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Dirección de Postgrado
Facultad de Ciencias Naturales - Programa de Doctorado en Oceanografía

Presencia acústica de ballenas azules (*Balaenoptera musculus*) y condiciones de forrajeo en el golfo Corcovado, Patagonia chilena

(Acoustic presence of blue whales (*Balaenoptera musculus*) and foraging conditions in the Corcovado Gulf, Chilean Patagonia)

Tesis para optar al grado de Doctor en Oceanografía

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La Tesis de Doctorado en Oceanografía titulada "*Presencia acústica de ballenas azules (Balaenoptera musculus) y condiciones de forrajeo en el golfo Corcovado, Patagonia Chilena*", de la Srta. Susannah J. Buchan y realizada bajo la Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, ha sido aprobada por la siguiente Comisión de Evaluación:

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A las investigadoras que me preceden, mi madre y mi bisabuela
A la Patagonia, su gente, sus paisajes y sus ballenas, que transformaron mi existencia
Por la esperanza de un océano lleno de vida siempre.

"*Eventually man, too, found his way back to the sea. Standing on its shores, he must have looked out upon it with wonder and curiosity, compounded with an unconscious recognition of his lineage. He could not physically re-enter the ocean as the seals and whales had done. But over the centuries, with all the skill and ingenuity and reasoning powers of his mind, he has sought to explore and investigate even its most remote parts so that he might re-enter in mentally and imaginatively.*"

- Rachel Carson, *The Sea Around Us*

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Finalizar con esta Tesis de Grado es también acabar con un primer capítulo de una larga y soñada, a veces dura pero bellísima aventura, que empezó de pequeña admirando las ballenas del Atlántico Norte, con la realización devastadora que ya quedaban tan pocas. Esto me llevó, años más tarde, a las costas del gran Pacífico Sur Austral en búsqueda de ellas. Estoy profundamente agradecida a estos animales asombrosos por sus enseñanzas y sus misterios, por darme la oportunidad de cumplir este sueño, y de poder seguir su camino adonde me lleve.

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RESUMEN

Esta Tesis de grado busca generar conocimiento relevante acerca de la distribución y ecología de la ballena azul *Balaenoptera musculus* y de la oceanografía de su hábitat de alimentación en la Patagonia chilena. Mediante dicho conocimiento, esta investigación busca contribuir a fomentar la conservación de este animal emblemático en peligro de extinción y de su ambiente marino único, el cual es expuesto a presiones antrópicas cada vez más importantes.

Los objetivos principales de la Tesis son:

1) Caracterizar el canto de las ballenas azules que se alimentan en la Patagonia chilena durante el verano austral y compararlo con los reportes de cantos regionales para el Océano Pacífico, con el fin de entender la identidad acústica de las ballenas azules del Pacífico Suroriental y los posibles nexos acústicos en el Pacífico Suroriental (Capitulo 1).
2) Determinar la ocurrencia estacional de cantos de ballenas azules del Pacífico Suroriental en su zona de alimentación en la Patagonia chilena, y en el Pacífico Tropical Oriental, el cual correspondería a una posible zona para invernar (Capitulo 2).
3) Analizar las características oceanográficas que explican la ocurrencia de sitios de alimentación y las condiciones óptimas para el forrajeo para ballenas azules en el golfo Corcovado (Capitulo 3).

La identidad, distribución y desplazamientos de ballenas azules que se alimentan en la ecorregión Chiloense de la Patagonia chilena son poco conocidos. Los estudios de cantos de ballenas azules han identificado poblaciones acústicas, las cuales se caracterizan por sus tipos de canto, rangos geográficos, rutas de migración y residencias estacionales. El Capítulo 1 presenta el primer estudio bioacústico (2008-2011) de ballenas azules en Chile y caracteriza el canto regional de este grupo de ballenas del Pacífico Suroriental mediante el uso de un hidrófono móvil en el Golfo Corcovado. Un nuevo tipo de canto se encontró para este grupo, además de establecer un nexo acústico con registros acústicos ya reportados para el Pacífico Tropical Oriental. Esta caracterización de los cantos regionales Pacifico Suroriental “SEP” permitirá rastrear el grupo de ballenas azules que se alimentan en la Patagonia chilena mediante el Monitoreo Acústico Pasivo en el futuro. El nexo acústico sugiere un rango de desplazamiento de este grupo de ballenas entre la Patagonia chilena y el Pacífico Tropical Oriental.

El Capítulo 2, mediante el Monitoreo Acústico Pasivo con hidrófonos anclados en el fondo marino, se focaliza en determinar la presencia estacional de cantos SEP en la Patagonia chilena (2012 - 2013), y el Pacífico Oriental Tropical (1996 - 2002). Se encontró un fuerte patrón estacional de una gran cantidad de cantos SEP en la Patagonia chilena entre diciembre y agosto, con una máxima en el periodo marzo-mayo. Así por primera vez, se obtiene información sobre la distribución anual de ballenas azules en la Patagonia chilena. En el Pacífico Tropical Oriental, los cantos fueron menos numerosos pero presentes todo el año, con una máxima alrededor de junio. Estos resultados sustentan la hipótesis de una residencia estacional de ballenas azules en la ERC durante el verano/otoño austral, y un desplazamiento estacional hacia el Pacífico Tropical Oriental durante junio/julio, retornando en diciembre. Estos datos también indican que algunas ballenas azules se quedarían todo el año en la región del Pacífico Tropical Oriental.

Por último, para lograr un mejor entendimiento de la presencia de ballenas azules en la Patagonia chilena, el Capítulo 3 presenta un estudio oceanográfico del sector suroriental del golfo Corcovado (43°38’-44°01’S, 73°38’-73°01’W), un lugar preferido por ballenas azules durante los meses de verano. Esta investigación evalúa la variabilidad temporal de condiciones ambientales asociadas a eventos de forrajeo y contrasta las diferencias de condiciones oceanográficas entre sitios de alimentación y temporadas de muestreo. Datos de avistamientos de ballenas azules y variables ambientales *in situ* y satelitales fueron colectados durante los veranos australes de 2011-2013 e invierno 2012 en un sitio de alimentación más oceánico (Archipiélago de los Chonos) y uno más continental (bahía de Raúl Marín Balmaceda). Estos son los primeros datos oceanográficos *in situ* asociados a avistamientos de ballenas azules en conducta de forrajeo en esta remota área del Pacífico Suroriental. Los resultados sugieren que las influencias de las distintas masas de agua (oceánicas y continentales) y la presencia de zonas de retención de plancton producido por la topografía podrían ser factores importantes para generar las condiciones adecuadas para la existencia de una abundancia suficiente de eufáusidos para el forrajeo de ballenas azules del Pacífico Suroriental en el sistema megaestuarino de la Patagonia chilena. Estos resultados se discuten en el contexto de la conservación de las ballenas azules en la Patagonia chilena.

ABSTRACT

This Doctoral Thesis seeks to fill certain key knowledge gaps relating to the distribution and ecology of blue whales *Balaenoptera musculus* and the oceanography of their feeding ground habitat in Chilean Patagonia. With this knowledge, this research aims to contribute to the conservation of this emblematic and endangered species and its unique marine environment, which is increasing exposed to growing anthropogenic threats.

The main objectives of this Thesis are to:

1) Characterize the song type of the blue whales which feed in Chilean Patagonia during the austral summer and compare it with reports of regional blue whales songs in the Pacific Ocean, with the aim of understanding the acoustic identity of Southeast Pacific blue whales and possible acoustic links in the Southeast Pacific (Chapter 1).
2) Determine the seasonal occurrence of Southeast Pacific blue whales songs within their feeding ground in Chilean Patagonia, but also in the Eastern Tropical Pacific, a possible wintering ground (Chapter 2).
3) Analyse the oceanographic characteristics that explain the occurrence of feeding sites and optimal foraging conditions for blue whales in the Corcovado Gulf (Chapter 3).

The identity, distribution and movements of blue whales which feed in the Chiloense Ecoregion in Chilean Patagonia are poorly understood. Studies of blue whales song types have been used to identify acoustic populations which share the same song type, geographic range, migration movements and seasonal residencies. Chapter 1 is the first bioacoustics study of blue whales in Chile (2008-2011) and characterizes the regional song type for this group of Southeast Pacific blue whales using dipping hydrophone recordings from the Corcovado Gulf. A new song type was recorded for this group, and an acoustic link was established with the Eastern Tropical Pacific. This characterization of the Southeast Pacific “SEP” regional song types will allow to track the blue whales that feed in Chilean Patagonia in future Passive Acoustic Monitoring studies. The acoustic link established suggests a movement range between Chilean Patagonia and the Eastern Tropical Pacific.

In Chapter 2, via Passive Acoustic Monitoring with fixed hydrophones, the seasonal occurrence of SEP blue whales songs was determined in Chilean Patagonia (2012 - 2013) and also in the Eastern Tropical Pacific (1996 - 2002). A strong seasonal pattern was found, with a high number of SEP blue whale songs, between December and August with a peak during March and May. This is the first data on the annual distribution of blue whales in Chilean

Patagonia. In the Eastern Tropical Pacific, songs were less numerous but present year round, with a maxima around June. These results support the hypothesis of seasonal residency of blue whales in Chilean Patagonia during the austral summer/autumn, with a seasonal movement towards the Eastern Tropical Pacific during June/July, returning south in December. These data also indicate that some blue whales remain in the Eastern Tropical Pacific year-round.

Lastly, to further the understanding of blue whale presence in Chilean Patagonia, Chapter 3 presents an oceanographic study of the southeast Corcovado Gulf (43°38’-44°01’S, 73°38’-73°01’W), a location preferred by blue whales during the summer months. This research assesses the temporal variability of environmental variables associated with feeding events and contrasts the differences in oceanographic conditions between feeding sites and sampling seasons. These are the first *in situ* oceanographic data associated with sightings of foraging blue whales in this remote area of the Southeast Pacific. The results suggest that the influence of different water masses (oceanic and continental) and the presence of topographically-driven retention areas for planktonic organisms could be important factors in generating suitable conditions for the occurrence of sufficient euphausiid densities for foraging Southeast Pacific blue whales in the megaestuarine system of Chilean Patagonia. These results are discussed within the conservation context of Chilean Patagonia.

INTRODUCCIÓN

1.1 De la caza a la conservación

Durante la época de caza industrial de ballena, las poblaciones de ballenas azules (*Balaenoptera musculus*) fueron reducidas a una fracción mínima de la abundancia existente pre-explotación, sobretodo en el hemisferio sur (Branch et al. 2004, 2007b). El casi exterminio de las especies de ballenas por la caza comercial fue el primer caso emblemático de colapso de un recurso biológico marino por causas antrópicas.

En Chile, las estadísticas oficiales registran 2.982 ballenas azules capturadas entre 1929 y 1971 en las costas de Chile continental. En el caso de la Antártica chilena, se capturaron 27.720 individuos entre 1911-1929, y 1.500 individuos entre 1946 y 1963 (Aguayo-Lobo et al. 1998). Así, la ballena azul representó el tercer recurso ballenero (31% del total comercial de misticetos) a nivel nacional, superado solo por el rorcual común (*Balaenoptera physalus*; 47% del total comercial de misticetos) y el cachalote (*Physeter macrocephalus*; 75% del total de cetáceos comerciales) (Aguayo-Lobo et al. 1998).

A nivel mundial, la población de ballenas azules permanece reducida a una cifra entre 10.000 y 25.000 individuos, es decir 3-11% de la población correspondiente a la etapa de pre-explotación (www.iucnredlist.org). Por consiguiente, es una de las especies de ballenas más amenazadas del mundo, y por tanto se encuentra clasificada en la categoría “En Peligro de Extinción” por la Unión Internacional para la Conservación de la Naturaleza (UICN; www.iucnredlist.org/) (Reilly et al. 2008). En el Hemisferio Sur, la Comisión Ballenera Internacional estima una población de ballenas azules de 2.300 individuos (www.iwcoffice.org/). En Antártica la población actual es de 1.700 individuos, es decir 0,7% de la población pre-caza (Branch et al. 2004). La población del Pacífico Suroriental (PSO) es aún menos conocida, pero la UICN infiere, a partir de lo reportado por Findlay et al. (1998), una abundancia de unos pocos miles de individuos. Esto coincide con Williams et al. (2011) quienes estimaron que la abundancia actual de ballenas azules del PSO es 4-18% de una población pre-explotación estimada en 2.000-6.200 individuos. Desafortunadamente, las ballenas azules del PSO corresponden a uno de los grupos menos entendidos y menos estudiados de esta especie a nivel global. A modo de ejemplo, las prospecciones realizadas por Findlay et al. (1998) y

William et al. (2011) no abarcaron el área de alimentación de la ecorregión Chiloense en el Sur de Chile que fue descubierta en el año 2003 por Hucke-Gaete et al. (2003).

Desde el término de la caza industrial en el año 1985, todos los países oficialmente protegen a las ballenas azules, prohibiendo su captura (www.iwcoffice.org/). En algunos pocos países, existen además medidas de conservación eficaces para reducir las amenazas antrópicas, por ejemplo el plan de manejo de la National Oceanic and Atmospheric Administration en EE.UU. para reducir el riesgo de colisión con embarcaciones mayores. En efecto, sin la amenaza de la caza comercial, el riesgo de colisiones con buques se ha transformado en la mayor amenaza para la conservación de ballenas azules, dado los altos y crecientes niveles de tráfico marítimo (Barlow et al. 1995; Irvine et al. 2014). Por otro lado, el pequeño tamaño poblacional de las ballenas azules junto a su dependencia sobre solo un grupo de presas (estenofagia), en este caso los eufáusidos, reducen la resiliencia de las poblaciones de ballenas azules frente a perturbaciones ambientales y antrópicas, limitando la recuperación del tamaño poblacional (Clapham et al. 1999). Es por eso que la protección de zonas de hábitat crítico, como son las zonas de alimentación, reproducción y rutas de migración, es fundamental para la recuperación de esta especie.

A nivel mundial, no se han identificado las zonas de reproducción de ballenas azules, aunque se asume que estas se encontrarían en latitudes bajas (Mackintosh & Wheeler 1929), y las rutas migratorias son difíciles de delimitar. Por lo tanto, los esfuerzos de conservación se han concentrado en la identificación y protección de las áreas de alimentación costeras (ej. en EE.UU.: http://sanctuaries.noaa.gov/).

1.2 Un área de alimentación en la Patagonia chilena

Áreas de alimentación de ballenas azules han sido reportadas para California (Calambokidis et al. 1990; Fiedler et al. 1998; Mate et al. 1999; Croll et al. 2005 entre otros), el golfo de Saint Lawrence (Sears et al. 1987), el sistema de surgencia del Sur de Australia (Gill 2002), el Océano Austral (Laws 1985), el Océano Indico (Alling et al. 1991; de Vos et al. 2014), Nueva Zelanda (Torres 2013), y la Patagonia chilena (Hucke-Gaete et al. 2003).

En la Patagonia chilena, la zona de alimentación abarca principalmente el golfo Corcovado, y las aguas oceánicas y del Mar Interior de la isla Grande de Chiloé (≈41-43°S). Estas localidades se ubican en la ecorregión marina Chiloense (ECR; 41°30-47°00’S) (Spalding et al. 2007). Una ecorregión marina es una clasificación biogeográfica que delimita un área en función de su composición común de especies, la predominancia de una cantidad limitada de ecosistemas distintos y/o características topográficas u oceanográficas particulares (Spalding et al. 2007). Más allá de la ERC, se han reportado avistamientos de ballenas azules en las costas de Chile Central y el Norte del país, así como en Isla de Pascua (Aguayo-Lobo et al. 1998), y más específicamente registros de ballenas azules alimentándose en verano en la costa de Valdivia (40°S; Hucke-Gaete *no publicado*) y en Chañaral de Aceituno (29°S; Moraga *no publicado*).

En base a prospecciones sistemáticas, se estima una abundancia total de 222 individuos ballenas azules (95% CI = 115-430) concentrados en la ECR (Hucke-Gaete et al. 2010). Por otra parte, Williams et al. (2011) realizó una estimación de abundancia para toda la zona Norte y Central de Chile (18-38°S), estimando una abundancia de 303 individuos (95% CI = 176-625), presentando una mayor abundancia entre los 26 y 33°S. Sin embargo, la aparente mayor densidad de ballenas azules observada en la ERC (Hucke-Gaete et al. 2010) sugiere que esta región sería una de las áreas de alimentación más importantes para las ballenas azules que habitan el PSO, lo cual otorga especial importancia a este ecosistema en la recuperación de este grupo de animales.

1.3 Conservación de la ballena azul y de su hábitat en la Patagonia chilena

Existen varias amenazas a la conservación marina en esta región de la Patagonia chilena, principalmente la salmonicultura (ej. McVicar 1997; Asche et al. 1999; Buschmann 2006; Cabello 2006; Costa-Pierce 2008) y la sobreexplotación pesquera (Neira et al. 2014; SUBPESCA 2014). Por otra parte, hasta la fecha no se ha evaluado el impacto del tráfico marítimo creciente sobre los cetáceos en la Patagonia chilena, el cual corresponde actualmente a la principal amenaza a nivel mundial para los cetáceos mayores (Barlow et al. 1995; Irvine et al. 2014). Asi, en la costa chilena, hay evidencias de colisiones fatales y no fatales entre buques mayores y ballenas (Van Waerebeek et al. 2007), incluyendo a ballenas azules en el Golfo Corcovado (Hucke-Gaete et al. 2005).

La necesidad de un ordenamiento territorial costero efectivo que incorpore la protección de cetáceos se hace cada vez más necesario en la Patagonia chilena. En este sentido, una especie tan emblemática como la ballena azul, el animal más grande que haya existido en la historia de nuestro planeta, puede servir como especie bandera (Simberloff 1998; Zacharias & Roff 2001) para fomentar estrategias de conservación de hábitats marinos en esta región, como por ejemplo la creación de Áreas Marinas Protegidas de Múltiples Usos (AMP-MU). De hecho, desde marzo 2014, la bahía de Raúl Marín Balmaceda y la bahía Tic Toc en el límite oriental del golfo Corcovado cuentan con figuras de protección (AMP-MU y Parque Marino, respectivamente; www.gob.cl), lo cual representa un importante y bienvenido avance, pero sigue siendo una fracción muy pequeña de la superficie marina de la región norte de la Patagonia chilena. Por otra parte, existe una propuesta para la creación de un AMP-MU más grande (Hucke-Gaete et al. 2010), en donde el golfo Corcovado se destaca como una zona prioritaria para la conservación marina, pero lamentablemente hasta la fecha este proyecto no se ha podido concretar.

Para el hábitat de la ballena azul en la Patagonia chilena, la mayoría de las zonas críticas de alimentación permanecen sin mecanismos legales de protección. Es necesario identificar estas zonas y fomentar estrategias de manejo y protección apropiados. Esta tesis se inserta en esta perspectiva, buscando contribuir en la generación de conocimiento para cubrir algunos vacíos de conocimientos, en especial en términos de la distribución estacional y la ecología del forrajeo de ballenas azules en la Patagonia chilena.

1.4 Las ballenas azules del Pacífico Suroriental: poblaciones y migraciones

Para lograr estrategias de manejo apropiadas para la conservación de la ballena azul y de sus hábitats críticos, es necesario determinar la identidad de grupos y poblaciones, y delimitar espacio-temporalmente sus distribuciones y migraciones. Específicamente, esta información es relevante para la creación de Áreas Marinas Protegidas y la planificación de rutas marítimas para evitar colisiones y la degradación de potenciales hábitats críticos (ej. http://sanctuaries.noaa.gov/).

Las subespecies de ballenas azules actualmente descritas son: *B. m. musculus* del hemisferio norte; la ballena azul Antártica *B. m. intermedia*; y la ballena azul pigmea *B. m. brevicauda* (Branch et al. 2007a, b). Se reconoce desde hace poco una cuarta subespecie para el Océano Indico (*B. m. indica)* (www.iucnredlist.org/). Anteriormente, se clasificaba las ballenas azules chilenas como *B. m. brevicauda* (Aguayo-Lobo et al. 1998) pero su identidad se ha cuestionado. En el año 1978, Clarke et al. (1978) planteó que este grupo podría ser una subespecie distinta y/o población delimitada. Esta noción se sustenta en datos morfológicos (Branch et al. 2007a), su distribución en verano (Branch et al. 2007b), análisis genéticos (Conway 2005; LeDuc et al. 2007; Torres-Florez et al. 2014a, b), y la existencia de un dialecto regional de canto distinto (Cummings & Thompson 1971; Buchan et al. 2010, 2014). Actualmente, la Sociedad de Mamíferos Marinos de EE.UU. (www.marinemammalscience.org/) clasifica las ballenas azules chilenas como una subespecie sin nombre; en tanto que la UICN se refiere simplemente a la población de ballenas azules del PSO.

En la Patagonia chilena, se pueden observar ballenas azules entre diciembre y abril en la zona de Chiloé y el golfo Corcovado (Hucke-Gaete et al. 2003; Cabrera et al. 2005; Zamorano-Abramson & Gibbons 2010; Galletti-Vernazzani et al. 2012). Hasta la presente investigación (Buchan et al. 2014, Capítulo 2), no había habido una serie de tiempo de un año completo para determinar la presencia de ballenas azules en la ERC durante los otros meses del año, lo cual estaría vinculado posiblemente a sus desplazamientos estacionales de migración.

