32	*O.flavescens*	Modern	-13,61	20,14
SP-Of33	*O.flavescens*	Modern	-12,52	20,50
SP-Of34	*O.flavescens*	Modern	-13,50	20,70
SP-Of35	*O.flavescens*	Modern	-13,10	20,60
SP-Of36	*O.flavescens*	Modern	-13,10	20,70
SP-Of37	*O.flavescens*	Modern	-13,42	21,07
SP-Of38	*O.flavescens*	Modern	-16,83	23,23
SP-Of39	*O.flavescens*	Modern	-13,65	20,66
SP-Of40	*O.flavescens*	Modern	-13,65	20,93
SP-Of41	*O.flavescens*	Modern	-12,30	23,40
SP-Sm1	*S. magellanicus*	Modern	-15,40	19,50
SP-Sm2	*S. magellanicus*	Modern	-16,50	18,10
SP-Sm3	*S. magellanicus*	Modern	-14,50	19,70
SP-Sm4	*S. magellanicus*	Modern	-17,10	19,00
SP-Sm5	*S. magellanicus*	Modern	-14,80	19,00
SP-Sm6	*S. magellanicus*	Modern	-15,10	20,10
SP-Sm7	*S. magellanicus*	Modern	-16,30	18,80
SP-Sm8	*S. magellanicus*	Modern	-14,80	18,80
SP-Sm9	*S. magellanicus*	Modern	-13,90	19,10
SP-Sm10	*S. magellanicus*	Modern	-15,50	19,50
SP-Sm11	*S. magellanicus*	Modern	-17,10	18,40
SP-Sm12	*S. magellanicus*	Modern	-16,90	19,50
SP-Sm13	*S. magellanicus*	Modern	-16,50	19,10
SP-Sm14	*S. magellanicus*	Modern	-17,00	19,20
SP-Sm15	*S. magellanicus*	Modern	-14,90	19,70
SP-Sm16	*S. magellanicus*	Modern	-16,20	19,30
SP-Sm17	*S. magellanicus*	Modern	-15,50	19,60
SP-Sm18	*S. magellanicus*	Modern	-16,00	19,40
SP-Sm19	*S. magellanicus*	Modern	-15,90	19,10
SP-Sm20	*S. magellanicus*	Modern	-15,90	18,80
SP-Sm21	*S. magellanicus*	Modern	-15,90	19,20
SP-Sm22	*S. magellanicus*	Modern	-15,20	20,30
SP-Sm23	*S. magellanicus*	Modern	-15,50	19,90
SP-Sm24	*S. magellanicus*	Modern	-14,80	20,00
SP-Sm25	*S. magellanicus*	Modern	-14,90	18,70

SP-Sm26	*S. magellanicus*	Modern	-14,60	19,10
SP-Sm27	*S. magellanicus*	Modern	-14,90	19,00
SP-Sm28	*S. magellanicus*	Modern	-14,60	19,10
SP-Sm29	*S. magellanicus*	Modern	-14,00	19,70
SP-Sm30	*S. magellanicus*	Modern	-14,30	19,50
SP-Sm31	*S. magellanicus*	Modern	-14,70	19,60
SP-Sm32	*S. magellanicus*	Modern	-14,70	18,50
SP-Sm33	*S. magellanicus*	Modern	-14,80	19,50
SP-Sm34	*S. magellanicus*	Modern	-14,40	19,10
SP-Sm35	*S. magellanicus*	Modern	-14,50	19,50
SP-Sm36	*S. magellanicus*	Modern	-15,00	19,70
SP-Sm37	*S. magellanicus*	Modern	-14,90	19,40
SP-Sm38	*S. magellanicus*	Modern	-17,30	20,00
SP-Sm39	*S. magellanicus*	Modern	-16,50	19,30
SP-Sm40	*S. magellanicus*	Modern	-17,10	18,10
A17-cM1	Herbivore	LAP	-20,07	13,01
A17-cM2	Herbivore	LAP	-19,59	13,32
A17-cM3	Herbivore	LAP	-20,27	14,30
A17-cM4	Herbivore	LAP	-21,35	14,01
A17-cM5	Herbivore	LAP	-21,09	12,15
A15-cM1	Herbivore	LAP	-14,32	12,86
A15-cM2	Herbivore	LAP	-14,99	13,43
A15-cM3	Herbivore	LAP	-14,53	13,72
A17-cL1	Herbivore	LAP	-16,74	13,11
A17-cL2	Herbivore	LAP	-17,35	12,00
A17-cL3	Herbivore	LAP	-20,99	13,02
A17-cL4	Herbivore	LAP	-22,15	11,73
A17-cL5	Herbivore	LAP	-19,52	12,59
A15-cL2	Herbivore	LAP	-11,44	11,17
A15-cL4	Herbivore	LAP	-14,52	12,66
44331	*A. australis*	LAP	-12,00	16,80
155288	*A. australis*	LAP	-11,70	17,46
150329	*A. australis*	LAP	-12,10	18,06
152253	*A. australis*	LAP	-11,60	16,71
152439	*A. australis*	LAP	-11,70	17,16
151607	*A. australis*	LAP	-12,00	16,13
154656	*A. australis*	LAP	-11,70	17,49
151575	*A. australis*	LAP	-11,80	17,01
151912	*A. australis*	LAP	-12,60	16,77
154284	*A. australis*	LAP	-12,40	17,22
153887	*A. australis*	LAP	-11,50	17,88