Se ha postulado, en base a información bioacústica, que las ballenas azules migrarían entre el golfo Corcovado y el Pacífico Tropical Oriental (PTO) (Stafford et al. 1999b; Buchan et al. 2014; Capítulo 2 de la presente Tesis). Desplazamientos norte-sur, consistentes con este patrón migratorio, han sido observadas por Hucke-Gaete (2004) en base al rastreo satelital de ballenas azules en el golfo Corcovado. Apoyando esta hipótesis son los avistamientos de ballenas azules en las costas de Chile Central y Norte (Aguayo-Lobo et al. 1998), así como en Perú (Gillpatrick & Perryman 2008); pero también en aguas más oceánicas frente a Perú y cerca de las islas Galápagos (Berzin 1978; Donovan 1984; Palacios 1999; Gilpatrick & Perryman 2008). Por otra parte, se ha postulado la existencia de ballenas azules residentes en el PTO denominado el “biostock de Galápagos” (Berzin 1978) o ‘población tropical’ (Donovan 1984), lo cual también explicaría los avistamientos en el PTO.

1.5 Identidad acústica de ballenas azules

Según McDonald et al. (2006), el estudio de los cantos de las ballenas azules provee un método para dilucidar la estructura de la población mundial de ballenas azules. Los dialectos regionales de cantos pueden ser un indicador de la identidad poblacional, dado que son señales sociales que pueden reflejar patrones de desplazamientos y asociaciones actuales y recientes. Se piensa que en ballenas azules existen alrededor de nueve tipos de cantos regionales que son de carácter estable a escala de décadas (McDonald et al. 2006). Los cantos, a diferencias de sonidos aislados, son producidos por los machos por lo que se ha sugerido podrían tener alguna función reproductiva (Oleson et al. 2007). Así, el tipo de canto regional indicaría la 'identidad acústica' de una población o grupo de ballenas (McDonald et al. 2006) y son producidos adentro del rango migratorio completo de una población (Stafford et al. 1999a, 2001). La existencia de 'nexos acústicos' de cantos (*sensu* Stafford et al. 1999a) entre regiones reflejaría los movimientos migratorios de cada grupo (ej. Mellinger & Barlow 2003; Stafford et al. 1999a, b; Stafford 2003; Samaran et al. 2010), y las variaciones estacionales en la ocurrencia de cantos de un cierto tipo reflejaría la presencia estacional de ballenas azules en un punto fijo (Stafford et al. 1999b, 2001; Širović et al. 2009; McCauley & Jenner 2010).

Ante lo anteriormente expuesto, los **Objetivos 1 y 2** de esta Tesis se focalizan en la identidad acústica y los patrones de desplazamiento estacional de las ballenas azules que se alimentan en el golfo Corcovado.

1.6 Ecología de forrajeo de ballenas azules

Para la implementación de estrategias de conservación eficaces en zonas de alimentación, hay que comprender la ecología de forrajeo de las ballenas azules y los procesos oceanográficos fundamentales que influencian estas zonas. Esto ha sido principalmente estudiado en sistemas de surgencia costera, como los de California (ej. Croll et al. 1998, 2005) y Australia (ej. Gill 2002; Gill et al. 2011), en donde los procesos oceanográficos que modulan la productividad biológica son muy distintos al sistema megaestuarino característico de la Patagonia chilena (Palma & Silva 2004).

La ballena azul puede llegar hasta una longitud de 33 m y un peso de hasta 150 t (Yochem & Leatherwood 1985). Estos gigantes son depredadores estenofágicos de eufáusidos (Nemoto 1970) que para cumplir con sus importantes demandas energéticas requieren un consumo diario de 1 a 3 t de eufáusidos por individuo (Reilly et al. 2004; Croll et al. 2006; Goldbogen et al. 2011). Además, la dinámica energética de su comportamiento de alimentación (embestida lateral o rotación 360°) depende directamente de la densidad de agregaciones de eufáusidos (Acevedo-Gutiérrez et al. 2002; Goldbogen et al. 2012).

Este alto consumo de eufáusidos por parte de las ballenas azules tiene lugar mayormente durante el verano, en latitudes intermedias y altas, en zonas de alimentación de alta productividad estacional (Mackintosh & Wheeler 1929; Mate et al. 1999; Hucke-Gaete et al. 2003; Croll et al. 2005; Gill et al. 2011). Las ballenas azules seleccionan hábitats de alimentación donde ocurren altas abundancias y densidades de eufáusidos de forma recurrente, lo cual está asociado a focos de alta producción primaria generados por una combinación de procesos oceanográficos y características topográficas y batimétricas (Croll et al. 1998, 2005). En la corriente de California, la máxima abundancia y la máxima densidad de eufáusidos coinciden al final del verano/principio de otoño, ocurriendo con un desfase respecto a la máxima estacional de productividad primaria en primavera (Croll et al. 2005). Burtenshaw et al. (2004) determinaron que la máxima ocurrencia de cantos de ballenas tiene lugar al final de verano, interpretando que esta máxima coincide con la máxima abundancia de eufáusidos.

Mediante el rastreo satelital de cinco ballenas azules en el golfo Corcovado, Hucke-Gaete (2004) observó la preferencia de zonas específicas de alimentación: Tres individuos prefirieron el sector sur-suroriente del golfo Corcovado cerca del canal Moraleda y el norte de la isla Guafo de igual manera; un individuo prefirió la zona sur-suroriente exclusivamente; y otro prefirió el sector noroeste de la isla Grande de Chiloé. Además, avistamientos sistemáticos también apoyan la noción de una preferencia por el sector sur-suroriental del Corcovado (Hucke-Gaete 2004; Hucke-Gaete et al. 2010). Sin embargo, las características ambientales que influencian el forrajeo de ballenas azules no son conocidas.

En este contexto, el **Objetivo 3** de esta tesis busca entender mejor la ecología de forrajeo de ballenas azules en el Corcovado y los procesos oceanográficos que la modulan. Para esto se utiliza como caso de estudio dos sitios (o parches) de alimentación en el sector suroriente del golfo Corcovado.

1.7 Antecedentes oceanográficos del golfo Corcovado

La Corriente de Deriva del Oeste (“West Wind Drift”) llega a la costa de Sudamérica a una latitud de 42°S aproximadamente (variando de forma estacional; Gatica et al. 2009), dando origen al sistema de la Corriente de Humboldt (SCH) y a la Corriente del Cabo de Hornos (Arntz et al. 2006; Quiñones et al. 2010). Los fiordos y canales Patagónicos constituyen uno de los sistemas estuarinos más importantes del planeta (Palma y Silva 2004), pero sus condiciones climáticas y difíciles accesos han limitados la investigación oceanográfica en esta región, la cual se ha incrementado fuertemente a nivel nacional en los últimos 10 años.

El golfo Corcovado (Fig. 3.1) es un golfo abierto en la región más productiva de la Patagonia chilena, es decir la región norte (Pizarro et al. 2000; Montecino y Pizarro 2006; Iriarte et al. 2007; González et al. 2010). En el golfo Corcovado los niveles de Clorofila-a (Cl-a) satelital superan los 10 mg Cl-a m^{-3} (Hucke-Gaete 2004; Montecino & Pizarro 2006) y la productividad primaria promedia 5476,6 $mgCm^{-2}d^{-1}$ (González et al. 2010). Aguas Subantárticas (ASAA) a profundidades intermedias y profundas, y ricas en macro-nutrientes, entran al golfo por la boca de Guafo desde el océano Pacífico y se dirigen hacia el continente (Silva & Guzmán 2006; Sievers & Silva 2008). A su vez, las aguas dulces ricas en silicato llegan al golfo desde el continente, formando una capa superficial de aguas estuarinas que fluye hacia el océano Pacífico (Silva & Guzmán 2006; Sievers & Silva 2008).

En el límite norte del Archipiélago de los Chonos, existe un cañón submarino desde la boca de Guafo hasta la entrada del canal Moraleda, el cual facilita el transporte de ASAA hacia el sector sur-suroriental del golfo Corcovado (Sievers & Silva 2008). La distribución de ballenas azules asociada a esta característica topográfica ha sido reportada por Hucke-Gaete (2004). En este mismo sector desemboca el canal Moraleda que recibe las descargas continentales de los fiordos y ríos localizados más hacia el sur (Sievers & Silva 2008). En el sector norte del Moraleda, la circulación de microcuenca aumenta los tiempos de residencia (Salinas & Hormazábal 2004). La mezcla de estas masas de agua junto a tiempos de residencia más altos, podría explicar la alta producción primaria en esta zona y la presencia recurrente de ballenas azules alimentándose año tras año.

Euphausia vallentini es una especie de eufáusido subantártico circumpolar que se distribuye latitudinalmente entre 42°S y 60°S (John 1936, Baker et al. 1990) y que ha colonizado de manera exitosa los fiordos Patagónicos. De hecho, *E. vallentini* es la especie de mesozooplancton más abundante en los fiordos, contribuyendo con el 98% de la abundancia total de eufáusidos (Antezana 1976; Palma & Silva 2004; González et al. 2010) y alcanzando densidades de 18.460 ind. $1000m^{-3}$ (CIMAR 3 52°45'-55°58'S; Palma & Silva 2004). Esta especie poseería características adaptivas que permitirían la existencia de una población auto-suficiente en la Patagonia (Hamamé & Antezana 2010). La biomasa de esta especie presenta importantes variaciones intra-anuales en la Patagonia (González et al. 2010).

2. HIPÓTESIS Y OBJETIVOS

2.1 Objetivo 1. Caracterizar el canto de las ballenas azules que se alimentan en la Patagonia chilena durante el verano austral y compararlo con los reportes de cantos regionales para el Pacífico Suroriental, con el fin de entender la identidad acústica y posibles nexos acústicos en las ballenas azules del Pacífico Suroriental.

Formulación de la Hipótesis 1:

Considerando que el canto refleja la identidad de una población o grupo de ballenas azules (McDonald et al. 2006) y que rutas de migración pueden ser identificadas mediante nexos acústicos en los cantos regionales entre regiones oceánicas (Stafford et al. 1999a), entonces,

Hipótesis 1: existe un nexo acústico entre los cantos de ballenas azules en el golfo Corcovado (Pacífico Suroriental; ca. 43°S) y el Pacífico Tropical Oriental (ca. 8°S).

2.2 Objetivo 2. Determinar la ocurrencia estacional de cantos de ballenas azules del Pacífico Suroriental en su zona de alimentación en la Patagonia chilena, y en el Pacífico Tropical Oriental, el cual correspondería a una posible zona para invernar.

Formulación de Hipótesis 2 y 3:

Considerando que a escala intra-anual las variaciones estacionales en la ocurrencia de cantos de ballenas azules refleja la residencia estacional de estas en un área y que esta residencia estacional refleja a su vez desplazamientos migracionales (Stafford et al. 1999b), entonces,

Hipótesis 2: Existe una máxima estacional en la ocurrencia de cantos de ballenas azules durante el verano austral (enero-marzo) en la zona de alimentación de la ecorregión Chiloense,

Hipótesis 3: Existe una máxima estacional en la ocurrencia de cantos de ballenas azules en el Pacífico Tropical Oriental durante el invierno austral (junio-septiembre).

2.3 Objetivo 3. Analizar características oceanográficas que explican la ocurrencia de sitios de alimentación y las condiciones óptimas para el forrajeo para ballenas azules en el golfo Corcovado.

Formulación Hipótesis 4 y 5

Hipótesis 4: Los eventos de alimentación de ballenas azules ocurren durante periodos de alta abundancia de eufáusidos y altas concentraciones de Cl-a.

Hipótesis 5: Las diferencias inter-anuales e inter-sitio en avistamientos de forrajeo de ballenas azules son generadas por variaciones en la abundancia local de eufáusidos.

3. MATERIAL Y MÉTODOS

3.1 Área de estudio

El estudio de bioacústica se realizó en el PTO (8°S, 95°W) y en la ERC (≈43°-44°S, 71°-73°W), incluyendo el golfo Corcovado. Por otra parte, el muestreo oceanográfico se realizó en dos sitios del golfo Corcovado (≈43°37'S, 73°26'W), los cuales se presentan en la Figura 3.1.

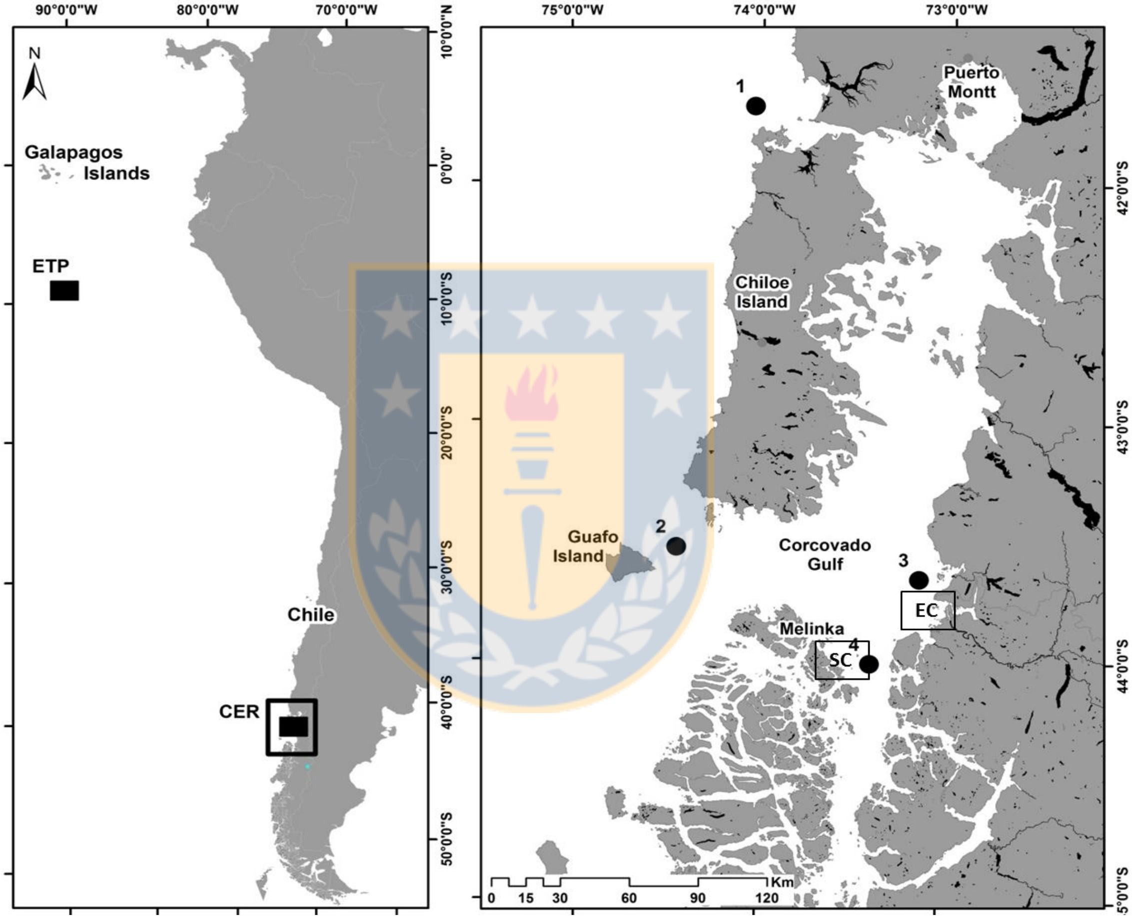

Figura 3.1 Zonas de muestreo en el Pacífico Suroriental. ETP: sitio de Monitoreo Acústico Pasivo fijo. CER: sitio de muestreo de la Ecorregión Chiloense en la Patagonia chilena. SC y EC corresponden a los sitios de alimentación Corcovado Sur y Corcovado Oriente, respectivamente. Los números 1 al 4 indican los sitios de Monitoreo Acústico Pasivo fijo en la ERC.

3.2 Monitoreo Acústico Pasivo

Para realizar el estudio bioacústica y contrastar las Hipótesis 1-3 de la presente Tesis (Buchan et al. 2014 y Capítulo 1), se ocuparon dos metodologías distintas de Monitoreo Acústico Pasivo (PAM por sus siglas en inglés: "Passive Acoustic Monitoring").

Monitoreo Acústico Pasivo móvil

En el caso de la **Hipótesis 1**, los datos acústicos se colectaron durante los veranos de 2008-2011 con un hidrófono móvil ("dipping hydrophone") (marca Cetacean Research Technology; modelo C54XRS) utilizado desde una embarcación de pesca artesanal. De esta forma fue posible acercarse a ballenas azules en la zona de alimentación del golfo Corcovado y grabar los cantos emitidos por ellas, según la metodología descrita por Buchan et al. (2010, 2014). Las ballenas azules fueron avistadas e identificadas por observadores experimentados de cetáceos. Las grabaciones con hidrófono realizadas desde el borde de la embarcación, se llevaron a cabo con el motor apagado, ya sea con o sin avistamientos de ballenas azules, pero nunca en presencia de otro cetáceo. Los puntos de grabación se presentan en la Figura 1 del Capítulo 1 (Buchan et al. 2014).

Los cantos registrados fueron visualizados en espectrogramas mediante el uso del software Raven Pro 1.3 (Bioacustic Research Program 2008) (Fig. 2 Capítulo 1; Buchan et al. 2014). Con este software se realizaron mediciones de frecuencia y duración de las unidades e intervalos inter-unidad de cada frase de canto grabado. Estos datos fueron compilados y los promedios de cada característica de frecuencia y duración de cada unidad e intervalo fueron calculados. Estos datos, junto a inspecciones visuales de espectrogramas, se utilizaron para comparar las frases de cantos de ballenas azules grabados en el golfo Corcovado con cantos regionales descritos en Cummings & Thompson (1971) y Stafford et al. (1999b).

Monitoreo Acústico Pasivo fijo

En el caso de la **Hipótesis 2 y 3** (Buchan et al. *en prensa*, Capítulo 2), se utilizó el PAM fijo ("fixed Passive Acoustic Monitoring") para la colección de datos acústicos mediante el uso de dos tipos distintos de hidrófonos anclados en el fondo marino en la ecorregión Chiloense y en la Pacífico Tropical Oriental (Fig. 3.1 Capítulo 2). En el caso de la ecorregión Chiloense, se instalaron un total de 6 hidrófonos de tipo Marine Autonomous Recording Units (MARU) fabricados y arrendados por el Bioacoustics Research Program de la Universidad de Cornell, EE.UU (www.birds.cornell.edu/) en cuatro localidades distintas (≈43°-44°S, 71°-73°W) entre enero 2012 y abril 2013. Los tres periodos de grabación fueron de 5 meses continuos a una frecuencia de muestreo (“sample rate”) de 2 kHz.

En el caso del Pacífico Tropical Oriental, se instaló un hidrófono modelo 1032 del International Transducer Corporation en un sitio (8°S, 95°W) a 500 mn SSO de las islas Galápagos, entre los años 1996 y 2002, descrito en Stafford et al. (1999b). La grabación se realizó una frecuencia de muestreo (“sample rate”) de 100 Hz.

Análisis bioacústico vía detección automática

Los datos en formato digital de ambas regiones de estudio fueron analizados con el software XBAT (Extensible Bioacoustic Tool; Bioacoustics Research Program 2012) para determinar la variación temporal de ocurrencia de dos tipos de cantos de ballenas azules del Pacífico Suroriental. Para realizar conteos mensuales de los cantos, se ocuparon detectores automáticos desarrollados en XBAT que seleccionan automáticamente los sonidos que se parecen a los sonidos objetivos del detector (Fig. 2 de Buchan et al. *en prensa*, Capítulo 2). Luego se contabilizó el número de detecciones por cada mes, el cual se dividió por la cantidad de días en el mes. El numero promedio de detecciones por día durante cada mes se reportó y se graficó para visualizar las tendencias temporales.

Cada detector se evaluó para definir el % de detecciones positivas falsas (es decir equivocadas por detector) y % detecciones negativas falsas (es decir omitidos por el detector). Para esto, se revisó una cantidad fija de detecciones cada mes y un tiempo fijo en horas visualmente, determinando el número de falsas positivas y falsas negativas (modificado desde Samaran et al. 2013; descrito en Buchan et al. *en prensa* y Capítulo 2). Los valores de detecciones por día en cada mes se corrigieron con estos porcentajes y se reportaron en los resultados.

3.3 Avistamientos de ballenas azules y muestreo oceanográfico

Sitios de muestreo en los sectores Sur y Oriente del golfo Corcovado

Dos sitios de alimentación fueron seleccionados en el Suroriente del golfo Corcovado (43°38’-44°01’S, 73°38’-73°01’W; Fig. 3.1 y Figura 1 en Capítulo 3), siendo donde ballenas azules fueron previamente avistadas de manera consistente en verano entre 2003 y 2009 (Hucke-Gaete e al. 2010). El sitio Corcovado Sur (CS) se localizó más en dirección hacia el océano Pacífico, entre el límite norte del Archipiélago de los Chonos (donde se encuentra la localidad de Melinka) y la entrada norte del canal Moraleda (Figura 1 en Capítulo 3). Por otra parte, el sitio Corcovado Oriente (CO) se localizó más cerca del continente, abarcando la bahía de Raúl Marín Balmaceda (Figura 1 en Capítulo 3), donde desemboca el río Palena.

En el verano 2011 (febrero), verano 2012 (febrero-abril), invierno 2012 (mayo-junio) y verano 2013 (febrero-marzo) se colectaron datos de avistamientos de ballenas azules en los dos sitios de estudio y se recopilaron datos oceanográficos satelitales para el sector suroriente del golfo Corcovado. Además, durante el verano 2012 (febrero-abril), invierno 2012 (mayo-junio) y verano 2013 (febrero-marzo), se colectaron datos oceanográficos *in situ* asociados a los avistamientos de forrajeo de ballenas azules y/o en estaciones oceanográficas fijas. Cuando las ballenas azules estaban presentes, se realizó un seguimiento de los animales y se muestreó en los sitios donde se observó el comportamiento de forrajeo, dando la prioridad al sondeo de temperatura, salinidad y oxígeno *in situ* y el muestreo de mesozooplancton, si las horas de luz o las condiciones climáticas fueron limitantes. En ausencia de ballenas azules, se realizó muestreo oceanográfico en las estaciones fijas para caracterizar el ambiente de los sitios de alimentación. Cada sitio de estudio contenía 12 estaciones fijas de muestreo separadas por 1-2 mn. Las profundidades máximas en dichos sitos eran entre 70 m y 230 m.

Para la contrastación de las **Hipótesis 4** y **5**, se examinaron datos de avistamientos junto a datos oceanográficos *in situ* y obtenidos mediante satélite para determinar las condiciones ambientales y la comunidad del zooplancton presente en los sitios de alimentación y durante los eventos de alimentación de ballenas azules, con especial énfasis en las diferencias observadas entre-veranos y entre-sitios.

Metodología de avistamiento de ballenas

Un esfuerzo de prospección visual de cetáceos se realizó durante los veranos 2011, 2012, 2013 e invierno 2012 por un observador experimentado de manera continua sobre la duración completa de los cruceros en los sitios CS y CO. Los siguientes datos fueron registrados durante los avistamientos de cetáceos: fecha, hora, posición, número de individuos en el grupo, número de crías, especie, comportamiento. En esta tesis solo se reportan los avistamientos de ballenas azules. También se registró el tipo de comportamiento de ballenas azules observado, clasificándolo en las siguientes categorías: (i) en tránsito, (ii) alimentación tipo “lunge-feeding” (embestida lateral), (iii) buceos profundos. Observaciones de embestida lateral y buceos profundos se consideraron una indicación de comportamiento de forrajeo (Goldbogen et al. 2012). En el caso de los buceos profundos, este comportamiento podría indicar búsqueda de alimento y/o alimentación en profundidad.

A partir de los avistamientos, se calcularon tasas de avistamiento (“sighting rates”) para cada campaña de muestreo (2011-2013) y para cada sitio de muestreo. La tasa (ind./día) fue calculada por el número de ballenas azules presentando comportamiento de forrajeo dividido por el número de días de esfuerzo (por sitio y campaña de muestreo).

Imágenes satelitales de variables oceanográficas

Imágenes satelitales diarias o mensuales, dependiendo de la disponibilidad, fueron analizadas para estimar la Línea de Referencia de la Fluorescencia (Fluorescence Line Height; nFLH), Clorofila-a (Cl-a), y la temperatura superficial del mar (TSM). Las imágenes fueron obtenidas, con 1 km de resolución, desde la base de datos MODIS (http://modis.gsfc.nasa.gov/data) para el área entre 43°15'-44°04'S y 74°39'-72°47'W. La data de sensoramiento remoto proveniente de MODIS (“Moderate Resolution Imaging Spectroradiometer:” Espectrorradiométro para la Captación de Imágenes de Resolución Moderada) fueron procesadas utilizando el software SeaDAS (SeaWIFS Data Analysis System, versión 6.4), siguiendo los procedimientos recomendados para archivos L1A.

Sondeo de temperatura y salinidad in situ

Para examinar la estructura vertical de la columna de agua (temperatura °C, salinidad y oxígeno disuelto mg/L) hasta una profundidad de 200 m. Se utilizó un CTD-O (SAIV A/S, modelo SD204); lamentablemente, el 11.02.2013, el CTD-O resultó dañado debido a condiciones climáticas desfavorables y por tanto no existen datos de CTD-O después de ésta fecha. Los datos del CTD-O se ocuparon para plotear perfiles verticales y diagramas de Temperatura-Salinidad (T-S). Además, se midió la temperatura y la salinidad *in situ* a 2 m de profundidad utilizando una sonda multiparámetros YSI 650 MDS.

Mediciones de nutrientes y Clorofila-a

Muestras para determinar la concentración *in situ* de los nutrientes (NO_3, NO_2, SiO_4 y PO_4) y clorofila-a fueron colectadas a 2 profundidades (2 y 50 m) utilizando una botella Niskin. La determinación de la concentración de los nutrientes se llevó a cabo utilizando la metodología de Hansen y Koroleff (2007). La concentración de Cl-a fue determinada mediante la metodología descrita por Holm-Hansen et al. (1965).

Muestreo y análisis de mesozooplancton

Las muestras de mesozooplancton fueron colectadas utilizando una red bongo (0.71 m de diámetro) provista de un flujómetro General Oceanics y con una trama de red de 250 µm. Los arrastres fueron de tipo oblicuos desde los 100 metros de profundidad o desde la mayor profundidad posible en sectores más someros. Los arrastres tuvieron una duración cercana a los 20 minutos a una velocidad de 2 nudos. Las muestras fueron preservadas en formaldehído en agua de mar a una concentración final de 5%. Todos los organismos fueron contados e identificados hasta el nivel de orden. En el caso de los eufáusidos, sin embargo, los organismos fueron identificados a nivel de especie y clasificados de acuerdo a su estadio de ciclo de vida (adulto, calyptopis, furcilia). La estructura de tamaños de los eufáusidos fue determinada midiendo los ejemplares desde la punta del rostrum hasta el extremo posterior del telson (Melo & Antezana 1980).

4. CAPÍTULOS DE RESULTADOS

4.1 Capítulo 1: Un nuevo canto grabado para ballenas azules en el golfo Corcovado, Sur de Chile, y un nexo acústico con el Pacífico Tropical Oriental

Manuscrito publicado en Endangered Species Research: Buchan, S. J., R. Hucke-Gaete, L. E. Rendell & K. M. Stafford. 2014. A new song recorded from blue whales in the Corcovado Gulf, Southern Chile, and an acoustic link to the Eastern Tropical Pacific. Endangered Species Research. 23: 241-252.

Resumen: La identidad, distribución y desplazamientos de ballenas azules (*Balaenoptera musculus*) que se alimentan en la ecorregión Chiloense en el Sur de Chile permanecen poco conocidos. Los estudios de cantos de ballenas azules han identificado poblaciones acústicas que se caracterizan por el tipo de canto, rangos geográficos, rutas de migración y residencias estacionales. En el presente estudio, se caracteriza las secuencias de cantos de las ballenas azules que se alimentan en el golfo Corcovado basado en registros acústicos colectados mediante un hidrófono móvil durante 3 temporadas de verano (2008, 2009, 2011), y se comparan con tipos de canto previamente descritos para el Pacífico Suroriental (PSO) y otras regiones con el fin de comprender mejor la variación a meso-escala (versus a escala de cuenca) del canto de la ballena azul. El análisis reveló dos cantos distintos, SEP1 y SEP2 (por sus siglas en inglés "Southeast Pacific"). Ninguno de estos cantos es producido por ballenas azules Antárticas. Si bien SEP1 fue el primer canto registrado en el golfo Corcovado en 1970, encontramos que SEP2 es mucho más común, a pesar de que nunca fue reportado en esta área. Nuestro reporte de SEP2 agrega un nuevo canto a la descripción actual del repertorio acústico de las ballenas azules del PSO. Nuestra grabación de SEP1 reafirma el nexo acústico con el Pacífico Tropical Oriental (PTO); nuestra grabación del canto SEP2 establece un nuevo vínculo acústico de este canto con el PTO. Estos resultados proveen una base para futuros estudios acústicos pasivos sobre la distribución espacio-temporal de las ballenas azules amenazadas del PSO y para entender como estos cantos se relacionan con la estructura poblacional.

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A new song recorded from blue whales in the Corcovado Gulf, Southern Chile, and an acoustic link to the Eastern Tropical Pacific

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ABSTRACT: The identity, distribution and movements of blue whales *Balaenoptera musculus* that forage in the Chiloense Ecoregion in Southern Chile remain unclear. Studies of blue whale songs have identified acoustic populations with distinct song types, geographic ranges, migration routes and seasonal residencies — information that is relevant to the conservation of this endangered species. Here, we characterized the song sequences of blue whales that use the Corcovado Gulf based on dipping hydrophone recordings from 3 austral summer field seasons (2008, 2009, 2011), and compare these data to previously described song types for the Southeast Pacific (SEP) in order to better understand meso-scale (versus basin-scale) variation in blue whale song. Two distinct songs, SEP1 and SEP2, emerged from our analysis. Neither of these songs is used by Antarctic blue whales. Although SEP1 was the first song recorded in the Corcovado Gulf area in 1970, we found SEP2 to be the more common song, despite never having been reported previously in this area. Our report of SEP2 adds a new song to the current description of the SEP blue whale repertoire. Our recording of SEP1 reaffirms the acoustic link already established between Chile and the Eastern Tropical Pacific (ETP); our recording of SEP2 establishes a new acoustic link for this song between Chile and the ETP. These findings provide the basis for future passive acoustic studies on the temporal and spatial distributions of endangered SEP blue whales and for understanding how these songs relate to the population structure.

KEY WORDS: Chile · Southeast Pacific · *Balaenoptera musculus* · Whale song · Bioacoustics

INTRODUCTION

Blue whales *Balaenoptera musculus* were hunted to near extinction during the twentieth century, and although the species was protected internationally in 1966, illegal whaling continued into the early 1970s (Branch et al. 2004). In the Southeast Pacific (SEP), most blue whale catches occurred off the coast of Chile, but also off Peru and Ecuador (Clarke et al. 1978, Ramírez 1983, Van Waerebeek et al. 1997). Commercial whalers caught approximately 3000 blue whales off the coast of Chile between 1927 and 1971 (Aguayo-Lobo et al. 1998). In 2003, a blue whale feeding ground was discovered off the Pacific coast of Chiloé Island, the Corcovado Gulf and the Guaitecas Archipelago (Hucke-Gaete et al. 2004), and was subsequently found to extend farther north of Chiloé Island (Cabrera et al. 2005, Galletti Vernaz-

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zani et al. 2012) and inshore, to the Inner Sea of Chiloé Island (Abramson & Gibbons 2010), thus spanning what is known as the Chiloense Ecoregion (Spalding et al. 2007). These reports indicate that this area could be important for the recovery of endangered SEP blue whales (Hucke-Gaete et al. 2004, Branch et al. 2007b). In December 1997, based on line-transect surveys following distance sampling protocols, an abundance estimate of 303 animals (95% CI: 176–625) was obtained for the exclusive economic zone waters off Chile between north (18° S) and central (38° S) Chile (Williams et al. 2011), excluding the more coastal waters of the Chiloense Ecoregion (within the 20 nautical mile limit).

In the Southern Hemisphere, 2 subspecies of blue whales are recognized, viz. the Antarctic blue whale *Balaenoptera musculus intermedia* and the pygmy blue whale *B. m. brevicauda*, although acoustic data suggest there may be at least 5 acoustically distinct populations (Stafford et al. 1999b, 2011, Širović et al. 2004, Samaran et al. 2013). There has been some confusion as to the type of blue whales present in the waters off the coast of Chile. Aguayo (1974) reported blue whales caught in Chilean waters as being either Antarctic or pygmy, while Clarke et al. (1978) proposed the Chilean blue whales to be a separate subspecies. More recently, Branch et al. (2007a) determined that the total lengths of blue whales were intermediate in size between the larger Antarctic blue whale and the smaller pygmy blue whale, suggesting that these were not only a separate population but also a unique unnamed subspecies. This is also supported by discrete summer distribution from Antarctic blue whales (Branch et al. 2007b), genetic analyses (Conway 2005, LeDuc et al. 2007) and a distinct acoustic repertoire (Cummings & Thompson 1971, Buchan et al. 2010). For management purposes, Chilean blue whales are considered a separate population from both Antarctic blue whales and Indian Ocean pygmy blue whales by the International Whaling Commission (www.iwc.int). Key questions thus remain regarding the identity, distribution and movements of this unnamed group of blue whales.

Blue whale vocalizations lend themselves particularly well to distinguishing among different populations of blue whales worldwide (e.g. Stafford et al. 1999b, 2001, McDonald et al. 2006). These sounds are some of the loudest sustained biological sounds in the ocean, capable of propagating over extremely long distances (Stafford et al. 1998, Širović et al. 2007). The biological function of many of these sounds remains unknown. Some appear to be used during feeding (D calls), while the patterned sequence of calls known as a 'song' has been attributed to male reproductive display, often produced during transit (Oleson et al. 2007). This patterned song sequence is made up of individual sounds or 'units' which occur in repeated 'phrases'. Blue whale song types have been characterized based on differences in some or all of the following criteria, most often determined by visual inspection of spectrograms: (1) song phrasing (e.g. ABABAB or ABCABC, where A, B and C represent different song units); (2) the inter-unit time interval; (3) total song phrase duration; and (4) song unit characteristics (frequency, duration, modulation) (e.g. Cummings & Thompson 1971, Thompson et al. 1996, Stafford et al. 1999b, McDonald et al. 2006).

Studies of blue whale song in particular have identified populations with distinct song types, geographic ranges, migration routes and seasonal residencies (e.g. Stafford et al. 1999a, 2001, 2011, McDonald et al. 2006, Samaran et al. 2013). Song characteristics are believed to remain relatively stable over a 40 yr period, and individual variability within song types is found to be minimal relative to the variation among song types (McDonald et al. 2006). Thus, song types may reflect recent distribution changes that are relevant to the conservation management of the various subspecies and populations of this endangered species. This is particularly useful in areas where different populations overlap, such as the North Pacific (Stafford et al. 2001), the Eastern Tropical Pacific (Stafford et al. 1999b) and the Indian Ocean (Stafford et al. 2011, Samaran et al. 2013).

Individuals from a single population of blue whales have been observed to produce variants of 1 basic song type (e.g. Stafford et al. 2001, Oleson et al. 2007), but have never been observed to produce more than 1 distinct song type. Variants have been described as being largely composed of the same units that define a given song type but in different proportions and temporal sequences, e.g. ABABAB versus ABBB. In the case of variants, the types of units and the order in which they occur remain stable over time. In contrast, a distinct song type consists of entirely different units, as characterized by peak frequency, duration and modulation characteristics. Proper characterization and classification of song types is essential prior to looking at patterns of overlap of song types in space and time that may reflect the seasonal passage of different whale populations through a given habitat (e.g. Stafford et al. 1999b, 2001, Samaran et al. 2010, 2013).

In the Chiloense Ecoregion of the SEP, only 1 song type has been reported (Cummings & Thompson 1971), which was the first ever documented recording of blue whale sounds obtained on 30 and 31 May 1970 near Guafo Island (Cummings & Thompson 1971), at the entrance to the Corcovado Gulf (Fig. 1). This song (see Fig. 2a) consisted of a 3-unit song, with A-B-C phrasing lasting a total of 36.5 s, with a 0.5 to 1.0 s pulse around 390 Hz described as a precursor to unit C. No further recordings were made of this song type until 1996 from a fixed hydrophone in the Eastern Tropical Pacific (ETP), at 8° S, 95° W (Stafford et al. 1999b). This SEP song was recorded in the ETP with greatest frequency during the austral winter (June to August). It was recorded along with a second song (see Fig. 2b) which followed the same temporal pattern, but had not been previously recorded elsewhere. This second song was considered a variant ('variant 2') of the first SEP song because both songs had similar phrasing and durations (Stafford et al. 1999b). Both songs were attributed to South Pacific blue whales.

Since the work in the 1970s, only 1 preliminary description of blue whale sounds from the Corcovado Gulf has been reported (Buchan et al. 2010). Buchan et al. (2010) made a coarse classification of the Chilean blue whale repertoire (isolated calls and song units), grouping all low-frequency long calls (>100 Hz, average duration 10 s) together and highlighting the presence of high-frequency short call precursors (approximate duration 1 s) at 350 and 420 Hz. These authors did not attempt song sequence characterization. Here, we analysed the data from Buchan et al. (2010) plus 2 additional years of data, and report a quantitative comparison of the specific song type characteristics recorded in the Corcovado Gulf.

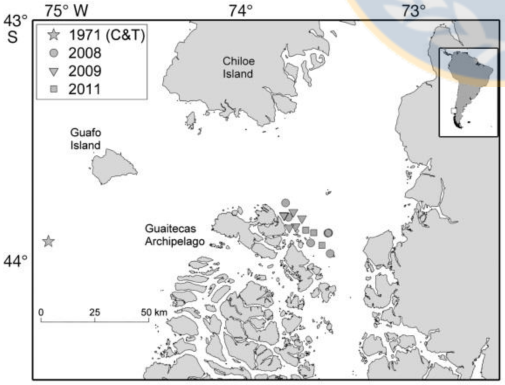

Fig. 1. Corcovado Gulf study area. Circles (2008), triangles (2009) and squares (2011) mark dipping hydrophone recording sites per year, and the star (labelled C & T) marks the recording location from Cummings & Thompson (1971)

In this study, our objective was to characterize the song of the blue whales that forage in the Corcovado Gulf during the austral summer months (February to April) based on dipping hydrophone recordings from 3 field seasons (2008, 2009 and 2011), and compare them to the 2 previously described song types/variants for the SEP by Cummings & Thompson (1971) and from the ETP by Stafford et al. (1999b), in order to better understand meso-scale (versus basin-scale) differences in blue whale songs within the SEP.

MATERIALS AND METHODS

Acoustic data collection

During the austral summers of 2008 (February to April; Buchan et al. 2010), 2009 (February to March) and 2011 (March), we conducted acoustic monitoring in our study area (1542 km^2 total) located in the coastal waters of the Guaitecas Archipelago and the Corcovado Gulf, Chile (43° 54′ S, 73° 44′ W; Fig. 1). Data were collected from an 8 m outboard-powered vessel. Blue whales were located with aid of land-based observers working with binoculars and a theodolite for tracking. Whales were identified visually from the vessel with binoculars and the naked eye, first by identifying their blow and then by confirming species upon closer approach.

Recording equipment and settings were selected in order to ensure that sufficient energy was captured at frequencies necessary to characterize song units (20–400 Hz) but also to diminish background noise at low frequencies. Nevertheless, high levels of low-frequency background noise were present. Hydrophone recordings were made in 2008 and 2009 with an omni-directional hydrophone (Cetacean Research Technology C54XRS) with a flat frequency response from 0.016 to 44 kHz (+2/−3 dB) and a usable frequency response of 0.006 to 203 kHz (+2/−20 dB), a digital high-pass filter set at 20 Hz (Cetacean Research Technology), an Edirol 96-bit USB sound card sampling at 96 kHz and a Panasonic Toughbook laptop computer with Raven Pro 1.3 recording software (Bioacoustics Research Program 2008). In 2011, single hydrophone recordings were made with an SQ26-MT portable underwater recording system (Cetacean Research Technology), which includes an omni-directional hydrophone with a flat frequency response from 0.020 to 20 kHz (+2/−2 dB) and a usable frequency response of 0.01 to 50 kHz (+2/−15 dB), and an M-Audio Microtrack recorder sampling at 96 kHz. Recording effort was carried out regardless of whether blue whales were in sight, but not in the presence of other cetaceans. All sightings (number of groups, number of individuals, approximate distance estimated visually) were noted.

Whale song characterization: phrases and units

A blue whale song sequence is composed of several repeated phrases. Each phrase is a patterned sequence of song units and shorter 'unit-precursor' sounds. Spectrograms of complete song phrases, with labelled song units and unit precursors, are presented (see Fig. 3). Songs were characterized from visual inspection of spectrograms between 0 and 500 Hz, using the following criteria: (1) song phrasing; (2) the inter-unit gaps between song units; (3) total song phrase duration; and (4) song unit characteristics (frequency, duration, modulation) (Cummings & Thompson 1971, Stafford et al. 1999b, Mellinger & Clark 2003). Within a song sequence, each unique unit within the repeated phrases was named according to its order of appearance in the phrase, e.g. A for the first unit, B for the second, C for the third (Cummings & Thompson 1971). In the literature, this method of labelling song units does not imply that, for example, unit A from the North Pacific song is identical to unit A from the Indian Ocean song; it merely expresses the position of the unit in the song phrase. However, in order to avoid this confusion, we additionally annotated units according to the song they belonged to, based on our classification of song. Thus, song units and phrases were described as A1-B1-C1 for the first song type, A2-B2-C2 for the second, and so on, to emphasize the song that units belonged to. Unit precursors were labelled according to the unit they preceded (pre-A1, pre-B1, pre-C1 etc.). The time (s) between 2 consecutive units (or between a unit and the precursor to the following unit) defined the inter-unit gap. Total song phrase duration was determined by the time between the start of the first unit and the end of the last unit; the last unit in the phrase was easily distinguishable since it was followed by a much longer time gap (>50 s) before the start of a new phrase. Song units were considered to be delimited by an abrupt change in the frequency or modulation rate, irrespective of a pause between song units (McDonald et al. 2006), and each unit was characterized by measuring its peak frequency (Hz) and duration (s), and assigned modulation characteristics (pulsed or tonal, where possible; Cummings & Thompson 1971).