155456	*A. australis*	LAP	-12,30	15,46
155447	*A. australis*	LAP	-11,60	17,15
OF 2a	*O.flavescens*	LAP	-13,81	17,40
OF 2b	*O.flavescens*	LAP	-15,65	16,81
OF 3	*O.flavescens*	LAP	-15,12	16,52
OF 9	*O.flavescens*	LAP	-14,24	16,31
OF 12	*O.flavescens*	LAP	-12,23	17,81
OF 14	*O.flavescens*	LAP	-13,17	17,81
OF 15	*O.flavescens*	LAP	-14,12	19,23
OF 5	*O.flavescens*	LAP	-15,65	16,92
OF 7	*O.flavescens*	LAP	-12,62	17,32
OF 10	*O.flavescens*	LAP	-12,62	17,32
43418	*O.flavescens*	LAP	-11,70	18,50
154286	*O.flavescens*	LAP	-11,30	17,67
10030	*S. magellanicus*	LAP	-12,38	16,89
10100	*S. magellanicus*	LAP	-12,96	15,42
pingüino 4b	*S. magellanicus*	LAP	-13,32	17,35
pingüino 6	*S. magellanicus*	LAP	-14,32	18,22
pingüino 4a	*S. magellanicus*	LAP	-15,59	17,14
9255	*S. magellanicus*	LAP	-12,79	17,61
19098	*S. magellanicus*	LAP	-14,70	16,00
19264	*S. magellanicus*	LAP	-14,07	17,30
10122	*S. magellanicus*	LAP	-14,26	17,41
12433	*S. magellanicus*	LAP	-14,82	18,20
12268	*S. magellanicus*	LAP	-15,84	17,55
10116	*S. magellanicus*	LAP	-15,92	17,72
10115	*S. magellanicus*	LAP	-16,63	17,46
A19-cM1	Herbivore	EAP	-22,34	15,06
A19-cM2	Herbivore	EAP	-17,07	14,35
A19-cM3	Herbivore	EAP	-17,25	16,95
A19-cM4	Herbivore	EAP	-17,09	16,28
A19-cM5	Herbivore	EAP	-17,40	14,30
A19-cL1	Herbivore	EAP	-18,40	12,81
A19-cL2	Herbivore	EAP	-19,79	13,61
A19-cL3	Herbivore	EAP	-20,43	13,32
A19-cL4	Herbivore	EAP	-15,05	14,19
A19-cL5	Herbivore	EAP	-18,33	13,03
CV6 4/-45-50cm	*A. australis*	EAP	-12,96	20,47
CdN2-0072	*A. australis*	EAP	-12,82	19,35
37295	*A. australis*	EAP	-11,70	18,68
37340	*A. australis*	EAP	-12,80	18,29

37456	*A. australis*	EAP	-12,00	16,17
67319	*A. australis*	EAP	-10,90	17,45
66397	*A. australis*	EAP	-11,40	16,75
186854	*A. australis*	EAP	-12,10	16,99
65989	*A. australis*	EAP	-12,20	17,13
202401	*A. australis*	EAP	-10,90	17,41
202083	*A. australis*	EAP	-11,80	16,36
193261	*A. australis*	EAP	-11,40	18,06
194047	*A. australis*	EAP	-12,10	17,22
43247	*A. australis*	EAP	-11,80	17,38
174498	*A. australis*	EAP	-11,90	16,36
217933	*A. australis*	EAP	-12,40	17,89
215241	*A. australis*	EAP	-12,70	17,38
223614	*A. australis*	EAP	-11,60	16,80
215940/215933	*A. australis*	EAP	-11,60	17,33
53580	*A. australis*	EAP	-11,20	17,56
68445	*A. australis*	EAP	-10,90	18,12
64460	*A. australis*	EAP	-11,70	17,22
213370	*A. australis*	EAP	-11,50	17,67
215074	*A. australis*	EAP	-12,20	17,29
58630	*A. australis*	EAP	-12,40	18,11
190846	*A. australis*	EAP	-12,00	17,68
63330	*A. australis*	EAP	-11,30	18,14
213732	*A. australis*	EAP	-11,50	17,88
52463	*A. australis*	EAP	-12,00	17,65
226119	*A. australis*	EAP	-10,80	17,15
69639	*A. australis*	EAP	-11,50	17,29
189603	*A. australis*	EAP	-12,50	17,54
216713	*A. australis*	EAP	-11,90	17,38
212616/212653	*A. australis*	EAP	-12,40	17,24
224151	*A. australis*	EAP	-12,40	17,99
30459	*O.flavescens*	EAP	-11,27	19,63
33459	*O.flavescens*	EAP	-11,45	18,72
33551	*O.flavescens*	EAP	-11,80	18,78
33571	*O.flavescens*	EAP	-12,46	19,04
33717	*O.flavescens*	EAP	-12,67	18,37
34177	*O.flavescens*	EAP	-12,33	18,58
34544	*O.flavescens*	EAP	-12,00	18,39
34751	*O.flavescens*	EAP	-11,61	18,86
33458	*O.flavescens*	EAP	-12,37	18,51
CV6 4/-60-65cm	*O.flavescens*	EAP	-13,92	20,75