Spectrogram analysis of whale songs

Recordings were analysed in spectrograms and waveform plots created in Raven Pro 1.3 (Hamming window; 90% overlap; window size 60000 samples; Fast Fourier Transform (FFT) 65536 samples, Bioacoustics Research Program 2008). All spectrograms were scanned visually for blue whale calls within the 0 to 500 Hz frequency range, and only blue whale song units and phrases were analysed. Blue whale song units and unit-precursors were selected manually on-screen using a cursor and committed to selection tables that compiled the following data for each selection: begin time (s), end time (s), low frequency (Hz), high frequency (Hz), peak frequency (Hz; the frequency at which peak power occurs), unit amplitude modulation (where signal-to-noise ratio was sufficient, modulation rate of pulsed sounds was determined as the number of pulses per second) and unit type (e.g. A1, B2).

Following the compilation of selection tables in Raven Pro 1.3 (Bioacoustics Research Program 2008), we calculated the duration of units (end time minus begin time in seconds), the average inter-unit interval for each set of consecutive units (time between the end of one unit and the beginning of the following unit, in seconds) and the average inter-phrase interval (from the beginning of one phrase to the beginning of the following phrase in seconds).

The final set of song characteristics determined from the data for song sequence characterization were (1) peak frequency of song units and unit precursors, (2) duration of song units and unit precursors, (3) duration of inter-unit gaps and (3) duration of total phrase.

Whale song comparison

Once blue whale song sequences were visually inspected and quantitatively characterized, they were compared to song descriptions by Cummings & Thompson (1971) from the Corcovado Gulf and Stafford et al. (1999b) for the ETP. In order to visually compare our song sequences with both of these previous studies, we decimated our data to a 100 Hz sample rate (see Fig. 2). Sounds from Cummings & Thompson (1971) were recorded with a hydrophone with a pre-amplifier (Wilcoxon, type M-H90-A) suspended ~28 m below a ~305 m (1000 ft) floating cable, with a low-frequency response of 3 dB at 12 Hz; sounds were recorded on a battery-powered magnetic tape recorder. A digital copy of the song sequence recorded by Cummings & Thompson (1971) was obtained from the Macaulay Library at Cornell University, USA, which we decimated to 100 Hz sample rate. Sounds from Stafford et al. (1999b) were recorded with an autonomous hydrophone logging system with an International Corporation 1032 hydrophone, preamplifier/filter (designed to prewhiten ocean ambient noise spectra from 1 to 40 Hz) and a digital recorder in a pressure resistant titanium housing. The hydrophone was suspended in the deep sound channel at depths of 650 to 750 m and set to record up to 6 mo at a sampling rate of 100 Hz with low pass filters set at 40 Hz. The methods employed in both of these studies make the data largely comparable with data from this study, although our signal-to-noise ratio (SNR) is somewhat poorer.

RESULTS

Sampling effort and context

In total, 29 h and 11 min were recorded during the austral summers in February to April 2008, February to March 2009 and March 2011 (Table 1) within the Corcovado Gulf study area. Song recordings coincided with sightings of groups of 1 to 3 blue whales first sighted at an observed distance of 500 m to 2 nautical miles of the research vessel. The distance to the source of sounds was not measured; therefore, it is possible that sounds recorded may have been produced by whales farther away than those animals sighted near the vessel. We selected a total of 345 units within 67 song phrases for analysis, excluding 157 sounds that were isolated calls (not clearly part of a song sequence) and song units/phrases with an SNR considered to be too poor to distinguish the start and end of each unit.

Table 1. *Balaenoptera musculus.* Total acoustic monitoring effort in hours, number of separate days when songs were recorded, total song units (including unit precursor sounds) and total song phrases of Southeast Pacific (SEP) blue whale song types SEP1 and SEP2, recorded during the austral summers of 2008, 2009 and 2011 in the Corcovado Gulf blue whale feeding ground

	2008 (Feb–Apr)	2009 (Feb–Mar)	2011 (Mar)	All years
Total hours:minutes of effort	16:03	10:46	2:49	29:11
Total days when songs were recorded	5	3	2	10
Total SEP1 song units	18	0	0	18
Total SEP2 song units	117	187	41	345
Total SEP1 song phrases	5	0	0	5
Total SEP2 song phrases	22	32	8	62

Description of the two SEP songs

Based on the frequency characteristics of song units and unit precursors (Table 2), and the temporal characteristics of song phrases and units (Table 3), we distinguished 2 different songs, which we named SEP1 (Southeast Pacific 1; Figs. 2a,c & 3a) and SEP2 (Southeast Pacific 2; Figs. 2b,d & 3b).

SEP1 (Figs. 2c & 3a; Tables 2 & 3) was only recorded during a single song sequence on 23 February 2008, and only 5 phrases were recorded; on that day no other song sequence was recorded. This small sample size is a clear limitation to the characterization of this song sequence. This song consisted of 3-unit phrases (A1-B1-C1) that each lasted on average 33.9 s. The first unit (A1) had a mean peak frequency of 21 Hz and an average duration of 11.4 s. It was followed immediately by unit B1 with mean peak frequency of 49 Hz and average duration of 9.2 s. Unit C1 had a mean peak frequency of 25 Hz and lasted 9.5 s and was almost always (4 times out of 5) preceded by a short (0.7 s), high-frequency pulse (350 Hz) that we named precursor-C (pre-C1; circled in Fig. 3a).

SEP2 (Figs. 2d & 3b; Tables 2 & 3) was recorded during all 3 field seasons (2008, 2009, 2011), totalling 62 phrases.

Table 2. *Balaenoptera musculus.* Frequency characteristics of Southeast Pacific (SEP) blue whale song types SEP1 and SEP2: mean peak frequencies (rounded to nearest whole number) ± SD (rounded to nearest decimal) of unit precursors (Pre-A, Pre-C, Pre-D) and song units (A–E); sample sizes are in parentheses. Peak frequency refers to the frequency at which peak power (amplitude) occurs within the selected sound; NA: not applicable

	Mean peak frequency (Hz)							
	Pre-A	Unit A	Unit B	Pre-C	Unit C	Pre-D	Unit D	Unit E
SEP1	NA	21 ± 0.8 (4)	49 ± 17.1 (5)	350 ± 3.3 (4)	25 ± 0.0 (5)	NA	NA	NA
SEP2	414 ± 15.5 (48)	55 ± 12.1 (57)	84 ± 7.6 (62)	NA	35 ± 16.6 (61)	356 ± 9.7 (53)	37 ± 17.3 (60)	85.3 ± 2.2 (4)

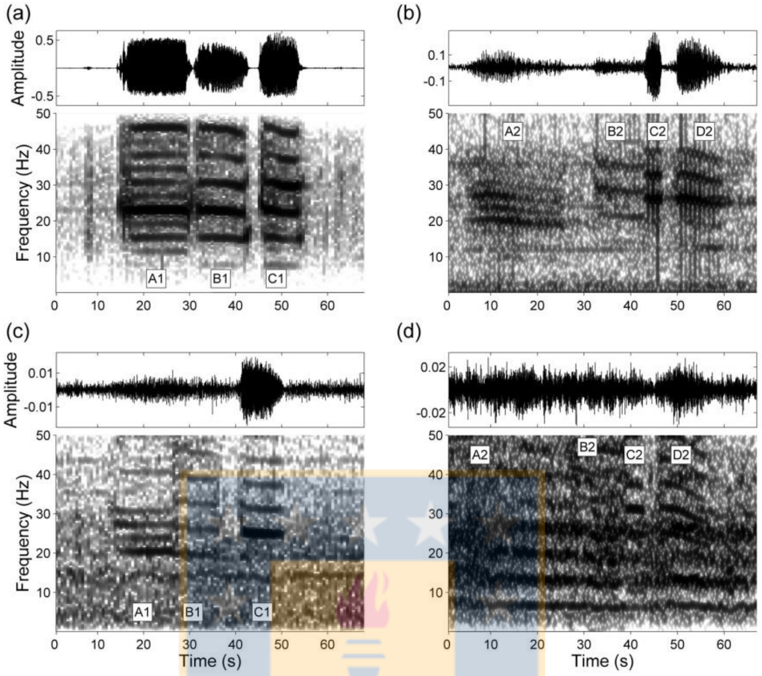

Fig. 2. *Balaenoptera musculus.* Waveforms (top panels) and spectrograms (bottom panels), of blue whale songs: (a) SEP1 from Cummings & Thompson (1971) obtained from the Macaulay Library (http://macaulaylibrary.org/) downsampled to 100 Hz; (b) SEP2 from Stafford et al. (1999b) sampled at 100 Hz; (c) SEP1 from this study downsampled to 100 Hz; (d) SEP2 from this study downsampled to 100 Hz. Song units are marked by A, B, C, D with song type 1 or 2 annotations. Unit precursors are not shown. Spectrogram parameters for (a) and (c) are FFT: 256, 128-point Hanning window, 50 % overlap; for (b) and (d), FFT: 1024, 128-point Hanning window, 90 % overlap. Note that (d) is poorly visualized due to high low-frequency background noise; Fig. 3 shows 0–500 Hz bandwidth spectrograms of sounds (c) and (d)

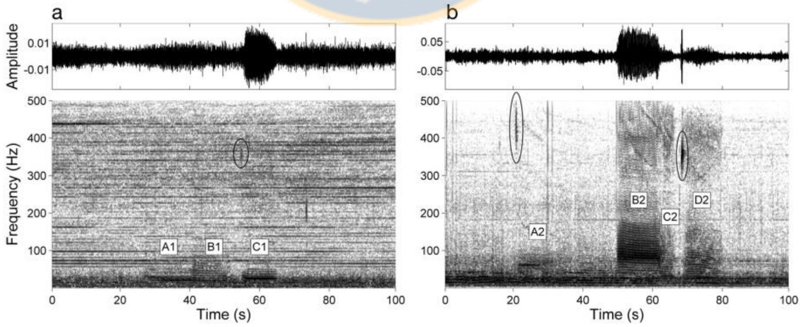

Fig. 3. *Balaenoptera musculus.* Waveforms (top panels) and spectrograms (bottom panels) of blue whale songs from this study downsampled to 1 kHz: (a) SEP1, (b) SEP2. Spectrogram parameters are FFT: 1024, 512-point Hanning window, 50 % overlap. Song units are marked by A, B, C, D with annotations 1 for SEP1, and 2 for SEP2, and circles indicate short duration higher frequency unit precursors (pre-C1 for SEP1; pre-A2 and pre-D2 for SEP2)

This song generally consisted of a 4-unit phrase (A2-B2-C2-D2; n = 58) lasting on average 60 s, with an additional unit E2 in 4 phrases from a single song sequence recorded in 2009. Unit A2 had a peak frequency of 55 Hz and an average duration of 9.5 s, and was almost always preceded by short (0.7 s) high-frequency pulse (414 Hz) that we named pre-A2 (circled in Fig. 3b). After an average inter-unit gap of 19.5 s, unit A2 was followed by unit B2, which had a mean maximum frequency of 84 Hz and a mean duration of 12.6 s. Unit B2 was strongly amplitude modulated, similar to B1 in SEP1, and where the SNR was sufficient (n = 10), a modulation rate of 6.62 s^{-1} ± 0.11 SD was determined (equal to an inter-pulse interval = 0.15 s). Unit C2 had a mean maximum frequency of 35 Hz and a mean duration of 4.5 s. Unit D2 had a mean maximum frequency of 37 Hz and a mean duration of 8.0 s, and was almost always preceded by a short (1 s) high-frequency (356 Hz) precursor that we named pre-D2 (circled in Fig. 3b). An additional unit E2 was recorded 4 times during 1 song sequence, with a mean maximum frequency of 37 Hz and a mean duration of 12.6 s.

Comparison between SEP songs

To graphically explore how similar or distinct the song units and unit precursors of both songs are, we plotted the peak frequencies and durations of all units and precursors (Fig. 4a,b, respectively). Given our relatively small sample size, no statistics were applied. Most units were distinct from one another; however, a high degree of similarity was clear between SEP1 unit B (B1) and SEP2 unit A (A2), as well as between SEP1 precursor C (pre-C1) and SEP2 precursor D (pre-D2). Unit B and unit E of SEP2 also appeared to be quite similar.

Higher bandwidth spectrogram examples of SEP1 and SEP2 are given in Fig. 3a and b, respectively, which show higher SNR compared to lower bandwidth spectrograms, given the high levels of low-frequency noise. Visual inspection of these spectrograms, as well as data in Tables 2 & 3, reveal the following differences between SEP1 and SEP2: (1) different song phrasing (A1-B1-C1 versus A2-B2-C2-D2); (2) different inter-unit gap durations (for A-B and B-C gaps); (3) the occurrence of precursors to different song units (pre-C1 in SEP1; pre-A2 and pre-D2 in SEP2); (4) different frequency and duration characteristics of song units (A1 versus A2; B1 versus B2; C1 versus C2); (5) different phrase durations (34 s for SEP1 versus 59 s for SEP2).

Table 3. *Balaenoptera musculus.* Temporal characteristics of Southeast Pacific (SEP) blue whale song types SEP1 and SEP2, from Cummings & Thompson (1971), Stafford et al. (1999b) and this study: mean duration (s) ± SD (sample size in parentheses) of unit precursors (pre-A, pre-C, pre-D), song units (A–E), inter-unit gaps (A-B, B-C, C-D, D-E), total song from start to end and song interval, measured from the start of a song to the start of the following song. NA: not applicable; –: no available data

Song type and source	Pre-A	Unit A	Gap A-B	Unit B	Gap B-C	Pre-C	Unit C	Gap C-D	Pre-D	Unit D	Gap D-E	Unit E	Total phrase	Inter-phrase interval
SEP1: this study	NA	11.4±2.7 (4)	0.07±0.1 (4)	9.2±0.5 (5)	5.0±0.8 (5)	0.7±0.1 (4)	9.5±0.4 (5)	NA	NA	NA	NA	NA	33.9±5.6 (5)	107.9±31.7 (3)
SEP1: Cummings & Thompson (1971)	NA	13.4[a] 15.3[b]	0[a] 1.6[b]	10.3[a] 9.6[b]	2.5[a] 3.7[b]	0.5–1.0	9.0[a] 7.9[b]	NA	NA	NA	NA	NA	36.9[a] 36.2[b]	100[a] 106[b]
SEP1: Stafford et al. (1999b)	NA	13.4±1.1 (25)	–	9.1±1.2 (25)	–	–	8.4±0.5 (25)	NA	NA	NA	NA	NA	38.8±1.8 (25)	–
SEP2: this study	0.7±0.1 (48)	9.5±6.9 (57)	19.5±1.7 (50)	12.6±0.4 (62)	0.3±0.3 (53)	NA	4.5±0.8 (61)	2.2±0.7 (52)	1.0±0.2 (53)	8.0±2.7 (60)	10.8±6.9 (4)	12.6±0.1 (62)	59.6±6.7 (62)	222.9±344.7 (46)
SEP2: Stafford et al. (1999b)	–	17.7±3.8 (23)	–	10.8±0.6 (9)	–	–	4.0±0 .5 (23)	–	–	10.8±1.5 (23)	–	–	53.5 NA	–

[a]Whale 1 and [b]Whale 2 from Cummings & Thompson (1971)

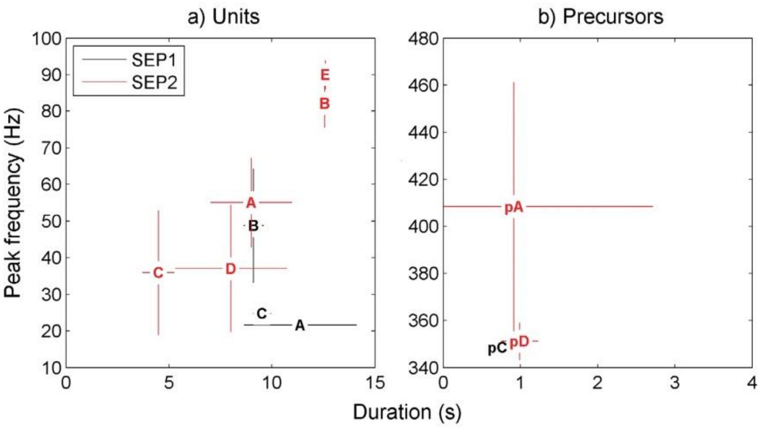

Fig. 4. *Balaenoptera musculus.* Plot of average peak frequency vs. duration of (a) blue whale song units and (b) unit precursors for SEP1 (in black) and SEP2 songs (in red). Bars indicate total range of values. Song units and unit precursors are marked as A, B, C, D, E. Unit precursors are marked as pA, pC and pD

Comparison of SEP songs with previous studies

In order to classify the SEP songs recorded here, we compared them to other blue whale songs described in the literature, in particular for the same study area by Cummings & Thompson (1971), and for the ETP by Stafford et al. (1999b). Overall, SEP1 and SEP2 phrases and individual units were more similar to each other than to any other blue whale song described for regions outside the SEP and the ETP; no song types currently attributed to blue whales in Antarctica (Širović et al. 2004) or elsewhere (e.g. McDonald et al. 2006) match the songs reported here.

When comparing our song measurements (Tables 2 & 3), and the spectrograms for SEP1 (Fig. 2c) and SEP2 (Fig. 2d), with the previously recorded songs by Cummings & Thompson (1971; Fig. 2a) and Stafford et al. (1999b; Fig. 2b), we found that SEP1 matched with the song described by Cummings & Thompson (1971) for the Corcovado Gulf and also matched 'variant 1' in Stafford et al. (1999b) from the ETP. SEP2 matched 'variant 2' reported by Stafford et al. (1999b) from the ETP.

DISCUSSION

The proper characterization and classification of song type is essential given the implications of song type in defining acoustic groups of blue whales. This analysis is particularly relevant given the current availability of fixed passive acoustic technologies that provide long-term data sets. These can be used to examine patterns of song type overlap in space and time that may reflect the seasonal passage of different acoustic groups through the same habitat (e.g. Stafford et al. 1999a, 2001, 2011, Samaran et al. 2010, 2013).

Blue whale song types and variants

In the literature, a single population, or acoustic group, of blue whales has been known to produce phrasing variations of 1 basic song type (e.g. Stafford et al. 2001, Oleson et al. 2007), but not to produce more than 1 distinct song type (i.e. with a completely different set of units). Song type characteristics are believed to remain relatively stable over a 40 yr period (McDonald et al. 2006). A variant of a song type is a song made up of a majority of the same song units (with matching peak frequency, duration and modulation characteristics) but with different phrasing, e.g. A1-B1-A1-B1 and A1-B1-B1-B1. These kinds of variants can be observed in songs produced by blue whales in the Northeast Pacific (Stafford et al. 2001, Oleson et al. 2007). It remains unclear whether these variants are caused by individual or some other source of variation. Based on limited observations, individual variation has been documented within blue whale song types, although it appears to be minimal relative to the variation among song types (McDonald et al. 2006 and references therein).

The 2 song sequences (patterned phrases and individual units) presented here are much more similar to each other than they are to song types from other geographic locations, e.g. Antarctica (Širović et al. 2004). However, there are distinct differences between SEP1 and SEP2, which are also apparent. The SEP1 song phrase consists of only 3 units while the SEP2 song phrase is made up of 4 units; the SEP2 phrase is roughly twice as long as the SEP1 phrase; lastly, units in each song are largely distinct from one another in peak frequency and duration, with the exception of B1 being similar to A2 and pre-C1 similar to pre-D2. At this stage, given the small sample size, particularly in the case of SEP1 (n = 5), it is not possible to determine whether these 2 songs are variants of each other or are altogether different song types. However, a clearer case of a variant, possibly due to individual variation, is that of SEP2, with the inclusion of additional end unit E2 in only 4 phrases, while the other phrases only had units A to D. Thus, A2-B2-C2-D2 and A2-B2-C2-D2-E2 phrasing can be considered variants of the SEP2 song. Continuous data and greater sample sizes of song phrases will be needed to clarify this issue.

SEP blue whale song classification

The 1970 recording of a song sequence from 2 blue whales at the entrance of the Corcovado Gulf by Cummings & Thompson (1971) is the only description of the SEP blue whale song up until now and is considered the only characteristic song type for SEP blue whales in the literature (Stafford et al. 1999b, McDonald et al. 2006). This song was later recorded on a fixed hydrophone in the ETP (8° S 95° W) during March to August, the austral winter (Stafford et al. 1999b). These authors also recorded another song, which they classified as a variant ('variant 2') of the song recorded by Cummings & Thompson (1971). Here, based on our analysis of the frequency characteristics of song units and song unit precursors, and the temporal characteristics of song phrases and song units of the song sequences produced by blue whales that feed in the Corcovado Gulf, we distinguished 2 songs, which we named SEP1 and SEP2. This adds a new song to the repertoire of blue whales in Chile. Based on the detailed comparison of SEP1 and SEP2 with the previous songs recorded by Cummings & Thompson (1971) and Stafford et al. (1999b), we conclude that SEP1 is the same song reported by Cummings & Thompson (1971), and SEP2 is variant 2 reported by Stafford et al. (1999b).