CV20 OF1	*O.flavescens*	EAP	-14,80	15,41
CV20 OF3	*O.flavescens*	EAP	-14,50	17,95
CV20 OF4	*O.flavescens*	EAP	-12,25	19,11
CV20 OF6	*O.flavescens*	EAP	-12,29	19,55
CV20 OF7	*O.flavescens*	EAP	-14,16	18,84
1925	*S. magellanicus*	EAP	-14,86	17,46
26006	*S. magellanicus*	EAP	-13,35	17,70
27597	*S. magellanicus*	EAP	-15,32	16,92
3761	*S. magellanicus*	EAP	-13,90	18,31
4179	*S. magellanicus*	EAP	-14,54	17,79
3522	*S. magellanicus*	EAP	-15,29	17,39
3641	*S. magellanicus*	EAP	-14,98	18,65

DISCUSIÓN Y CONCLUSIONES

DISCUSIÓN GENERAL

La abundancia natural y el papel ecológico de los grandes vertebrados en ecosistemas marinos no alterados por el hombre resultan, en general, desconocidos, a pesar de ser una información clave para comprender su papel ecológico original. Hace ya dos décadas, Daniel Pauly (1995) acuño el concepto de "*shifting baseline*" para referirse al sesgo provocado en la gestión de pesquería por la falta de perspetiva histórica. En otras palabras: ignorando las condiciones previas al impacto humano en los ecosistemas marinos, corremos el riesgo de considerar como prístinas las condiciones en las que nosotros mismos empezamos a tener conciencia de dicha alteración. Lo mismo sucedería en la biología de la conservación, que puede orientar sus esfuerzos a recuperar ecosistemas en realidad ya muy alejados de su estructura natural, debido a dicha falta de perspectiva histórica.

Recientemente se está colmando este vacío a través de estudios históricos, que utilizan series temporales basadas en indicadores biogeoquímicos, físicos, históricos y de biodiversidad (Jackson et al. 2001). El análisis del registro subfósil y zooarqueológico, por ejemplo, ha permitido aclarar los mecanismos y las causas subyacentes de algunas extinciones y colapsos de especies marinas, por ejemplo tras la colonización de Nueva Zelanda por los maories, (Anderson 2008). Sin embargo, los métodos tradicionales ofrecen muy poca información acerca de las paleodietas, del nivel trófico de la especie y de la estructura de la red trófica a la que pertenecía. Recientemente, se han desarrollado una serie de métodos cuantitativos para estudiar la topología de las redes tróficas en base a los datos proporcionados por el análisis de isótopos estables (Bearhop et al. 2004, Layman et al. 2007a, Schmidt et al. 2007) gracias a los cuales es posible ir un paso más allá y empezar a obtener este tipo de información.

Uno de los factores limitantes para la interpretación de los datos históricos de razones isotópicas es el conocimiento de los cambios en la línea de base. Como la abundancia relativa de los dos isótopos estables del nitrógeno, indicadora del nivel trófico de un consumidor, se ve fuertemente influida por cambios en las tasas de fijación y desnitrificación, se puede llegar a conclusiones erróneas en ausencia de dicha información. Esto podría explicar la disparidad de resultados obtenidos durante los últimos años. Así, el nivel trófico de los pinnípedos del Mar del Norte parece haber aumentado desde el Holoceno (Bailey et al. 2008), mientras que el de los lobos marinos antárticos de Georgia del Sur (*Arctocephalus gazella*) ha disminuido al recuperarse la población tras el cese de la persecución humana (Hanson et al. 2009). Sin embargo, no parecen existir diferencias entre el nivel trófico de los pinnípedos del Holoceno de California y Alaska o de las nutrias marinas en el mar de Alaska y el del sus equivalentes modernos (Burton et al. 2001, Corbett et al. 2008). Tampoco se han encontrado diferencias en los valores de $\delta^{15}N$ del bacalao recuperado en los asentamientos medievales noruegos del Ártico y el bacalao moderno del Mar de Barents (Barrett et al. 2008), o en los lobos marinos comunes (*O. flavescens*) en el norte de la Patagonia durante el período de explotación comercial, durante su nadir demográfico y en la actualidad (Drago et al. 2009). Todo ello sugiere la estabilidad o incluso el incremento del nivel trófico de los depredadores a medida que la actividad humana altera los ecosistemas marinos.

Sin embargo, otros estudios indican lo contrario. Así, el nivel trófico de los pingüinos de Adélie (*Pygoscelis adeliae*) que nidifican en la Península Antártica parece haber disminuido durante los últimos 200 años, pero esto se debe a que la explotación ballenera del siglo XX causó indirectamente un fuerte aumento del krill, anteriormente no disponible para los pingüinos (Emslie y Patterson 2007). El mismo patrón se observa durante el siglo XIX con la marsopa (*Phocoena phocoena*) del Mar del Norte (Christensen y Richardson 2008) y el delfín listado (*Stenella caeruleoalba*) del Mediterráneo occidental durante la segunda mitad del siglo XX (Gómez-Campos et al. 2011).