The small sample size for SEP1 (n = 5) makes song sequence characterization based on this study alone problematic, but we believe that its similarity to reports by Cummings & Thompson (1971) and Stafford et al. (1999b), which both document its existence, supports the robustness of our classification. We recognize that the high levels of low-frequency noise in our recordings may have affected quantitative song unit measurements due to poor SNR. For some sounds, high noise levels at low bandwidths (0–25 Hz) meant that any potential peak frequency of units at these lower bandwidths could not be measured (e.g. SEP2 in Fig. 2d) or that the measurements of duration of less intense song units were highly variable, like unit A in SEP2 (Table 3). However, there is no reason to believe that these quantitative measurement errors were sufficiently consistent in magnitude or direction to systematically bias the results enough to render the obvious distinctions between the 2 songs spurious. Furthermore, it is the case that different sample rates could have affected comparisons with data described in previous studies. The Stafford et al. (1999b) data were sampled at a very low sample rate (100 Hz, versus 96 kHz in our study) such that the bandwidth was only 0.1 to 40 Hz and therefore many of the elements that help to characterize the 2 songs in our study were not recorded by those authors. We attempted to mitigate this by decimating our data and the data of Cummings & Thompson (1971) to a sample rate of 100 Hz for visual comparison (Fig. 2).

High-frequency song unit precursors

The occurrence of short (~1 s), higher frequency (>350 Hz) precursors to unit C1 in SEP1 and to units A2 and D2 in SEP2 (Fig. 3a,b), is noteworthy since they have seldom been reported in the literature and lie well above the frequency ranges generally reported for blue whales. These sounds may have been often overlooked in previous analyses or missed by low sampling rates. However, Cummings & Thompson (1971, p. 1195) did mention the occurrence of 'a 0.5- to 1-sec pulse of about 390 Hz' prior to the start of unit C1 in the SEP1 song; McDonald et al. (2001) also reported a high-frequency precursor to unit B in the blue whale song recorded off California. These precursors were useful in distinguishing between SEP1 and SEP2 in this study; we therefore recommend that sufficient sample rates (>1 kHz) be used and these sounds be reported in future blue whale song studies to enable more robust classification.

SEP2: a new song described for SEP blue whales

We describe 2 songs, SEP1 and SEP2, the latter of which was largely predominant with 62 phrases recorded compared with 5 phrases of SEP1. In the Chiloense Ecoregion, only SEP1 had been previously described (Cummings & Thompson 1971), so the present study is the first to describe the SEP2 song in the Chiloense Ecoregion. The song type was previously described as 'variant 2' in the ETP by Stafford et al. (1999b), who attributed it to southern blue whales based on its seasonality, i.e. higher call intensities during the austral winter. Our recording of SEP2 much farther south of the ETP confirms this interpretation. We propose that it be considered as part of the SEP blue whale repertoire for future acoustic studies in this region. These findings also suggest that most blue whales using the Corcovado Gulf feeding area in the austral summer use the SEP2 song and not the SEP1 song, although a longer data set will be necessary to confirm this.

An acoustic link between the ETP and the Chiloense Ecoregion

The occurrence of SEP1 and SEP2 in the Corcovado Gulf (Cummings & Thompson 1971, this study) and in the ETP (Stafford et al. 1999b) establishes an acoustic link between the Chiloense Ecoregion and the ETP, which suggests that the same group(s) of blue whales migrate between these 2 locations. Stafford et al. (1999b) recorded both songs in roughly equal proportions at a fixed hydrophone array in the ETP, at 8° S, 95° W, but rarely above the Equator. Both songs displayed a clear, similar, seasonal pattern: significantly more frequent calling between late January and the end of August, indicating that at least a proportion of SEP blue whales migrate south from the ETP during the austral summer. Unfortunately, the inherent limitations of our sampling method mean that it was not possible to determine the temporal and spatial distribution patterns of SEP songs. Satellite tagging data suggest that some proportion of the animals that feed in the Corcovado Gulf during the austral summer travel north to spend the winter in the ETP (Hucke-Gaete 2004). However, sighting data (Findlay et al. 1998), as well as some recent records (Abramson & Gibbons 2010, Försterra & Häussermann 2012), have documented the presence of blue whales in the Chiloense Ecoregion until the beginning of July. It is still unclear, therefore, whether some blue whales remain year-round in the Chiloense Ecoregion or whether some whales start to migrate out of the area later in the year, past the month of July. Until we have year-round acoustic data from fixed hydrophone systems and sighting data for the feeding sites in the Chiloense Ecoregion (e.g. Corral, Northeast Chiloe, Corcovado Gulf), it will be difficult to fill these knowledge gaps.

Blue whale acoustic groups

The overlap of distinct song types temporally and/or spatially is not uncommon in blue whales, and it is thought to reflect the seasonal passage of different acoustic populations through different areas. In the North Pacific, one song type has been recorded in the Northeast Pacific, and a different song in the Northwest Pacific, both with similar seasonal variations, but largely spatially distinct (Stafford et al. 2001). These songs overlap in space and time in the Gulf of Alaska (Stafford 2003), and both occur in the central North Pacific but not at the same time (Stafford et al. 2001). In the Indian Ocean, where multiple acoustic populations exist, the overall distribution of song types suggests that, although these acoustic populations have some limited overlap, they do mostly have distinct ranges (Alling et al. 1991, McCauley et al. 2000, Samaran et al. 2013). In some cases, where different song types overlap spatially, recorded at the same fixed location, they displayed largely different seasonalities and proportions of occurrence, as seen in the ETP where both Northeast Pacific and SEP blue whale songs have been recorded (Stafford et al. 1999b).

In this study, the possible occurrence of 2 song types, as opposed to 2 variants, in the Corcovado Gulf could indicate (1) the presence of 2 distinct blue whale acoustic groups that exploit this feeding area at similar times of year, but have different distributions (e.g. onshore or offshore), seasonal residencies and migration routes; or (2) the presence of one acoustic group with higher levels of song type variation than have been previously described for a single population of blue whales, for example due to individual variation or different behavioural contexts. In the ETP, both SEP1 and SEP2 were recorded with similar seasonality (austral winter) according to Stafford et al. (1999b), which suggests common migration and thus that both songs could stem from the same population. The similarities between the song units of SEP1 and SEP2 could suggest their evolution from a common stock source. Given the limited temporal and spatial coverage of our acoustic data, and the lack of integrated photo-identification and genetic data for these animals, it is unclear how these 2 songs reflect population structure.

CONCLUSIONS

These data from the austral summers of 2008, 2009 and 2011, which include the data reported by Buchan et al. (2010), are the first recordings of blue whales in the Chiloense Ecoregion of Southern Chile since 1970 (Cummings & Thompson 1971). Two distinct songs emerged from our analysis that should be used to monitor the temporal and spatial distribution of SEP blue whales in future passive acoustic studies. SEP1 matched the song described by Cummings & Thompson (1971) recorded at the entrance of the Corcovado Gulf, although we only recorded this song on 1 day throughout our 3-summer study period. The SEP2 song, on the other hand, was much more common, recorded on multiple days during all 3 summer seasons. Our report of SEP2 adds a new song to the current description of the SEP blue whale repertoire. Our findings suggest that most blue whales using the Corcovado Gulf feeding ground during the austral summer use the SEP2 song and not the SEP1 song. Both SEP1 and SEP2 songs were recorded by Stafford et al. (1999b) in the ETP. This acoustic link suggests a north–south migration of SEP blue whales between Chile and the ETP.

Given the importance of song type studies in defining acoustic groups of blue whales, by characterizing the songs of SEP blue whales, our findings open up questions for future passive acoustic research on SEP blue whales. Future studies should focus on the use of fixed passive acoustic techniques that provide greater spatial and temporal coverage in order to answer certain key questions: (1) Are these SEP songs sufficiently different to be classified as different song types or are they variants of each other? (2) How do SEP blue whale songs overlap in space and time within the Chiloense Ecoregion feeding ground and the wider SEP region? (3) How do these songs relate to SEP blue whale population structure? Answering these questions will bring us closer to resolving the issue of population identity, distribution and movements of endangered SEP blue whales. Moreover, whale song studies will need to be integrated with photo-identification, genetics studies and satellite tracking, due to likely mixing of groups in the Chiloense Ecoregion and the SEP.

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4.2 Capítulo 2: Presencia estacional de ballenas azules del Pacífico Suroriental en el Sur de Chile y el Pacífico Tropical Oriental

Manuscrito en prensa en Marine Mammal Science: Buchan, S. J., K. M. Stafford & R. Hucke-Gaete. *En prensa*. Seasonal occurrence of southeast Pacific blue whale songs in southern Chile and the eastern tropical Pacific. Marine Mammal Science.

Resumen: Datos de Monitoreo Acústico Pasivo fijo fueron colectados entre enero 2012 y abril 2013 en cuatro sitios de la ecorregión Chiloense (ERC) en el Sur de Chile (≈43°-44°S, 71°-73°W) y en 1996-2002 en un sitio del Pacífico Oriental Tropical (ETP) (8°S, 95°W). Detectores automáticos fueron utilizados para detectar dos cantos (SEP1 y SEP2) descritos para las ballenas azules del Pacífico Suroriental (PSO). Hubo un patrón estacional fuerte de una alta cantidad de cantos SEP en la ERC de diciembre a agosto, con una máxima en marzo-mayo. En el PTO, los cantos fueron menos numerosos pero estuvieron presentes todo el año, con una máxima alrededor de junio. Estos resultados sustentan una residencia estacional de las ballenas azules en la ERC durante el verano/otoño austral, y un desplazamiento estacional hacia el PTO durante junio/julio, retornando en diciembre. Variaciones interanuales en el PTO estuvieron posiblemente asociadas al evento El Niño de 1997-1998. En ambos sitios de estudio, SEP2 fue mucho más común que el SEP1; aunque ambos cantos siguieron las mismas tendencias temporales. Estos resultados contribuyen al conocimiento de los desplazamientos estacionales de las ballenas azules amenazadas del PSO y pueden contribuir a la generación de estrategias de conservación, particularmente en el área de alimentación de la ERC. Se recomienda el Monitoreo Acústico Pasivo con cobertura anual en la ERC y la PTO (ej. cerca de las islas Galápagos), idealmente acoplado a la colección de datos oceanográficos.

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Seasonal occurrence of southeast Pacific blue whale songs in southern Chile and the eastern tropical Pacific

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Abstract

Passive acoustic data were collected January 2012 to April 2013 at four sites in the Chiloense Ecoregion (CER) in southern Chile (≈43°S–44°S, 71°W–73°W) and 1996–2002 from one site in the eastern tropical Pacific (ETP) (8°S, 95°W). Automatic detectors were used to detect the two songs (SEP1 and SEP2) described for southeast Pacific (SEP) blue whales. There was a strong seasonal pattern of occurrence of SEP songs in the CER from December to August, peaking March to May. In the ETP, the occurrence of songs was an order of magnitude lower but songs were present year-round, with a peak around June. These findings support austral summer/autumn seasonal residency in the CER and a seasonal movement of blue whales towards the ETP during June/July, returning in December. Interannual differences in the ETP were possibly linked to the 1997–1998 El Niño event. At both study sites, SEP2 was significantly more common than SEP1; both songs largely followed the same temporal trends. These findings contribute to our understanding of the seasonal movements of endangered SEP blue whales and can inform conservation strategies, particularly in the CER coastal feeding ground. We recommend future year-round passive acoustic studies in the CER and the ETP (*e.g.*, near the Galapagos Islands), ideally coupled with oceanographic data.

Key words: blue whale, *Balaenoptera musculus*, passive acoustic monitoring, whale song, Chiloense Ecoregion, southeast Pacific, eastern tropical Pacific.

Throughout the Southern Hemisphere, blue whales (*Balaenoptera musculus* spp.) were decimated by industrial whaling and are currently listed as Endangered on the IUCN Red List of Threatened Species (Reilly *et al.* 2008). In the southeast Pacific (SEP), approximately 3,000 blue whales were caught between 1827 and 1971 (Aguayo-Lobo *et al.* 1998), principally off the coast of Chile, but also off Peru and Ecuador (Clarke *et al.* 1978, Ramirez 1983, Van Waerebeek *et al.* 1997). The current abundance estimate for blue whales in Chilean waters is 303 animals (95% CI = 176–625) between north (18°S) and central Chile (38°S) (Williams *et al.* 2011). However, this does not include the Chiloense Ecoregion (CER; Spalding *et al.*

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2007) feeding ground in southern Chile (≈41°S–44°S) (Hucke-Gaete *et al.* 2003, Cabrera *et al.* 2005, Zamorano-Abramson and Gibbons 2010, Galletti Vernazzani *et al.* 2012), that hosts an estimated 222 animals (95% CI = 115–430) (Hucke-Gaete *et al.* 2010).

Sighting data have indicated high concentrations of blue whales throughout the CER during the austral summer months (Hucke-Gaete *et al.* 2010). There have been limited reports of blue whales as late as July (Zamorano-Abramson and Gibbons 2010, Försterra and Häussermann 2012) and anecdotal accounts from the local community of year-round presence of blue whales in this area; however climatic conditions in this part of Chilean Patagonia mean that systematic visual observation effort has been largely restricted to summer months. Up to this point, the lack of year-round data has meant that it has not been possible to systematically determine the seasonal residency of blue whales in the CER.

It is generally thought that Southern Hemisphere blue whales undergo north-south migrations, between high-latitude summer feeding grounds and low-latitude calving grounds (Mackintosh and Wheeler 1929). In the Southern Hemisphere, feeding grounds have been identified in southern Chile (Hucke-Gaete *et al.* 2003), the Indian Ocean (Samaran *et al.* 2010, Stafford *et al.* 2011), the Southern Ocean (Mackintosh and Wheeler 1929), New Zealand (Torres 2013), and Australia (Gill 2002). Where reproduction occurs is unknown, but calving is speculated to occur at low-latitude wintering grounds, such as the ETP, where blue whales are known to congregate (Berzin 1978; Donovan 1984; Reilly and Thayer 1990; Wade and Gerrodette, 1993; Palacios 1999; Stafford *et al.* 1999*a*, *b*; Gilpatrick and Perryman 2008).

Southeast Pacific blue whales are thought to follow a north-south migration route based on satellite tracking data from the CER feeding ground (Hucke-Gaete 2004) and an acoustic link established between the CER and the ETP (Stafford *et al.* 1999*b*, Buchan *et al.* 2014). However, it has also been suggested that blue whales off the north coast of South America are part of a resident ETP population or "Galapagos biostock" (Berzin 1978, Donovan 1984, Palacios 1999, Gilpatrick and Perryman 2008). New findings by Torres-Florez *et al.* (2014) based on molecular techniques suggest that Chilean blue whales sampled in the Corcovado Gulf could be part of a larger SEP population, which separates into smaller subgroups during the austral summer feeding season.

Two subspecies of blue whale are widely recognized in the literature (*e.g.*, Branch *et al.* 2007*a* for the Southern Hemisphere: Antarctic blue whales, *Balaenoptera musculus intermedia* and pygmy blue whales, *Balaenoptera musculus brevicauda*). Both subspecies were caught off the coast of Chile (Aguayo 1974). However, later evidence suggests that the blue whales present off the coast of Chile are in fact a separate subspecies, as originally proposed by Clarke *et al.* (1978), supported by body length data (Branch *et al.* 2007*a*, Gilpatrick and Perryman 2008), discrete summertime distribution (Branch *et al.* 2007*b*), genetic analyses (Conway 2005, LeDuc *et al.* 2007), and a distinct acoustic repertoire (Cummings and Thompson 1971; Buchan *et al.* 2010, 2014). Chilean blue whales are now recognized as a separate unnamed subspecies (Committee on Taxonomy 2014), but remain one of the most poorly understood groups of blue whales worldwide. The population identity and movements of Chilean blue whales remain largely open questions.

Beyond these subspecies distinctions, blue whales worldwide can be further classified into acoustically distinct populations, or acoustic groups, with distinct song types, geographic ranges, migration routes and seasonal residencies (*e.g.*, Stafford *et al.* 1999*a*, *b*, 2001, 2011; Mellinger and Clark 2003; McDonald *et al.* 2006;

Samaran *et al.* 2013). Song, the patterned sequence of call sounds (as opposed to isolated calls), is believed to be produced only by male blue whales and therefore thought to have some reproductive function (Oleson *et al.* 2007*a*). Blue whales produce these population-specific songs throughout their migratory range (Stafford *et al.* 1999*a*, 2001). Song types are characterized by the frequency and duration characteristics of the individual sounds, *i.e.*, song units (A, B, C, *etc.*) and unit precursors (McDonald *et al.* 2001), which make up song phrases (A-B-C-A-B-C or A-B-A-B) (see McDonald *et al.* 2006). These characteristics are believed to remain stable over decades, except for gradual shifts in frequency (McDonald *et al.* 2009, Gavrilov *et al.* 2011). The degree of variation within song types is much lower than the variation among song types (McDonald *et al.* 2006).

In the Southern Hemisphere, there are thought to be at least five distinct acoustic groups: Antarctic, Sri Lankan, Madagascar, Australian, and Chilean or southeast Pacific (Cummings and Thompson 1971, McDonald *et al.* 2006, Stafford *et al.* 2011, Samaran *et al.* 2013, Miller *et al.* 2013, Buchan *et al.* 2014). Two distinct song types in the SEP, known as SEP1 and SEP2, have been recorded from blue whales both in the CER in southern Chile (Buchan *et al.* 2014) and in the ETP (8°S, 95°W; Stafford *et al.* 1999*b*), suggesting spatial and temporal overlap of blue whales that produce each of these songs. SEP1 matches the previously reported Chilean song type by Cummings and Thompson (1971) (Stafford *et al.* 1999*a*, Buchan *et al.* 2014). It remains unclear whether the presence of these two distinct SEP songs reflects the presence of two distinct acoustic groups or one acoustic group that produces more than one distinct song type, which has not been previously documented for blue whales. In the ETP where fixed hydrophone data are available, SEP songs were present year-round, although less frequent between September and March (Stafford *et al.* 1999*a*). Up until now, no fixed hydrophone data have been available for the CER.

The aim of this study was to employ passive acoustic monitoring (PAM) techniques to determine the temporal variation of the presence of each SEP blue whale song in the CER (14 mo of data) and the ETP (6 yr of data), in order to (1) determine the seasonal pattern of occurrence of SEP blue whale songs at each study site, (2) verify the acoustic link between the two regions, and (3) examine any interannual differences in the ETP data set.

MATERIALS AND METHODS

Acoustic Data Collection in the CER

Acoustic data from the CER in the south of Chile (≈43°S–44°S, 71°W–73°W) were collected during three 5 mo deployment periods between the end of January 2012 to the end of April 2013 using six Marine Autonomous Recording Units (MARUs) deployed at four different coastal study sites: Northwest Chiloe, Guafo North, Tic Toc Bay, and Locos Islet (Fig. 1). Deployment details of MARUs are listed in Table 1. MARUs were leased from the Cornell University Laboratory of Ornithology's Bioacoustics Research Program. MARUs were programmed to record continuously at a sampling rate of 2 kHz. Acoustic data were recorded to an internal hard drive and only accessible upon instrument recovery. Deployment sites were chosen to provide wide geographic coverage of the CER feeding ground from the northwest of Chiloe Island to the southern section of the Corcovado Gulf, as well as from the more offshore area of Guafo Island to nearshore areas closer to the

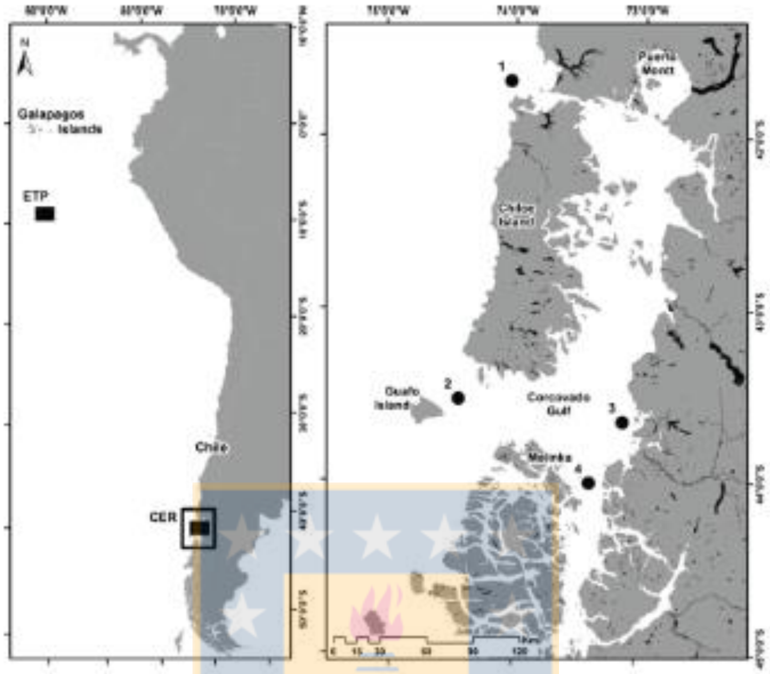

Figure 1. Map of study areas showing, left panel: the ETP study site (one hydrophone deployment location) and the CER study site (four hydrophone deployment locations); right panel: the three hydrophone deployment sites in the CER: 1. Northwest Chiloe, 2. Guafo North, 3. Tic Toc Bay, and 4. Locos Islet.

Chilean continent. Three MARU recovery attempts were unsuccessful, therefore some temporal coverage was lost at certain sites, which is an inherent shortcoming of the data set. The recovered data were extracted onto a hard drive.