Por todo ello, uno de los primeros objetivos de esta tesis doctoral fue determinar la variabilidad histórica de la línea de base isotópica. El método aquí empleado para ello ya había sido propuesto por Bailey et al. (2008), pero no había sido empleado aún en ningún trabajo publicado que sepamos. Un factor clave para el éxito del método es la existencia de una elevada correlación actual entre los niveles de productivida primaria y los valores de $\delta^{15}N$ en las valvas de los moluscos. Dicha correlación se ha podido comprobar a lo largo del litoral de Argentina para dos de las especies empleadas, la lapa (*N. magellanica*) y la cholga (*A. atra atra*), pero no para el mejillón (*M. edulis*). Esto puede ser debido a que esta especie emplee como alimento no sólo productores primarios marinos, sino también materia orgánica particulada de origen terrestre. En cualquier caso, gracias a la relación que existe entre la productividad primaria y el valor de $\delta^{15}N$ de las valvas de dos especies del intermareal rocoso, comprobamos que a lo largo del Holoceno medio-tardío se produjeron grandes cambios en la productividad marina. Tanto en la zona de la Península Valdés (Patagonia septentrional) cómo en el Canal del Beagle (Tierra del Fuego) la productividad marina fue más alta en todas las épocas pasadas consideradas pero, mientras que en el sur se produjo un descenso paulatino, en el norte se registraron algunas fluctuaciones. En concreto, hacia finales del Holoceno medio la productividad primaria era alta y se mantuvo constante (incluso subió) hasta hace unos 2000 años AP. Hace aproximadamente 1700 años AP la productividad primaria disminuyó, para luego volver a aumentar hace 600 años AP. A partir de ese momento se registró una disminución constante hasta llegar al día de hoy.

Aunque se hayan registrado diferencias en los patrones de productividad entre las dos zonas estudiadas, tanto en el centro-norte como en el sur de la Patagonia las épocas de intensa explotación de los pinnípedos, tal cómo aparece en el registro zooarqueológico (Gómez Otero 2006; Favier Dubois et al. 2009; Yesner et al. 2003; Tivoli y Zangrando 2011), coinciden con épocas de elevada productividad marina. Por lo tanto se puede concluir que la disminución de pinnípedos en el registro subfósil en ambas zonas está más relacionada con un control del ecosistema por los productores primaros (contro desde debajo) que no con una sobreexplotación por parte de lo cazadores-recolectores. La reducción de la talla media de los lobos finos capturado durante la segunda mitad del Holoceno, interpretada como una consecuencia de la rarefacción de la especie debido a la caza (Zangrando et al. 2013), también puede ser explicada por la reducción de la productividad primaria, pues el tamaño corporal de los pinnípedos disminuye al hacerlo la disponibilidad de alimento per capita (Hanson et al., 2009; Drago et al. 2010).

La productividad primaria no es el único factor ambiental que pudo haber cambiado durante la segunda mitad del Holoceno, por lo que también se afrontaron los posibles cambios de temperatura superficial del mar. La concentración de isótopos estables de oxígeno ($\delta^{18}O$) en valvas de moluscos es actualmente uno de los indicadores más robustos de la temperatura superficial del mar (SST), no presentando aparentemente cambios ontogenéticos durante el crecimiento del animal (Schone et al. 2004). Sin embargo hay que considerar que la salinidad también afecta a la ratio $^{18}O/^{16}O$ en la muestra (Bowen 2010) y por lo tanto no hay que confundir variaciones en la temperatura con variaciones en la salinidad (Epstein et al. 1951, Wefer et al. 1991, Schone et al. 2004, LeGrande y Schmidt 2006). En la presente tesis doctoral hemos visto que los valores de $\delta^{18}O$, inversamente proporcionales a la temperatura, tienen un patrón temporal similar en el centro-norte de Patagonia y en el Canal del Beagle (Tierra del Fuego). En concreto eran más altos (temperaturas más bajas) a finales del Holoceno medio (hace 6000-5000 años) que en la actualidad y más bajos que los actuales a lo largo de la mayor parte del Holoceno tardío (correspondientes a temperaturas más altas), salvo en el pico correspondiente a la Pequeña Edad de Hielo. Estos valores pueden traducirse, en el caso del centro-norte de Patagonia, en valores de SST, pues hay estudios que confirman que a lo largo del Holoceno no se produjeron cambios de salinidad en la zona (Aguirre et al. 2006). No puede decirse lo mismo para el Canal del Beagle, donde actualmente hay continuas aportaciones de agua dulce desde los glaciares, y por el clima lluvioso. La acción sinérgica de temperatura y salinidad, por ejemplo, puede explicar los valores tan elevados de $\delta^{18}O$ que se observaron hace alrededor de 890 años AP.

Teniendo en consideración estas aclaraciones se puede afirmar que, mientras los patrones de temperatura varían de forma paralela en las dos zonas, no sucede lo mismo con la abundancia de pinnípedos en el registro subfósil. En el centro-norte de Patagonia, por ejemplo, el aumento de la explotación del lobo marino común coincide con épocas más cálidas y su disminución lo hace con una época de temperaturas estables, hace uno 700-1500 años. Lo contrario sucede en el Canal del Beagle, donde el inicio de la explotación de lobos marinos finos coincide con temperaturas bajas, disminuye a medida que aumenta la temperatura, pero no remonta en la siguiente época fría, correspondiente a la Pequeña Edad de Hielo. En consecuencia parece poco probable que los cambios en la SST fueran el principal motor de las variaciones observadas en los patrones de explotación de los recursos marinos por los cazadores-recolectores de las dos zonas estudiadas, y en particular de los pinnípedos. En cambio, dichas variaciones seguramente fueron motivadas por cambios en la producción pimaria marina y los cambios subsiguientes en las poblaciones de pinnípedos.