Acoustic Data Collection in the Eastern Tropical Pacific

Acoustic data from the ETP (8°S, 95°W; Fig. 1) were collected between 1996 and 2002 (data were not available for 2000). Deployment details are listed in Table 1. This site is located in a low-latitude offshore area, almost 1,575 km (850 nmi) from the coast of Peru and almost 925 km (500 nmi) SSW of the Galapagos Islands. Acoustic data from this hydrophone were chosen for analysis following Stafford *et al.* (1999*b*), who found SEP song detections to be highest at this site out of the total six sites. The hydrophone package used included an autonomous hydrophone logging system composed of an International Transducer Corporation 1032 hydrophone, pre-amplifier/filter (designed to prewhiten ocean ambient noise spectra below 40 Hz) and a digital recorder in pressure-resistant titanium housing. Acoustic data were collected continuously at a sample rate of 100 Hz. They were archived within the instrument until it was recovered, then downloaded onto 8 mm digital tape (Fox *et al.* 2001).

Table 1. Fixed hydrophone deployment details for the ETP and CER study sites: location, latitude, longitude, total water column depth (m), deployment depth (m), start and end dates of recording, total number of hours of acoustic data in data set, sample rate of recording.

Hydro-phone code	Location	Latitude, longitude	Water column total depth (m)	Deployment depth (m)	Start date	End date	Total hours	Sample rate
MARU 1	Guafo North	43°31.889′S, 74°26.488′W	200	200	31 January 2012	17 June 2012	3,370	2 kHz
MARU 2	Guafo North	43°31.918′S, 74°26.092′W	210	210	4 December 2012	28 April 2013	3,497	2 kHz
MARU 3	Locos Islet	44°00.966′S, 73°23.379′W	170	170	19 June 2012	6 December 2012	4,077	2 kHz
MARU 4	Locos Islet	44°01.015′S, 73°23.419′W	170	170	6 December 2012	29 April 2013	3,492	2 kHz
MARU 5	Northwest Chiloe	41°41.179′S, 74°02.442′W	140	140	23 January 2012	25 June 2012	3,688	2 kHz
MARU 6	Tic Toc	43°39.618′S, 73°07.789′W	200	200	6 December 2012	29 April 2013	3,495	2 kHz
ETP 1	Eastern Tropical Pacific	8°S, 95°W	~1,000	650–750	13 May 1996	20 October 2002 (no data for 2000)	≈46,464	100 Hz (1996–1999) 250 Hz (2001–2002)

Blue Whale Song Detections

Acoustic data were analyzed as spectrograms using XBAT (Extensible Bioacoustic Tool; Bioacoustics Research Program 2012). For the CER data sets, spectrograms were made with FFT: 4,096 samples, 25% overlap, Hann window. For the ETP data set, spectrograms were made with FFT: 512, 25% overlap, Hann window. Automated detectors were built in XBAT targeting the two previously described blue whale songs for the southeast Pacific, referred to as SEP1 and SEP2 (Buchan *et al.* 2014). In XBAT, automatic detection is done by spectrogram correlation, which quantifies the similarity between a signal and a template or kernel of a target sound (*cf.* Mellinger and Clark 2000). Antarctic blue whale songs were ignored as they had been treated in a previous publication for the ETP (Stafford *et al.* 2004). SEP1 and SEP2 detectors targeted parts of the song phrase (one or more song units) considered to be most characteristic of each specific song type (Fig. 2), *i.e.*, a section of each phrase of the respective song types, which was distinct from the other song type and that also had the highest signal to noise ratio (SNR), even in very faint phrases. Because of sampling rate differences, separate detectors were built for the CER and ETP data sets. Once the detectors were run on the respective data sets, the total number of detections was counted per month per song; this was then divided by the total

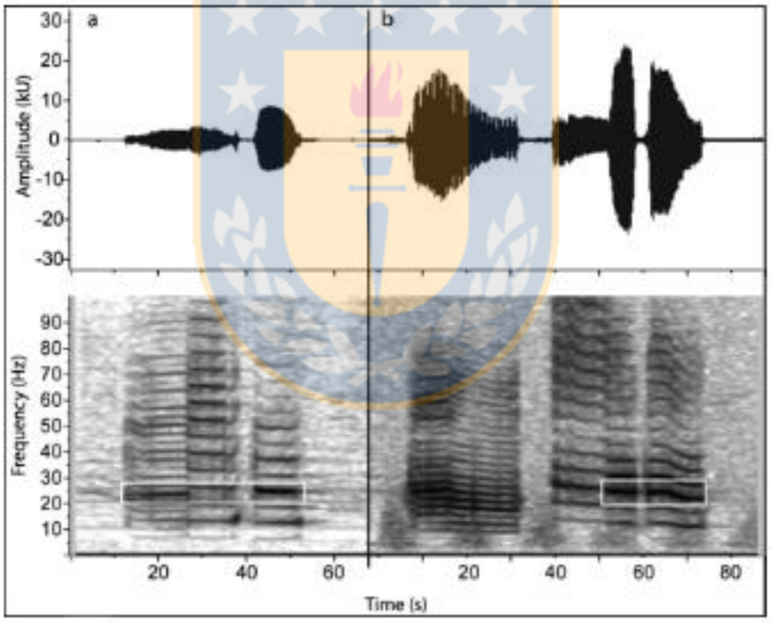

Figure 2. Waveforms (top panels) and spectrograms (lower panels) of southeast Pacific blue whale songs, (a) SEP1 and (b) SEP2, from acoustic data in the CER. Spectrogram parameters: FFT: 4,096, 50% overlap, Hann window. White boxes indicate the parts of the song selected as a template for automatic detection in XBAT.

days of acoustic monitoring effort in the given month, to obtain the average number of detections per day during each month and thereby examine temporal variations in song occurrence.

To determine statistical differences between the total detections of each SEP song at both study sites, Student's *t*-tests were applied to monthly detections of each song at each site.

Detector Performance

For the CER data sets, the high number of SEP1 and SEP2 song units initially detected by the detector meant that it was not practical to verify all detections as being true positives (correct detections). Where the number of detections per month was fewer than 500, each detection was scanned visually and deleted if a false positive (incorrect detection). In order to assess detector performance, the first 48 h of data of every month recorded by MARUs 1, 2, and 3 were scanned visually to determine the number of false positives and false negatives (missed target sounds) as a percentage of the total number of detections. A total of 912 h (4% of the 21,728 h data set) were assessed. It was found that 3% of detections by the SEP1 detector and 3% of detections by the SEP2 detector were false positives and 33% of the SEP1 detections and 28% of the SEP2 detections were false negatives. Corrected detections were calculated by subtracting the percent of false positive detections from initial detections (except for those months with 500 detections or fewer where all detections were reviewed) and adding the percent of false negatives on to all months.

For the ETP data set, initial detections were also too numerous to make it possible to review each detection visually, so where the number of detections per month was less than 50, each detection was scanned visually and deleted if false positive. Additionally, the first 48 h of every month from years 1997 and 1999 were assessed visually to determine the number of false negatives as a percentage of the total number of detections. A total of 912 h (2% of 46,800 h data set) were assessed, and found that 7% of the SEP1 detections and 13% of the SEP2 detections were false positives, while 6% of SEP1 detections and 17% of SEP2 detections were false negatives. For both SEP and ETP data, corrected detections were reported.

RESULTS

SEP Songs in the Chiloense Ecoregion

Both SEP blue whale songs, SEP1 and SEP2 (Fig. 3), were detected in the CER in high numbers, with a total of 397,752 corrected SEP detections from the 21,728 h of data.

SEP blue whales were detected in this study area between December and August over the three 5 mo study periods, with a very strong seasonal pattern for both SEP1 and SEP2 detections (Fig. 3a–f). Detections peaked above 1,000 detections/day (30,000 detections/month) between March and May during 2012 and 2013 at all four study sites, and then decreased dramatically in June (≈150 detections/day), although data from this month were incomplete and only available for Guafo North 2012 (Fig. 3a), Locos Islet 2012 (Fig. 3c), and Northwest Chiloe 2012 (Fig. 3e). No SEP blue whale songs were detected between September and November 2012 (only Locos Islet data available; Fig. 3c). There was a significant difference (t_{42} = -5.22,

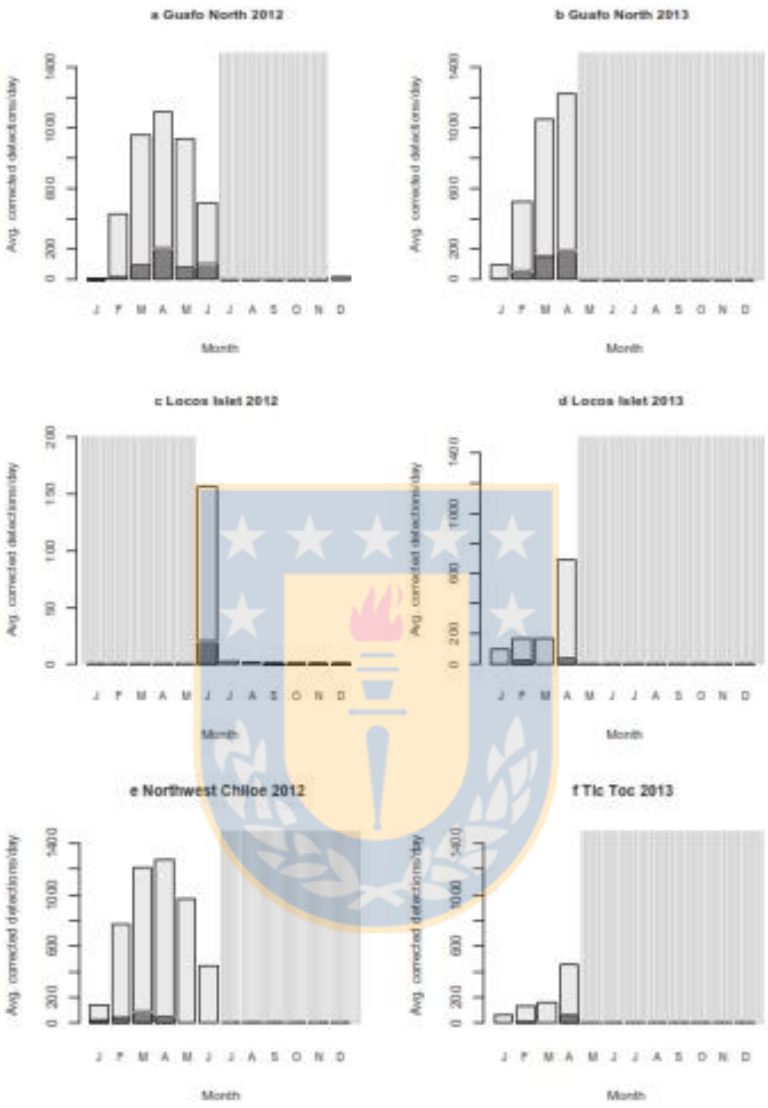

Figure 3. Temporal variation of southeast Pacific blue whale song detections of SEP1 and SEP2 in the CER, south of Chile, during 2012/2013 at (a) Guafo North 2012, (b) Guafo North 2013, (c) Locos Islet 2012, (d) Locos Islet 2013, (e) Northwest Chiloe 2012, and (f) Tic Toc 2013. Dark bars indicate SEP1 songs, light bars indicate SEP2 songs. Vertical shading indicates lack of data for these months.

$P < 0.0001$, $\alpha = 0.01$) between the total detections of SEP1 and SEP2. SEP2 (n = 362,486 corrected detections) was the dominant song throughout the data set, making up over 90% of total detections, as compared with SEP1 (n = 35,266 corrected detections). Both, however, largely followed the same seasonal trend, peaking during summer months; however, no SEP1 song units were detected beyond June 2012, while SEP2 song units were detected until August 2012 (Fig. 3c).

SEP Blue Whale Songs in the Eastern Tropical Pacific

Both southeast Pacific blue whale songs were detected in the ETP over the 6 yr study period, with a total of 51,838 corrected SEP detections during the 46,800 h of data. Total SEP detections in the ETP over the 6 yr study period were much lower than detections over the 14 mo study period in the CER; detections in the ETP occurred in an order of magnitude lower than in the CER, roughly the same as wintertime detections in the CER (n < 3,000 per month).

The seasonal pattern was much weaker in the ETP than the CER. SEP2 was detected in the ETP during all months of most years, while SEP1 was principally detected June–August (Fig. 4a–f). A slight seasonal pattern for SEP2 was apparent, with most detections occurring in June, although year-to-year this peak shifted by a month or two.

Interannual differences in SEP2 detections were apparent in the ETP. The lowest numbers of detections per year occurred during 1999 (n = 3,815) and 2001 (n = 2,487), compared with the highest during 1996 (n = 17,835). No data were available for 2000.

As in the CER, SEP2 (n = 49,747 detections) was the dominant song throughout the data set compared with SEP1 (n = 2,091), and occurred significantly more often ($t_{142} = -5.59$, $P < 0.0001$, $\alpha = 0.01$) accounting for over 95% of total detections.

DISCUSSION

Seasonal Occurrence of SEP Blue Whale Songs in the Chiloense Ecoregion

The seasonal residency of SEP blue whales on the CER feeding ground was unknown prior to this study. The passive acoustic data presented here are the first data to provide near-annual coverage on the presence of SEP blue whales in the CER. Sighting data have documented the presence of blue whales in the CER between January and the beginning of July (Findlay *et al.* 1998; Hucke-Gaete 1998, 2004; Hucke-Gaete *et al.* 2003; Cabrera *et al.* 2005; Zamorano-Abramson and Gibbons 2010; Försterra and Häussermann 2012; Galletti Vernazzani *et al.* 2012), in addition to anecdotal accounts from the local community of year-round presence. Satellite tracking data indicated that some blue whales that feed during the austral summer in the CER migrate north in winter to the Nazca Ridge region in the ETP (Hucke-Gaete 2004).

The acoustic data presented here reveal a strong seasonal pattern in SEP blue whale songs. Singing SEP blue whales were present between December and August in the CER, with a dramatic peak between March and May, and decreased several-fold in June. Although there are no year-round visual sighting data, this compares well with the abovementioned sighting data during the austral summer and late autumn (*e.g.*,

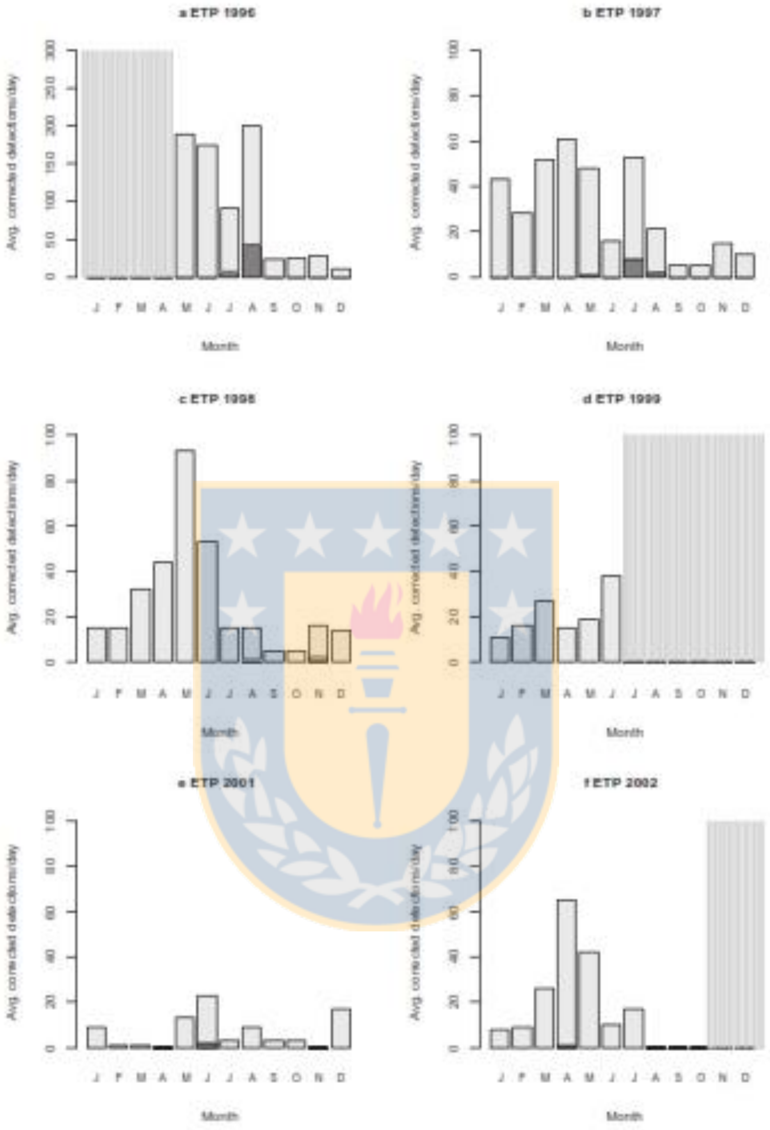

Figure 4. Temporal variation of southeast Pacific blue whale songs SEP1 and SEP2 in the ETP during (a) 1996, (b) 1997, (c) 1998, (d) 1999, (e) 2001, and (f) 2002. Dark bars indicate SEP1 songs, light bars indicate SEP2 songs. Vertical shading indicates lack of data for these months.

Findlay *et al.* 1998, Hucke-Gaete *et al.* 2003, Försterra and Häussermann 2012). It also compares well with lower occurrences of SEP songs between September and March at the same ETP location (1996–1997) by Stafford *et al.* (1999*b*).

Blue whale distribution in mid- and high-latitude feeding grounds, where biological productivity is characteristically seasonal (Fleming 1957), is driven by the attraction of whales to areas where high euphausiid densities are predictable as a result of high levels of primary productivity caused by coastal upwelling, topographic breaks, and/or frontal regions (*e.g.*, Croll *et al.* 1998, 2005; Branch *et al.* 2007*b*; Gill *et al.* 2011). The CER blue whale feeding ground is a complex mega-estuarine system that receives important inputs of both oceanic subantarctic and continental freshwater into an intricate network of channels, fjords, and open gulfs (Palma and Silva 2004), leading to an array of frontal features. Primary production is high and strongly seasonal, peaking in spring/summer (González *et al.* 2010), exceeding 10 mg Chl-a m^{-3} (Hucke-Gaete 2004, Montecino and Pizarro 2006). The dominant mesozooplankton species in this area, the euphausiid *Euphausia vallentini* (Antezana 1976), doubles in abundance between winter and spring (González *et al.* 2010) and probably peaks in late summer (Croll *et al.* 2005). We hypothesize that the peak we observed in SEP detections during the late austral summer and early autumn (March–May) coincides with the annual peak in euphausiid abundance, also postulated by Burtenshaw *et al.* (2004) in the northeast Pacific. Long-term coupled oceanographic and passive acoustic data are necessary to better understand how the seasonal residency of SEP blue whales is linked to underlying oceanographic processes in the CER feeding ground.

The acoustic data analyzed here were from three different sites in the CER located 93–185 (50–100 nmi) apart. Due to several unsuccessful MARU deployments, there were no continuous data from one single site for more than 5 mo, except for the Locos Islet 2012 deployment between June 2012 and April 2013. This reduced coverage may have induced geographic variation into the temporal patterns observed, especially between inner (Locos Islet and Tic Toc) and outer gulf (Guafo North and Northwest Chiloe) areas, where detection ranges at hydrophones may differ due to site-specific sound propagation conditions. However, we consider this geographic variation to be minimal compared to the strong temporal pattern observed at the deployment sites. Moreover, Hucke-Gaete (2004) showed that three out of five blue whales tagged with satellite tracking devices used the inner (near Locos Islet) and outer gulf (near Guafo North) areas equally; one preferred primarily the northwest of Chiloe Island; and one primarily the inner gulf area (near Locos Islet).

While blue whales have been found to sing throughout their migration range (Stafford *et al.* 1999, 2001), singing behavior does not remain constant throughout the year, which could have affected detections rates at specific times of year. Off southern California, Oleson *et al.* (2007*b*) found that although blue whales were present and feeding during spring, song production started in summer, and peaked in late summer (as observed in this study). These authors speculated that the time lag between the arrival of blue whales at the feeding ground and the time when whales start singing could indicate the time necessary for males to obtain sufficient food resources to allocate energy to singing following low food intake during winter in less productive southern calving grounds.

Lastly, gradual interannual frequency shift in blue whale calls, as reported for other parts of the world (McDonald *et al.* 2006) could have led to a higher number of missed calls, especially for the multiyear ETP data, although that did not appear to be true based on our detector performance assessment. The percentage of false negatives by both SEP1 and SEP2 detectors for the CER data is nonnegligible and may have also affected results, especially in parts of the data set with less singing. This high percentage was a trade-off for obtaining detectors that had a very low rate of confusion between them, *i.e.*, SEP1 sounds were almost never detected as SEP2 sounds and *vice versa*. This high percentage is also a trade-off for a very low proportion of false positives, most of which occurred due to confusion with instrument noise at 5 Hz intervals throughout the MARU data sets. Achieving low levels of false positives and no confusion between SEP1 and SEP2 were prioritized given the emphasis placed on differentiating between song types in this study; additionally we found that temporal trends were found to be largely unchanged by a lower proportion of false negatives. Lastly, many studies do not report the percent of false negatives at all, only false positives, and it is therefore difficult to compare these values with the literature.

Seasonal Movements of SEP Blue Whales to the ETP

The migration of blue whales between high-latitude feeding grounds and low-latitude calving grounds was first put forward by Mackintosh and Wheeler (1929). Blue whales in the CER have seemingly specialized in selecting and exploiting areas of predictable high productivity at mid-latitudes to maximize feeding success (Hucke-Gaete *et al.* 2003). The passive acoustic data presented here provides further support for the acoustic link between the CER and the ETP (Buchan *et al.* 2014) and shows SEP blue whales songs peaking March–May in the CER and around June in the ETP. Unfortunately, the data for ETP and CER were recorded 10 yr apart, which is a potential limitation and we recommend that future studies aim to obtain data from overlapping periods. Ideally, data should be collected with identical sample rates to apply identical automatic detectors to data sets, which would improve comparative analyses. Nevertheless, based on the seasonal peaks from the data available to us, we conclude that SEP blue whales undergo a seasonal movement from the CER to the ETP during June/July and arrive back in the CER from December onwards. If indeed singing activity is low in early summer and peaks in late summer (Oleson *et al.* 2007*b*), and given that the seasonal pattern is much weaker in the ETP than the CER, then the timing of the departure from the CER towards the ETP in June/July is a more reliable estimate than the estimated departure from the ETP towards the CER. If this seasonal movement pattern is true, then the SEP population could be supported by the highly productive CER system (44°S) during the austral summer, but also by the productive coastal upwelling of the Humboldt Current System (≈39°S–5°S), and by local topographic and equatorial upwelling foci offshore in the ETP, including the Galapagos, (≈10°S–0°) during winter when calving is likely to take place. This seasonal movement pattern is supported by sighting and historical catch data (Clarke 1980, Donovan 1984, Reilly and Thayer 1990, Capella *et al.* 1999, Palacios 1999, Branch *et al.* 2007*b*, Felix *et al.* 2007), acoustic data on both SEP songs (Stafford *et al.* 1999*b*, Buchan *et al.* 2014), and satellite tracking data (Hucke-Gaete 2004).

Although we assume that the seasonal differences in song occurrence between the two areas indicate a seasonal movement between the CER and the ETP for SEP blue whales, SEP song unit detections occurred in the ETP during all months of the year, indicating that some SEP animals remain year-round in the ETP. If indeed these SEP blue whales have developed modified migrations to optimize feeding success (Hucke-Gaete *et al.* 2003), then it is also possible that some individuals choose not to migrate south to the CER, possibly due to high energetic costs, or other unknown reasons, and remain year-round in the ETP. This may also apply to animals in the CER who remain undetected by PAM between September and November due to a possible seasonal pause in their singing activity. Given that females do not sing (Oleson *et al.* 2007*a*), no conclusions can be drawn regarding the seasonal movements of females, which may differ from males. This nonmigrating strategy would only work if areas in the ETP were able to supply sufficient food resources to blue whales year-round, as discussed below. It is also possible that there might be a constant flow of animals between the two sites whereby animals are not resident in one or another, but each area is occupied year-round.

At the low-latitude ETP study site, primary production is an order of magnitude lower than the CER (0.16 mg Chl-a m^{-3}, Pennington *et al.* 2006 *vs.* >10 mg Chl-a m^{-3}, Hucke-Gaete 2004, Montecino and Pizarro 2006) and does not vary seasonally (Fleming 1957), which could explain the order of magnitude lower and the much weaker seasonal signal in detections in the ETP. In the ETP, blue whales have been associated with the cold, nutrient-rich waters of the Peru Current and the Costa Rica Dome (Reilly and Thayer 1990, Wade and Gerodette 1993), and west and southwest of the Galapagos (Palacios 1999). For SEP blue whales, whose calls have not been detected north of the equator (Stafford *et al.* 1999*b*), the Galapagos, 926 km (500 nmi) to the northeast of our ETP study site, could be one of several productive hot spots where blue whales can potentially feed during the austral winter, and even year-round. Palacios (1999) reported seasonal blue whale sightings during the austral winter and spring months, and observations of blue whales feeding on surface swarms of the euphausiid *Nyctiphanes simplex*. Palacios (1999) speculated that aggregations of blue whales probably occur primarily offshore in this region, given the lack of near-shore sightings. More dispersed blue whale spatial distribution throughout a larger offshore area in the ETP could also explain overall fewer detections relative to the CER. However, fewer detections could also be due to seasonal differences in singing activity (Oleson *et al.* 2007*b*). On the other hand, the ETP site likely has a greater detection range than the CER site due to differences in water depth (deeper) and greater distance from the coast, which would mean that the difference in numbers of detections between both sites could be even greater than reported here. Off the coast of California, blue whale densities were an order of magnitude higher in feeding grounds than in the wintering grounds further south off Mexico (Forney and Barlow 1998, Calambokidis and Barlow 2004). Nevertheless, we cannot exclude the possibility that the ETP study site is located away from the main concentrations of SEP blue whales in winter, possibly near the Galapagos, where detections in winter may be much higher. Long-term PAM near the Galapagos Islands could provide valuable insights into the seasonal occurrence of blue whales near this productive area.

Interannual Variability in SEP Songs in the Eastern Tropical Pacific

Long-term acoustic data from the ETP for 1996–1999 and 2001–2002 presented here, showed interannual differences in total SEP song detections. Detections were highest during 1996, dropped in 1997 and remained low until 2002, with very few detections in 2001. A seasonal peak around June was observed during most years, except for 1997 when the seasonal peak was less marked and detections were higher earlier in the year, during the austral summer, relative to the rest of the year. We speculate that these interannual differences could be linked to the 1997–1998 El Niño event, the strongest in 50 yr (*e.g.*, Chavez *et al.* 1999). However, under this scenario, persistently low detections after 1998 are not easily explained. This El Niño event lead to well-documented reductions in ocean biological productivity (Chavez *et al.* 1999, 2002), sea lion (Sielfield and Guzmán 2002, Salazar *et al.* 2003) and sea bird abundance (Velarde *et al.* 2004, Vargas *et al.* 2006), and commercial fish catches (Niquen and Bouchon 2004) across the ETP. In the North Pacific, during the 1997–1998 El Niño, a reduction in acoustic energy in the blue whale frequency band in southern California was reported, coinciding with an increase in the more productive northern California feeding ground (Burtenshaw *et al.* 2004). It is possible that during El Niño years, SEP blue whales might have preferred the CER feeding ground in response to the El Niño affecting ETP productivity. Hucke-Gaete *et al.* (2003) reported visual sightings of over 60 blue whales within 4 h in January 1998 at the Corcovado Gulf, Chiloense Ecoregion. Based on visual surveys during the austral summer of 1997/1998 along the Chilean coast between 18°S and 53°S, Hucke-Gaete (2004) put forward that blue whales may have favored the Chiloense Ecoregion as a feeding ground during this El Niño event compared to the rest of the Chilean coast north of ≈39°S, where El Niño more directly affects the wind driven coastal upwelling system. Unfortunately, there are no long term PAM or sighting data during these years to validate this hypothesis, which remains untested.

Acoustic Groups

Two distinct songs have been reported for SEP blue whales in the CER (Buchan *et al.* 2014) and in the ETP (Stafford *et al.* 1999*b*), *i.e.*, SEP1 (a three-part song) and SEP2 (a four-part song) with marked differences in the temporal and frequency characteristics of their individual song units and song phrases (Buchan *et al.* 2014). Although both songs follow a largely similar seasonal pattern in both the CER and the ETP, SEP2 was much more common than SEP1 in both regions.

Stafford *et al.* (1999*b*) described these SEP songs as being the "most complex calls" recorded at the ETP site, compared to northeast and northwest Pacific, and Antarctic blue whale songs. The differences in SEP1 and SEP2 song characteristics could be considered as important as the differences among three pygmy blue whale song types recorded in the Indian Ocean, which have each been suggested to delineate populations with distinct geographical distributions (Stafford *et al.* 2012, Samaran *et al.* 2013). This has also been found to be true in the North Pacific, where the northeast Pacific and northwest Pacific song types have similar seasonal patterns but are mostly spatially distinct (Stafford *et al.* 2001).

The existence of a distinct SEP blue whale population or subspecies off the coast of Chile, with a distinct acoustic signature, has been widely supported (Cummings and Thompson 1971; Clarke *et al.* 1978; Branch *et al.* 2007*a*, *b*; Gilpatrick and Perryman 2008; Conway 2005; LeDuc *et al.* 2007; Buchan *et al.* 2014; Torres-Florez *et al.* 2014; this study). It is possible that this population may in fact segregate to different feeding grounds during the austral summer (Torres-Florez *et al.* 2014). In addition, there have also been suggestions of a resident ETP population or "Galapagos biostock" (Berzin 1978, Donovan 1984, Palacios 1999, Gilpatrick and Perryman 2008), a distinction that remains uncertain. These possible subpopulation distinctions are noteworthy in light of the very different proportions of each song detected both in the CER and the ETP. Conclusions regarding the presence of two SEP blue whale acoustic groups should be based not only on distinct songs types and their distributions, but also on distinct distribution ranges and/or migrations from sighting or satellite tracking data. The evidence we present here does not make a clear case either way. Therefore, no firm conclusions can be drawn at this time, but we call for greater spatial and temporal PAM, coupled with other monitoring and tracking methods.

Conclusions

This is the first report of year-round passive acoustic data for the CER blue whale feeding ground in southern Chile. Based on three consecutive 5 mo PAM periods, we found SEP blue whale songs occur between December and August, with a clear peak between March and May, coinciding with the late austral summer and autumn; we detected SEP songs in the ETP year-round, with a loose seasonal peak around June. We conclude that there is a seasonal movement of SEP blue whales between the CER and the ETP, where animals start to leave the CER in June/July and return in December.

These findings contribute to our understanding of SEP blue whale residents on their summer feeding ground in southern Chile and lead to hypotheses about a potential winter calving ground in the ETP. This information is useful for building conservation strategies, particularly in the CER coastal feeding ground in southern Chile. We recommend that future passive acoustic studies focus on a longer-term data set for the CER and on obtaining year-round data near the Galapagos Islands. These data sets should overlap temporally in order to help confirm the seasonal movements suggested by the results of this study. We also recommend that PAM studies be coupled with oceanographic data, which will help elucidate the underlying factors that drive blue whale temporal and spatial distribution.

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4.3 Capítulo 3: Condiciones oceanográficas para el forrajeo de ballenas azules en el golfo Corcovado, Patagonia chilena

Manuscrito en preparación para Conservation Biology: Buchan, S. J. and R. Quiñones. Oceanographic conditions for foraging blue whales at two feeding sites in the Corcovado Gulf, Chilean Patagonia.

Resumen: Comprender la ecología de forrajeo de las ballenas azules (*Balaenoptera musculus*) del Pacífico Suroriental (PSO) es una tarea crucial para lograr la protección de su crítico hábitat de alimentación en la ecorregión Chiloense (ERC) de la Patagonia chilena. El sector suroriental de golfo Corcovado (43°38’-44°01’S, 73°38’-73°01’W) es una zona preferencial de forrajeo de las ballenas azules en su área de alimentación de la ERC. El objetivo del estudio fue evaluar la variabilidad temporal de las condiciones ambientales asociadas a eventos de forrajeo y contrastar las diferencias de condiciones oceanográficas entre sitios de alimentación y entre temporadas de muestreo. Datos sobre avistamientos de ballenas azules, meso-zooplancton y variables oceanográficas fueron colectados durante los veranos australes de 2011-2013 e invierno 2012 en un sitio de alimentación más oceánico (Archipiélago de los Chonos) y uno más continental (bahía de Raúl Marín). Se presentan los primeros datos oceanográficos *in situ* asociados a avistamientos de ballenas azules en conducta de forrajeo en esta remota área del Pacífico Suroriental. Encontramos una asociación entre la variación temporal de clorofila-a (Cl-a) y los eventos de alimentación de ballenas azules. Durante los veranos de 2011 y 2913, hubo más avistamientos de ballenas azules alimentándose, comparado con el verano 2012, en donde hubo temperaturas, salinidades, concentraciones de silicato y Cl-a más bajos, además de una dominancia de salpas en el mesozooplancton (vs. dominancia de eufáusidos en 2013). Esto podría haber sido el resultado de un aumento en la cantidad de aguas oceánicas y/o una reducción en descargas de aguas continentales hacia la zona de estudio. El sitio de alimentación más oceánico presentó, de manera consistente, mayores salinidades, temperaturas, concentraciones de Cl-a y densidades de eufáusidos y otros grupos planctónicos, y también fue el preferido por las ballenas azules. Esto se podría relacionar con la presencia de una zona de retención de plancton debido a la topografía y recomendamos esfuerzos de conservación a futuro en este sitio. Los resultados son discutidos en el contexto de la conservación de las ballenas azules en la Patagonia chilena.

Manuscrito en Preparación

Oceanographic conditions for foraging blue whales at two feeding sites in the Corcovado Gulf, Chilean Patagonia

“Condiciones oceanográficas para el forrajeo de ballenas azules en dos sitios de alimentación en el golfo Corcovado, Patagonia chilena”

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Abstract

Understanding the foraging ecology of Southeast Pacific (SEP) blue whales (*Balaenoptera musculus*), is central to the protection of their critical feeding ground habitat in the Chiloense Ecoregion (CER) in Chilean Patagonia. The southeast Corcovado Gulf (43°38’ - 44°01’S, 73°38’ - 73°01’W) is a preferred foraging zone by blue whales within their CER feeding ground. Blue whale visual sighting, zooplankton and oceanographic data were collected during austral summers 2011-2013 and winter 2012 at a more oceanic (Chonos Archipelago) and more continental (Raúl Marín BalmacedaBay) feeding site. We provide the first *in situ* oceanographic data associated with blue whales sighting data in this remote region the Southeast Pacific in order to assess the temporal variability of environmental conditions up to blue whale feeding events and to contrast the differences in oceanographic conditions between feeding sites and sampling seasons. We found an association between the temporal variation of chlorophyll a (Chl-a) concentrations and the timing of blue whale feeding events. During summers 2011 and 2013, more foraging blue whales were sighted compared with summer 2012, when temperatures, salinities, and silicate and *in situ* Chl-a concentrations were all lower, and salps dominated the mesozooplankton (compared to euphausiid dominated assemblage during 2013). This may have been the results of increased oceanic water inflow and/or a decrease in continental water discharges to the study area. The more oceanic feeding site had consistently higher salinities, temperatures, Chl-a concentrations and densities of zooplankton groups, (including euphausiids), and was also largely preferred by foraging blue whales. This may be due to a topographically-driven plankton retention zone and we recommend future conservation effort at this site. These findings are discussed within the context of the conservation of blue whales in the Chilean Patagonia.

Introduction

Understanding the foraging ecology of blue whales (*Balaenoptera musculus*) is fundamental for the protection of their critical feeding habitat and the conservation of this species, which remains endangered after centuries of commercial whaling (Reilly et al. 2008).

Blue whales are the largest of all animals to have existed on Earth and can reach up to 33 m in length and 150 t in weight (Yochem & Leatherwood 1985). Blue whales are stenophagous feeders on euphausiids (Nemoto 1970) and in order to meet their energetic demands, blue whales require 1120±359 kg euphausiids individual^{-1} day^{-1} (Goldbogen et al. 2011 and references therein), consumed largely during the summer in seasonally productive high- and mid-latitude feeding grounds.

Blue whale feeding grounds have been reported in Southern Chile (Hucke-Gaete et al. 2003), the Indian Ocean (Samaran et al. 2010, Stafford et al. 2011), the Southern Ocean (Mackintosh & Wheeler 1929), Australia (Gill 2002, 2011), and along the Pacific coast of North America (e.g. Fiedler et al. 1998, Forney & Barlow 1998, Croll et al. 2005, Calambokidis et al. 2008).

In Southern Chile, a summer feeding ground for southeast Pacific (SEP) blue whales was reported in the Corcovado Gulf and the Pacific coast of Chiloé Island in 2003 based on sighting data from boat-based and aerial systematic surveys (Hucke-Gaete et al. 2003). This feeding ground was later found to extend to the northwest of Chiloé Island (Cabrera et al. 2005, Galletti-Vernazzani et al. 2012) and further inshore, into the Inner Sea of Chiloé Island (Zamorano-Abramson & Gibbons 2010), thus spanning what is known as the Chiloense Ecoregion (CER; 41°30-47°00'S) (Spalding et al. 2007). The CER is part of one of the largest estuarine systems in the world, the Chilean Patagonian fjords and channels (Palma & Silva 2004), where primary productivity is not driven by wind-driven costal upwelling processes, in contrast to the Humboldt Current System (HCS) further north (≈42°S; Quiñones et al. 2010). An estimated 222 animals (CI 95% = 115 - 430) use the Corcovado Gulf and the wider Chiloense Ecoregion feeding ground (Hucke-Gaete et al. 2010). Additionally, 303 animals (CI 95% = 176 - 625) blue whales have been estimated between North (18°S) and Central Chile (38°S) (Williams et al. 2011).

The energetics of lunge-feeding means that blue whales rely not only on abundant, but also on highly dense patches of euphausiids (Acevedo-Gutierrez et al. 2002, Goldbogen et al. 2011) and tend to forage in relatively small areas, under 1km^2 (or 0.3 nm^2) (Acevedo-Gutierrez et al. 2002). Thus, blue whales have been found to select feeding habitats where high densities of euphausiids dependably arise, which in turn have been associated with centers of high primary productivity linked to coastal upwelling processes and topographic features, mainly studied in wind-driven coastal upwelling regions (e.g. Croll et al. 1998, 2005; Gill 2002; Gill et al. 2011).

The Corcovado Gulf (≈43°37'S, 73°26'W) receives intermediate-depth oceanic macronutrient-rich waters, identified as Subantarctic Water (SAAW), through the Guafo Island entrance, which flow towards the continent (Silva & Guzmán 2006; Sievers & Silva 2008). It also receives silicate-rich Estuarine Water (EW), which flows oceanwards in surface layers from the Chilean continent (Sievers & Silva 2008). This mix of oceanic macronutrients and continental silicate contributes to the formation of dense and abundant phytoplankton blooms (González et al. 2010). In effect, the Corcovado Gulf and Chiloe Island area presents the highest levels of remote-sensed Chl-a for the whole of Chilean Patagonia (>10 mgChl-a m^{-3}) (Montecino & Pizarro 2006). González et al. (2011) also found highest primary production in the Corcovado Gulf compared to areas further south.

Euphausia vallentini is a Subantarctic circumpolar euphausiid distributed between 42°S and 60°S (John 1936) and has successfully colonized the Patagonian fjords, displaying adaptive features in extent of diel migration, diet, and ontogenetic cycles that indicate a self-sustaining population (Hamamé & Antezana 2010). It is the most abundant mesozooplankton species in the Patagonian Fjords (Antezana 1976; Palma & Silva 2004; González et al. 2010). In the Inner Sea of Chiloe, González et al. (2010) found euphausiid (largely *E. vallentini*) biomass to double between winter and spring; no data were available for summer.

It is highly likely that the blue whales that forage in the Corcovado Gulf primarily target dense aggregations of *E. vallentini*, but this has not been confirmed. High numbers of visual sightings of blue whales are recorded during the austral summer (Hucke-Gaete 2004, Hucke-Gaete et al.

2010) and year-round Passive Acoustic Monitoring data have identified a seasonal peak in the occurrence of blue whale songs at the end of the austral summer, i.e. March-May, (Buchan et al. *in press*), which may coincide with the seasonal peak in euphausiid abundance.

With the satellite tracking of five blue whales, Hucke-Gaete (2004) described blue whale spatial preference for the southeast Corcovado Gulf, primarily, as well as the zones north of Guafo Island and the northwest of Chiloe. Land-based sighting data also confirms a preference for the southeast Corcovado Gulf (Hucke-Gaete et al. 2010). Particularly high satellite Chl-a concentrations (>20 mgChl-a m^{-3}) and the presence of a submarine canyon could be important factors in explaining blue whale preference for this zone (Hucke-Gaete 2004).

At present the underlying oceanographic processes which explain the dependable occurrence of dense euphausiid aggregations and, therefore, blue whale preference for the southeast Corcovado Gulf remain entirely unclear and no studies so far have provided *in situ* oceanographic data associated with foraging events at appropriate scales for examining blue whale foraging ecology. This has not been aided by the harsh weather conditions in this Subantarctic region and the logistical difficulties of fieldwork in Chilean Patagonia, one of the most remote regions on Earth.

Here, by analyzing *in situ* and remote-sensed oceanographic data associated with blue whales sightings at two blue whale feeding sites in the southeast Corcovado Gulf over three consecutive summer seasons and one winter season, we seek to characterize the oceanographic conditions and zooplankton community at feeding sites and during feeding events. Specifically, we aim to i) assess the temporal variability of environmental conditions (sea surface temperature, fluorescence, Chl-a and euphausiid density) leading up to blue whale feeding events; and ii) contrast differences in sighting rates of foraging blue whales and oceanographic conditions between a southern and an eastern feeding site and between summer seasons (2011, 2012, 2013).