Si realmente el impacto de los cazadores-recolectores fue mínimo sobre las poblaciones de pinnípedos, entonces podemos emplear la razón isotópica de los huesos de lobo fino y lobo común procedentes de los fogones aborígenes para comparar el nicho trófico de estas especies durante la segunda mitad del Holoceno con el actual, así como la estructura de las redes tróficas pasadas y modernas.

La dieta del lobo marino común (*O. flavescens*) ha sido reconstruida a partir de las razones de isótopos estables de carbono y nitrógeno en hueso arqueológico en dos zonas del litoral argentino: el centro-norte de Patagonia (Chubut y Río Negro) y el sur de Patagonia (Canal del Beagle). En los fogones del centro-norte de Patagonia no se encontraron restos de lobo común anteriores a 3000 años AP, con lo cual hay que considerar que sólo se ha podido reconstruir su dieta en una época bien posterior a la llegada del hombre y a su impacto en el ambiente litoral (Grammer 2005; Gómez Otero 2007). Gracias a estudios previos en esta zona se sabe que los recursos marinos, como peces, moluscos, y crustáceos eran importantes para el sustento de los cazadores-recolectores de Río Negro y Chubut ya desde hace 6000 años AP aproximadamente, y que su uso se intensificó a partir de 3500 años AP (Gómez Otero 2006, 2007; Favier Dubois et al. 2009). De todas formas, ninguno de los autores citados apunta a una sobreexplotación de los recursos, con lo cual, y con las oportunas precauciones, se puede considerar la dieta reconstruida en este apartado para la zona de centro-norte Patagonia como representativa de unas condiciones prístinas. Por lo que concierne el sur de la Patagonia, se usaron restos procedentes de fogones más antiguos, de unos 5000 años AP. Aquí, aunque el uso de los recursos marinos por parte de los canoeros fue sin duda más intenso y más antiguo (Orquera et al. 2011), la especie más afectada fue en todo caso el lobo fino (*A. australis*), con lo cual los resultados para la dieta originaria del lobo común (*O. flavescens*) pueden considerarse concluyentes.

Gracias al uso de las conchas subfósiles encontradas en los fogones y pertenecientes a varias épocas del Holoceno medio y tardío, se han corregido las razones isotópicas de los huesos de los depredadores con los valores de la línea de base correspondiente por época y zona, para así poder interpretar correctamente las razones isotópicas de los depredadores.

En general se observa un aumento del $\delta^{15}N$ en el hueso del lobo común, y en consecuencia de su nivel trófico, en ambas zonas desde el Holoceno tardío hasta hoy pero de forma más marcada en el norte, mientras que el $\delta^{13}C$ aumenta de manera significativa sólo en el norte. Actualmente en la Patagonia septentrional las presas pelágicas tienen una razón isotópica más empobrecida en ^{15}N y ^{13}C respeto a las presas demersales con lo cual se puede concluir que en esa zona hubo un cambio en la dieta del lobo común de más pelágica a más demersal a lo largo del Holoceno tardío, concretamente a partir de 1300 años AP. Las causas de este cambio se desconocen, ya que tanto el impacto humano (Orquera y Gómez Otero

2007), como la temperatura superficial del mar (*capítulo 1.1*) o la productividad marina (*capítulo 1.2*) no parecen estar involucrados. En cualquier caso, sí se produce un gran cambio durante el siglo XX, cuando los lobos comunes del norte de Patagonia adoptan una dieta claramente más demersal que durante el Holoceno a la vez que sus poblaciones se reducen en sus mínimos históricos en consecuencia a la caza por parte de los europeos. Este mecanismo de denso-dependencia ya había sido estudiado para el lobo común a lo largo del siglo XX en la Península Valdés (norte Patagonia). Aquí se observó que su dieta no se modificaba tanto como consecuencia de la pesca moderna de la merluza (su presa potencial más importante en esa zona), sino más bien a medida que aumentaba la población de lobo común y con ello el grado de competencia intraespecífica (Drago et al. 2009). En el mismo período, es decir cuando la población de lobo común se estaba recuperando tras la época de caza, se observó una reducción de la talla corporal en su población (Drago et al. 2010), hecho que podría explicar la reducción del nivel trófico (Jennings y Warr 2003) y el consumo de presas más pequeñas (Costa et al. 2004). En el sur, en cambio, la razón isotópica de nitrógeno no cambia a lo largo de todo el Holoceno medio y tardío, para luego aumentar en el siglo XX, indicando por lo tanto un aumento del nivel trófico de las presas consumidas por el lobo común en el siglo XX con respeto a las épocas anteriores. Este resultado por un lado confirma que la presión de los cazadores-recolectores sobre esta especie no fue tan intensa en el Canal del Beagle como fue para el lobo fino, y por el otro que la caza moderna sí que influyó sobre su ecología trófica. En este caso, el cambio de $\delta^{15}N$ en el depredador se debe más probablemente al consumo de especies de nivel trófico más elevado, como la merluza (*Merluccius hubbsi*), la nototenia (*Patagonotothen ramsayi*) y el langostino argentino (*Pleoticus muelleri*), más que un cambio en el conjunto de presas, como pasaba en la Patagonia septentrional, ya que en esta zona las presas pelágicas y demersales tienen señales de carbono y nitrógeno parecidas en su conjunto. Destacar también que la razón isotópica de carbono correspondiente al siglo XIX queda completamente fuera del paisaje isotópico actual. Estos animales pertenecían a una época en la que ya prácticamente no quedaban lobos comunes en la costa Patagónica, como consecuencia de la caza comercial actuada por los Europeos, y su presencia era meramente esporádica (Bridges, 1949). Es probable por lo tanto que fuesen individuos divagantes, y que procedieran de otras zonas, verosímilmente de las islas Falklands/Malvinas, ya que en la actualidad la razón de carbono de esa zona es mucho más empobrecida en ^{13}C que la de la costa de Patagonia (Weiss et al., 2009).

Así como el lobo común ha cambiado su nicho trófico en el último siglo, y en la Patagonia centro-septentrional posiblemente antes, el lobo fino en la misma zona ha mantenido su dieta prácticamente sin alterar en los últimos 2200 años, comiendo básicamente pequeños peces pelágicos y crustáceos decápodos. Más al norte, en la región de Río de la Plata se observa que la dieta del lobo fino era posiblemente más pelágica hace 7000 años que hoy en día, aunque el nivel trófico se ha mantenido sin cambios. Estos resultados preliminares (ya que no disponemos de datos sobre la línea de base de esta región, sino que se utilizaron los del norte de la Patagonia) podrían tener una explicación paleoceanográfica, ya que parece altamente improbable que los cazadores-recolectores de esta zona hayan podido influir sobre la ecología trófica de la especie (Bonomo et al. 2013), igual que en la Patagonia centro-norte.

Por el contrario, en el sur de la Patagonia (Canal del Beagle) los canoeros explotaron durante varios milenios al lobo fino, cazándolo directamente en el medio marino mediante canoas y arpones con punta separable ya desde 6400 años AP (Orquera y Gómez Otero 2007). Sin embargo, y una vez corregidos para los cambios en el nivel de base, las razones isotópicas de los lobos cazados entre 6000 y 2600 AP no muestran cambios significativos. La dieta de la especie, durante todo el Holoceno medio y parte del tardío, estaría basada en especies con una razón isotópica similar a la de la nototenia (*Patagonotothen ramsayi*). Estos resultados confirmarían que en época pre-contacto el impacto humano sobre esta especie no fue relevante. Por otra parte, la gran mayoría de los restos encontrados en los fogones pertenecían a machos adultos o sub-adultos y la cacería no se realizaba en zonas de crías (Schiavini 1993), por lo que el impacto demográfico debería ser escaso.

Como ya se ha comentado con anterioridad, la disminución en la proporción de pinnípedos en el registro zooarqueológico (Yesner et al. 2003; Tivoli y Zangrando 2011) y la disminución en la longitud de la mandíbula (Zangrando et al. 2013) podría estar explicado por la disminución de la productividad primaria marina (*capítulo 1.2*). Entre 2600 años AP y las muestras inmediatamente posteriores transcurren casi 2500 años, tiempo en el que se registran cambios de temperatura, disminución de productividad primaria (*capítulos 1.1* y

1.2) y por encima de todo, se inicia la explotación por parte de lo europeos, que finalmente llevó a la extinció virtual de la especie en esta zona (Schiavini 1992). Las consecuencias de la caza se manifiestan en los restos de hace aproximadamente 100 años AP, donde se observa un cambio radical en las razones de carbono y nitrógeno con respeto a las épocas anteriores. La explicación más razonable de estas señales tan diferentes es que los animales analizados procedieran de otros sitios, externos al paisaje isotópico del Canal del Beagle, por ejemplo desde la Isla de los Estados, al sur de Tierra del Fuego, o de las islas Malvinas/Falkland, y se alimentaban de presas en gran medida con unas razones isotópicas muy diferentes. Para concluir, según los datos presentados en este apartado, la dieta del lobo fino habría cambiado de forma significativa al menos en la costa Pampeana, pasando de una dieta más pelágica (7000 años AP) a una dieta menos pelágica (presente). Mientras estos cambios podrían estar más relacionados con cambios de tipo ambiental, los cambios observados hace 100 años en el sur de Patagonia tendrían una explicación totalmente diferente, ya que la caza perpetrada a lo largo del siglo XVIII y XIX sobre esta especie habría llevado a su extinción local.

Si las dietas de dos de los tres depredadores apicales más abundantes en el ecosistema han cambiado en el último siglo como consecuencia del impacto humano, esto debería verse reflejado en las relaciones tróficas entre ellos y con la tercera especie aquí estudiada, el pingüino de Magallanes. Actualmente se ha visto que el reparto de recursos entre estas tres especies no se explica bien por las dimensiones corporales, salvo en Río de la Plata, sino que la identidad de la especie es más importante. En otras palabras los nichos tróficos de machos y hembras de lobo común, lobo fino y pingüino de Magallanes se solapan de una forma impredecible, si sólo se consideran la masa corporal y la anchura de su boca/pico, excepto en la zona de Río de la Plata, pero machos y hembras de la misma especie siempre son más parecidos entre sí de lo esperado. Así vemos como la hembra de lobo común se solapa con el macho de la misma especie, que es mucho más grande y por lo tanto podría estar comiendo a una profundidad mucho mayor y cazar presas más grandes. Por el contrario, los machos de lobo fino y las hembras de lobo común, morfológicamente muy parecidos, no se solapan, ya que los primeros tienen una dieta mucho más pelágica que las segundas. Finalmente la topología de los depredadores dentro del espacio $\delta^{13}C$-$\delta^{15}N$ varía regionalmente, siendo positiva la relación entre el solapamiento y la latitud. Una explicación por el aumento del solapamiento en latitudes altas podría ser la disminución de diversidad que se observa en la plataforma continental patagónica (Cousseau y Perrotta 2000; Miloslavich et al. 2011), y por lo tanto la convergencia de los tres depredadores hacia las mismas especies de presa.

En realidad, este acortamiento de la red trófica y el incremento del solapamiento al aumentar la latitud no sucede sólo entre estas tres especies, sino en el conjunto del ecosistema, como se pone de manifiesto en el *capítulo 3.2*. Las causas de estos resultados podrían ser de origen natural, como la disponibilidad de los recursos, la talla de los animales que la constituyen, la talla del ecosistema, su historia y el régimen de perturbación natural (Cohen et al. 1993, Post 2002a, Jennings 2005), pero también antropogénico (Post 2002a, Koen-Alonso y Yodzis 2005). Sin embargo en nuestro caso es difícil relacionar este patrón con factores naturales claros ya que, por ejemplo, se observa una relación inversa entre la longitud de la cadena trófica y la variabilidad estacional en la temperatura superficial del mar, un patrón opuesto al que se propuso para otras zonas (Jennings y Warr 2003). La productividad marina no parece tampoco explicar el patrón encontrado en nuestro estudio, puesto que el valor más elevado de productividad se halla en el norte de Patagonia (Piola y Falabella 2009), pero la longitud de esa zona es intermedia entre Río de la Plata y sur de Patagonia. Por lo tanto el acortamiento de la cadena hacía el sur y el aumento de su redundancia, a la vez que la disminución de la diversidad trófica, parecen estar relacionados más con un cambio en la dieta de los depredadores apicales hacia presas de un menor nivel trófico que a otros factores ambientales (Post y Takimoto 2007). Esta explicación tendría sentido también a la luz de los resultados de *capítulo 3.1*, donde hemos visto que en el sur de la Patagonia los tres depredadores se solapaban mucho más que en las otras zonas y a pesar de sus diferecias morfológicas, convergiendo hacia las mismas especies de presa (p. ej. *Sprattus fueguensis* o *Munida subrugosa*). El impacto humano es también otro factor a tener en cuenta en el análisis de las redes tróficas en el Mar Argentino, como ya hemos visto en apartados anteriores. En particular el comportamiento denso-dependiente del lobo común, el depredador que tiene el nivel trófico más altos en la comunidad considerada, apuntaría a este tipo de explicación.

Para poder aclarar definitivamente la estructura original de las redes tróficas de la región y por lo tanto para entender mejor hacia donde debería evolver este ecosistema en el futuro, hemos recurrido nuevamente al registro zooarqueológico, esta vez, desde un punto de visto más amplio. Las muestras arqueológicas, tanto de la línea de base (lapas, mejillones y cholgas) como de los depredadores apicales (huesos de lobo común, lobo fino y pingüino de Magallanes), han sido agrupadas por épocas, ya que el análisis requería un cierto tamaño muestral y sucesivamente se han comparado con las muestras actuales. Por lo tanto, en la zona del centro-norte de Patagonia se han comparado la estructura de la red trófica del período pre-contacto (entre 5200 y 380 años AP aproximadamente) con la de la red trófica actual, mientras que en la zona del sur de Patagonia se han podido comparar tres períodos distintos: el período aborigen temprano (entre *ca.* 6000 y 1100 años AP), el período aborigen tardío (entre 1000 y 100 años AP) y el período actual.

En ambas regiones se ha observado un aumento en la longitud de la cadena trófica al desplazarnos del pasado al presente, además de un aumento en la diversidad trófica y a la disminución de la redundancia. Estos soprendentes resultados parecen contradecir la idea, ampliamente extendida, de que el impacto humano acortaría las cadenas tróficas (Pauly et al. 1998), pero en realidad confirman que el ecosistema ha sufrido unos cambios radicales a lo largo del Holoceno, sobre todo en los últimos dos siglos. En el sur de la Patagonia, de hecho, las redes tróficas correspondientes a las dos épocas arqueológicas consideradas no se distinguen sustancialmente la una de la otra, teniendo la misma longitud, el mismo rango de recursos a la base de la red y la misma diversidad, aunque el área de los nichos del lobo fino y del pingüino de Magallanes aumentan de más antiguo a menos antiguo. En consecuencia el solapamiento entre especies también aumenta, aunque este dato hay que tomarlo con cierta precaución, ya que la proporción de sexos en la muestra se desconoce y se ha demostrado que ello puede afectar al resultado.

Las mayores diferencias se observan tras la llegada de los europeos, y sobre todo después de la explotación masiva de pinnípedos a lo largo de los siglos XVIII y XIX. Explicaciones alternativas, como los cambios en la temperatura del mar y/o en la productividad, quedan descartadas, ya que no se observa ninguna corelación con los resultados obtenidos. Sin embargo hay que observar que, tanto en el presente como en el pasado, la red trófica del norte de Patagonia es mas larga de la del sur, lo cual confirmaría que lo que se observa en la actualidad tiene una explicación natural.

En conclusión, los resultados apoyan firmemente la hipótesis de que la explotación selectiva de los ecosistemas marinos, cuando se centra principalmente en depredadores apicales, lleva a cadenas más largas y menos solapadas, siempre y cuando los principales depredadores no están extintos, sino que sobreviven muy por debajo de la capacidad de carga del ecosistema. De esta manera se estarían alimentando ahora a un nivel trófico más alto que en el pasado, cuando la competencia intraespecífica era más alta. La situación podría ser muy diferente si la explotación humana fuese dirigida a niveles tróficos intermedios, como sucede en la pesca industrial, y a la vez los principales depredadores estuviesen protegidos legalmente, que es la situación esperable en el futuro más próximo. En este caso, cabe esperar una disminución de los recursos disponibles per capita, un incremento de la competencia intraespecífica y una nueva reducción del nivel trófico.

CONCLUSIONES

- ✓ La temperatura superficial del Mar Argentino aumentó al comienzo del Holoceno tardío y fue ligeramente más alta que en la actualidad durante la mayor parte de ese período, excepto durante la Pequeña Edad de Hielo.
- ✓ Si bien los cambios de temperatura fueron paralelos en la Patagonia septentrional y meridional lo mismo no puede afirmarse en los patrones de explotación de lo pinnípedos según como aparece en el registro zooarqueológico, ya que no susistió ninguna relación entre estas dos variables.
- ✓ La productividad primaria marina en el sur de la Patagonia disminuyó paulatinamente durante el Holoceno medio y tardío, mientras que en la Patagonia centro-septentrional fluctuó para luego disminuir en los últimos 600 años.
- ✓ Se observó una clara relación entre productividad marina y patrón de explotación de los pinnípedos en ambas zonas, evidenciando que los cazadores-recolectores dependían intensamente de los pinnípedos sólo en épocas de productividad alta. Por lo tanto la disminución en la abundancia de pinnípedos observada en el registro zooarqueológico fue causado por un control *bottom-up* y no por la sobreexplotación de los cazadores-recolectores.
- ✓ La dieta del lobo marino común en el centro-norte de Patagonia fue más pelágica hace 3000-2000 AP que en la actualidad, aunque ya hace 1000 AP hubo un primer cambio a una dieta más demersal.
- ✓ Viceversa en el sur de la Patagonia su dieta fue prácticamente estable durante todo el Holoceno medio y tardío para luego cambiar de repente hace 100 años. Actualmente el nivel trófico del lobo común es más alto que en todas las épocas anteriores, hecho que estaría relacionado con la reducción drástica de la población local por parte de los europeos en los siglos XIX y XX y por lo tanto por una disminución intraespecifica de los sobrevivientes.
- ✓ La dieta del lobo fino en la costa pampeana era más pelágica hace 7000 años AP que ahora, hecho que no se relacionaría con el impacto humano (prácticamente nulo), sino con cambios en los regímenes oceanográficos.

- ✓ En la región del centro-norte de Patagonia no se observaron cambios en la dieta del lobo fino en los últimos 2200 años ya que tanto en el pasado como ahora estaría basada en pequeños peces pelágicos y crustáceos decápodos.
- ✓ En cambio en el sur de Patagonia la dieta se mantuvo estable entre 6000 y 2600 años AP, no obstante la caza perpetrada por los canoeros para su subsistencia. Hace 100, igual que para el lobo común, el lobo fino parece "escaparse" del paisaje isotópico actual para ir a forrajear en otras áreas geográficas, verosímilmente en la Isla de los Estados o en las Falklands/Malvinas. Actualmente su dieta ha vuelto a ser parecida a lo que era hace 5000-2600 años AP, pero con un nivel trófico ligeramente inferior. Los cambios recientes en la dieta del lobo fino estarían otra vez relacionados con el impacto humano de los siglos XVIII y XIX.
- ✓ Se observó que actualmente la repartición de los recursos entre lobos comunes, lobos finos y pingüinos de Magallanes no está relacionada con las dimensiones del cuerpo, sino con la identidad específica.
- ✓ En la red trófica actual se observó un gradiente latitudinal decreciente en la longitud y creciente en la redundancia, probablemente debido a la disminución de la diversidad que se observa en la plataforma patagónica argentina.
- ✓ Viceversa el alargamiento de la red trófica actual, el aumento de su diversidad y la reducción de su redundancia comparado con épocas anteriores estarían relacionados con los cambios radicales que sufrió el ecosistema por causa humana a lo largo del Holoceno, y sobre todo en los últimos dos siglos.


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APÉNDICE: ARTÍCULOS PUBLICADOS