Methods

Study area and sampling approach

Within the CER blue whale feeding ground, we selected two study sites (each no more than 30 nm^2) where blue whales are known to forage (Hucke-Gaete 2004). We operationally define these as feeding sites. The Southern Corcovado Gulf feeding site (SC; ≈S43°50-43°59; W73°36-73°29) is near Locos Islet between the Chonos Archipelago and the Moraleda Channel, and is nearer the Pacific Ocean (Fig. 1). The Eastern Corcovado Gulf feeding site (EC; ≈ S43°42-43°49; W73°09-73°03) includes Raúl Marín BalmacedaBay and Tic Toc Bay, both of which are near the Chilean continent and receive direct river discharges. Each study site was divided up into 12 fixed stations, approximately 1-2 nm apart. Total water column depths at sampling stations ranged between 70 and 230 m.

Boat-based blue whale sighting data were collected during summers 2011 (February), 2012 (February-April), early winter 2012 (May-June), and summer 2013 (February-March). *In situ* oceanographic data was collected during summers 2012, 2013 and winter 2012, associated with blue whale feeding events at the SC and EC feeding sites: When foraging blue whales were sighted, *in situ* sampling was carried out at the foraging location, with priority given to zooplankton sampling and CTD-O casts if weather conditions and/or daylight hours were limiting. When blue whales were absent, all oceanographic variables were measured at fixed sampling stations within the SC and EC feeding sites, with the aim to collect baseline oceanographic data. Sighting and i*n situ* data collection was carried out on board a coastal research vessel powered by two 250 hp outboard motors, with a steel arm from which to manually deploy sampling equipment, providing that the weather conditions were suitable for the safe deployment of instruments.

In addition, remote-sensed oceanographic data were obtained for the 2011, 2012 and 2013 study periods.

Blue whale sightings

Cetacean visual survey effort was carried out by experienced observers continuously during summers 2011 (February), 2012 (February-April), early winter 2012 (May-June), and summer

2013 (February-March) at the SC and EC study sites. All cetacean species encountered were recorded (date, time, GPS position, species, number of calves). When blue whales were sighted, they were followed in order to photograph individuals for later photo-identification and classify their behaviour as follows: 1) Transit (fast directional swimming), 2) Lunges (subsurface lateral feeding lunges where one of the pectoral flippers is exposed), and 3) Deep dives (repeated dives revealing tail fluke or tail stock, about 10 min long, often revealing a circular movement track). Lunges and deep dives are considered indicative of foraging behavior in blue whales, either feeding on subsurface or deep aggregations of euphausiids (Goldbogen et al. 2011, 2012), or possibly searching for euphausiid aggregations.

Sighting rates were calculated per season by the number of foraging individuals sighted divided by the number of days of survey effort at sites and during sampling seasons.

Temperature, salinity and oxygen vertical profiles at selected stations

In order to examine the physical vertical structure of the water column at each site, vertical profiles for salinity, temperature (in 0.000°C) and oxygen (mg L^{-1}) down to 200 m were taken at a selected SC station and a selected EC station, measured with a CTD-O (SAIV A/S, model SD204). The CTD-O was calibrated before and after the field season; no decalibration was detected. On the 11.02.2013, the CTD-O was irreparably damaged due to bad weather conditions and casts were not available after this date.

The CTD-O data was cleaned and processed, by removing values with a negative sigma-t value, and the "upcast" data. Vertical profiles with vertically smoother data (1 m resolution) and Temperature-Salinity (T-S) diagrams were plotted.

In situ SST, surface salinity, nutrients and Chl-a

Salinity and SST (°C) readings were taken at 2m depth at each station with a multiparameter probe (YSI 650 MDS).

Seawater samples for nutrient analysis were collected at each station at 2 different depths, 2m and 50m using a Niskin bottle. 100 ml of seawater was filtered through a 0.7µm pore Millipore glass fiber filter of 25 mm diameter in order to eliminate particulate material, and the remaining water sample was frozen until laboratory analysis. The concentrations of nitrate (NO_3), nitrite (NO_2), silicate (SiO_4) and phosphate (PO_4) to 0.00µM were determined at the Laboratory of Geochemistry of the University of Concepción using standard techniques according to Hansen & Koroleff (2007). Average concentrations were tabled per site and per sampling season; and nutrient ratios were determined for comparison with a Redfield ratio of N:Si:P = 16:15:1 (Redfield et al. 1963) (N was calculated as [NO_3] + [NO_2]). NO_3 and SiO_4 concentrations were reported graphically in scatter plot to examine differences in NO_3:SiO_4 ratios between study seasons and sites.

Seawater samples for determining Chlorophyll-a concentrations were collected at each station at 2 different depths, 2m and 50m using a Niskin bottle. 500 ml of seawater were filtered through a 0.7µm pore Millipore glass fiber filter of 47 mm diameter, which was then wrapped in aluminum foil and frozen until laboratory analysis. The Chl-a concentration to 0.00 mg m^{-3} of each sample was determined according to Holm-Hansen et al. (1965).

Zooplankton assemblage

Mesozooplankton samples were collected at each station with mid-water oblique tows down to 100 m depth, or 15 m from the maximum depth in shallower zones, with bongo net trawls with a 250 µm mesh net and a mouth opening of 0.71 m diameter during 20 minutes at 2 knots. Trawls were conducted during daylight hours to coincide with the collection of blue whales sighting data. A General Oceanics flowmeter model 2030R was attached across the opening of the net to record the volume of water filtered. Once the trawl net was onboard, the net and cod end were fully rinsed and the sample was transferred into a 500 ml plastic container, and then fixed with 5% formaldehyde until laboratory analysis.

All organisms were counted and identified to order level; the most abundant orders were reported. Euphausiids were identified to species level and classified by life stage (adults, calyptopis, furcilia). For early euphausiid lifestages, species level identification was generally not possible. Density of species and lifestages were calculated and reported as ind./1000m^3.

Euphausiid size structure was also determined by measuring the body length (tip of rostrum to tip of telson) to 0.000 mm, according to Melo & Antezana (1980). Given that *E. vallentini* was by far the more abundant euphausiid species (identified to species level in adult individuals), we assume that the juvenile life stages are also *E. vallentini* although their small size did not allow species identification. Based on this assumption, adult *E. vallentini* and juvenile euphausiid size structure data was grouped together and presented in size structure histograms for summer 2012, winter 2012 and summer 2013.

Satellite fluorescence, chlorophyll-a and sea surface temperature

Monthly and daily (or several days depending on data availability) average satellite images for normalized Fluorescence Line Height (nFLH), Chl-a and sea surface temperature (SST) were obtained with a resolution of 1 km from the MODIS database (http://modis.gsfc.nasa.gov/data) for the area between 43°15' - 44°04'S and 74°39' - 72°47'W. Daily average images were selected to coincide with blue whale foraging events and on days when *in situ* sampling was carried out. Ocean color remote sensing data from MODIS (Moderate Resolution Imaging Spectroradiometer) were processed using the software SeaDAS (SeaWIFS Data Analysis System, version 6.4), following recommended procedures for L1A files. All available high-resolution L1A files for the study area (swaths inside the box LAT AND LON) were obtained from the NASA web site (http://oceancolor.gsfc.nasa.gov/) and processed for Chl-a and normalized Fluorescence Line Height (nFLH) outputs. The NIR–SWIR combined algorithm was selected for producing atmospherically corrected daily images (Wang & Shi 2007) at 1 km resolution. For SST, L2 files were downloaded and processed with SeaDAS for producing final projected outputs at 1 km resolution. Monthly and daily (or several days depending on data availability) average composites were computed for selected periods of time. These images were examined visually to determined qualitative changes in the parameters between the SC and the EC, and overtime (within-season and inter-annual).

Results

Blue whale sightings

Thirty-five sightings of a total of 51 blue whale individuals were recorded (Table 1, Fig. 1) on 9 separate days of a total of 44 boat days (5 days summer 2011; 15 days summer 2012; 9 days winter 2012; 19 days summer 2013). Most of the sightings were of foraging blue whales, i.e. diving or lunge feeding behavior, (94%). Most foraging individuals were sighted during summer 2011 (51%), followed by summer 2013 (29%), summer 2012 (13%) and winter 2012 (6%). The sighting rate per day effort of foraging blue whales was 6.0 ind./day in summer 2011, 0.43 ind./day in summer 2012; 0.33 ind./day in winter 2012; and 0.65 ind./day in 2013 (Table 2).

During summers 2011 and 2012, foraging blue whales were mostly in the SC; during summer 2012, blue whales were sighted mostly in the EC; during winter 2012 blue whales were sighted exclusively in the EC (Table 2). Associated oceanographic data were collected for almost all foraging events during 2012 and 2013, except due to highly adverse weather conditions.

Temporal variation of blue whales sightings in relation to oceanographic variables

During summer 2011, because of the lack of *in situ* oceanographic sampling, it was not possible to explore the temporal variation of blue whale foraging events relative to oceanographic variables. During summer 2012, blue whales were sighted on days when no clear change of *in situ* Chl-a concentrations or SST had occurred relative to previous days; sightings coincided with a slight increase in juvenile and adult euphausiid densities (Fig. 2). Moreover, sightings of foraging blue whales did not appear to coincided with any clear change in satellite SST, Chl-a or nFLH (e.g. 22 vs. 29 February; Annex 8.1).

Similar to summer 2012, during winter 2012, on the one day when blue whales were sighted (07.06.2012), there was no clear change in SST or Chl-a (*in situ* or remote sensed; Fig. 3 and Annex 8.2, respectively). Blue whale sightings appeared to coincided with a slight increase in juvenile and adult euphausiid densities (Fig. 3).

The clearest temporal variation pattern occurred during summer 2013: Blue whale sightings coincided with a drop in *in situ* Chl-a but no clear change in *in situ* temperature (Fig. 4). Whales were sighted on days when satellite SST, nFLH and Chl-a was lower relative to previous days, having reached a visible maxima ≈10 days prior, i.e. 2-4 February vs. 16 February (Fig. 5) and 3 March vs. 14 March (Fig. 6). Sightings in the SC coincided with a drop in the density of juvenile euphausiids from as high as 50,000 ind. 1000m^{-3} to <10,000 ind. 1000m^{-3}; no clear trend was seen at the EC (Fig. 4). In terms of adult density, sightings in the EC appeared to coincide with lower values (<500 ind. 1000m^{-3}); no clear trend was seen in the SC (Fig. 4).

In situ surface temperature and salinity

Average *in situ* SST was highest (and most variable) during summer 2013 (avg. 14.17°C at SC) and lowest during winter 2012 (avg. 9.82°C at SC) (Table 3). SST values between both sites were similar during summer and winter 2012; however during summer 2013 the SC was almost 1°C warmer compared to the EC, but also compared to values at the same site during summer 2012. Average surface salinities (Table 4) at both sites were highest during winter 2012 (32.97 at SC; 30.96 at EC) compared to both summer seasons (e.g. summer 2012 31.60 at SC; 28.82 at EC). Between sites, salinities were lower and more variable at the EC. During summer 2013, salinities were similar at both sites; in 2012 salinities were higher in the SC compared to the EC.

Temperature, salinity and oxygen vertical profiles

Temperature, salinity and oxygen vertical profiles revealed inter-season and inter-site differences (Fig. 10). Salinity vertical profiles were largely similar between years, but surface salinities appeared overall slightly higher in winter compared to the summers, and generally lower at the EC (≈20) compared to the SC (>28). Temperature profiles were similar between sites, although during summer 2013, the temperature gradient (warmer surface layers) at the SC appeared sharper than at the EC. Between sampling seasons, temperature profiles were clearly different: cooler (≈10°C), more vertically mixed, with an temperature inversion at the surface during winter 2012; higher surface temperatures (>12°C) and stronger temperature gradients during both summers compared with winter; higher overall surface temperatures (up to 17°C) and temperature gradients during summer 2013 compared with 2012. At depth (>100 m), across feeding sites and seasons, conditions were similar: ≈10°C and 33). Oxygen vertical profiles were similar between sites, with values ranging mostly ranging between 4-8 mg/L and a typical inversion at the ocean-air boundary. Oxygen concentrations were slightly lower during winter, higher during summer 2013 and highly variable during summer 2012.

Temperature-salinity diagrams

Temperature-salinity (T-S) diagrams (Fig. 11) reflect similar conditions at depth across sites and seasons, (≈10°C and 33). The following inter-seasonal differences in surface conditions were apparent: lower temperatures (≈10°C) and intermediate salinities ≈28-33 during winter compared relative to both summers; lower surface temperatures (≈13°C) and lower but more variable salinities (24-33) during summer 2012 compared with summer 2013 (≈15°C and salinities 28-32). The main differences between sites were seen during the summers, when surface salinities were surface salinities and temperatures were higher at the SC compared with the EC.

Nutrients

Nitrate ranged 6.24-32.71 µM at 2m depth (Table 6) and 6.13-40.43 µM at 10 m (Table 7) across all sites and sampling seasons, and was highly variable (high standard deviations). Nitrate was always higher in winter compared with both summers, at 2m and 50m depth. Surface nitrate was slightly lower at SC compared with EC during summer 2012 and winter 2012 but similar during summer 2013; at 50m depth, concentrations between both sites were similar.

Nitrite ranged 0.00-2.60 µM at 2m (Table 6) and 0.00-1.47 µM at 50 m (Table 7) across all sample sites and seasons; values were relatively similar, but variable, at both depths. Nitrite was lower in winter compared to summer, and highest during summer 2013, at both depths.

Silicate ranged between 0.09 and 33.32 µM at 2m (Table 6); and 0.82 and 43.87 µM at 50m (Table 7) across all samples, and similar to nitrate, was highly variable. Silicate was notably lower during summer 2012 (<9 µM) compared with summer 2013 (>16 µM at both depths) and winter 2012 (≈12 µM at 2m; 18 µM at 50 m depth) at both the SC and the EC. During both summers, silicate concentrations were similar at both depths; but during winter 2012, silicate was always lower at the surface at both sites. During each season, there was no clear difference between silicate concentrations between the SC and the EC.

Phosphate ranged 0.00-2.04 at 2m (Table 6) and 0.06-2.27 at 50m (Table 7) reflecting similar averages at both depths. Values at 2m and 50m were higher during summer 2012 and similar during winter 2012 and summer 2013. Phosphate concentrations at both sites were relatively similar during respective sampling seasons.

Comparing the nutrient ratios to a Redfield ratio of N:Si:P of 16:15:1 (Redfield et al. (1963) (see Table 8), N was slightly below Redfield during summer 2012 at 2 m, but not at 50 m. Si was well below Redfield at both 2m and 50m, and more so at SC. This is the most striking result of the nutrient data. Phosphate was slightly above Redfield at both depth during summer 2012; during winter 2012 and summer 2013, phosphate was slightly below Redfield. For a given sampling season or depth, the N:Si:P ratio was similar between sites.

The NO_3:SiO_4 scatter plot at 2 m and 50 m for stations in the SC and EC (Fig. 12) reiterated the patterns evident from the nutrient data in Tables 6-8. Specifically, the low SiO_4 conditions during 2012, particularly obvious at the SC, affecting both 2m (Fig 12a) and 50m depth (Fig. 12b). At the SC, SiO_4 was <12 µM during summer 2012 and >12 µM during summer 2013; there was little overlap in NO_3:SiO_4 values between summers 2012 and 2013 at this site.

In situ surface Chl-a

In situ Chl-a concentrations (Table 5) were highest during summer 2013, as high as 15.08 mgChl-a m^{-3} in the SC, but also highly variable (avg. 3.25 mgChl-a m^{-3}, standard deviation 3.92). Chl-a was lowest during winter 2012 (0.7 mgChl-a m^{-3} at the SC and 0.45 mgChl-a m^{-3} at the EC), but also low during summer 2012, with similar concentrations for both the SC (avg. 0.75 mgChl-a m^{-3}) and the EC (avg. 0.79 mgChl-a m^{-3}).

Zooplankton assemblage

The mesozooplankton assemblage at the SC and EC feeding sites was mostly constituted of the following orders: euphausiids, amphipods, salps, ctenophores and siphonophores. The two species of euphausiid identified were *Euphausia vallentini* and *Nematocelis megalops*. *E. vallentini* was largely more abundant.

There were clear differences in mesozooplankton community composition (Table 6) between sampling seasons. During the summer of 2012, the mesozooplankton was dominated by gelatinous zooplankton groups, particularly salps, averaging 5,000-6,000 ind. $1000m^{-3}$, although highly variable, followed by euphausiids and amphipods. During winter 2012, densities of all groups were low (<40 ind. $1000m^{-3}$), with a greater contribution of amphipods. During summer 2013, euphausiids dominated the zooplankton community, in particular due to important numbers of juvenile life stages compared with summer 2012 (e.g. 3,280 ind. $1000m^{-3}$ furcilia vs. 10 ind. $1000m^{-3}$ adults at SC), although no changes were observed in adult *E. vallentini* between summers 2012 and 2013. Amphipods remained important secondary components.

Both sites reflected the same inter-seasonal trends described above, but densities of all mesozooplankton groups, including euphausiids and salps, were generally higher at the SC compared with EC, regardless of sampling season (Table 6). This was particularly obvious during summer 2013, when juvenile euphausiid life stages were an order of magnitude greater at the SC site compared to the EC (e.g. 1,980 ind. $1000m^{-3}$ calyptopis vs. 330 ind. 1000 m^{-3} adults).

Euphausiid temporal variability and size structure

Euphausiid densities plotted over time revealed increasing densities of juvenile and adult euphausiids towards the end of summer 2012 (Fig. 2). During summer 2013 (Fig. 4), there was a shift from high juvenile densities at the beginning of the sampling period (early February 2013) to high adult *Euphausia vallentini* densities at the end of the sampling period (mid-March 2013).

Baker et al. (1990) describe adult lengths of *E. vallentini* between 13-28 mm. Seasonal size structure histograms for *E. vallentini* during each sampling campaign (Fig. 13) revealed size structures centred around 9 mm (juveniles) and 13 mm (adults) during summer 2012 (bimodal); 13 mm (adults) during winter 2012 (unimodal); and 3 mm (adults), 9 mm (juveniles) and 15 mm (adults) during summer 2013 (trimodal). It also appeared that juveniles were generally more present at the SC and adults at the EC.

Daily size structures histograms for all sampling campaigns (Fig. 14) revealed a shift over time from smaller sizes at the beginning of the summer to larger sizes as the year progressed. There was a distinct lack of small size classes (juveniles) during summer and winter 2012, compared with summer 2013, particularly due to high abundances of juveniles at the SC during 2013.

Monthly-averaged summer satellite data

Satellite images of monthly averages for January (Fig. 7), February (Fig. 8) and March (Fig. 9) reveal differences in oceanographic conditions between summer seasons (2011, 2012, 2013) and between blue whale feeding sites. Overall, SST ranged between 8-18°C; nFLH between 0.00-0.06 mW cm^{-2} um^{-1} sr^{-1}; and Chl-a between 0-30 mgChl-a m^{-3}.

SST, nFLH and Chl-a were all highest for the summer of 2013 (e.g. 14-16°C, 0.02-0.04 mW cm^{-2} um^{-1} sr^{-1}, 3-10 mgChl-a m^{-3} during February) compared with 2011 (e.g. 13-15°C, 0.01-0.03 mW cm^{-2} um^{-1} sr^{-1}, 1-10 mgChl-a m^{-3} during February) and 2012 (e.g. 12-14°C, 0.01 mW cm^{-2} um^{-1} sr^{-1}, 1-3 mgChl-a m^{-3} during February). Monthly images did not reflect the lower *in situ* SST measurements during 2012, but did reflect the drop in *in situ* Chl-a and nFLH concentrations during February, which was not so clear for January and March. During all three summers, SST was highest in January and February (≈15°C) compared with March (≈13°C). During all three summers, nFLH and Chl-a were highest in January compared with February and March, especially during 2013 (0.03-0.05 mW cm^{-2} um^{-1} sr^{-1} vs. 0.00-0.03 mW cm^{-2} um^{-1} sr^{-1} and 5-20 mgChl-a m^{-3} vs. 1-3 mgChl-a m^{-3}).

Between sites, monthly average images revealed similar SST conditions. nFLH was often slightly higher in the SC site (e.g. 0.04 mW cm^{-2} um^{-1} sr^{-1} January 2011) compared with the EC site (e.g. 0.02 mW cm^{-2} um^{-1} sr^{-1} January 2011); Chl-a was always higher at the EC (e.g. <10 mgChl-a m^{-3} January 2011) compared to the SC (e.g. >10 mgChl-a m^{-3} January 2011). The difference in the spatial patterns seen in the nFLH and Chl-a images is likely due to an erroneous Chl-a signal caused by sediment carried by the Palena River into the coastal zone. *In situ* measurements indicated generally higher Chl-a at the SC.

Discussion

General oceanographic conditions in the southeast Corcovado Gulf

Sea surface temperatures (approx. 9-18°C) and salinities (approx. 22-33) reflected the range of estuarine conditions present in the northern Patagonian Fjords (Sievers & Silva 2008). *In situ* SST measurements during winter 2012 were within the range for winter SST reported by for the Inner Sea of Chiloe (8.7-11.5°C by González et al. 2010), the Corcovado Gulf (Silva & Guzman 2006, González et al. 2010) and the Moraleda Channel (Silva & Guzman 2006); our summer SST was higher than SST recorded in spring (approx. 11-12°C) by González et al. (2010) due to the difference in sampling season. *In situ* salinities were in line with reports for the Corcovado Gulf by González et al. (2010; winter and spring) and Silva & Guzman (2006; winter only). Lower average salinities at the EC reflected the presence of the Palena River. Lower salinities are always recorded further inland in this estuarine region due to important freshwater influences from the continent (Sievers & Silva 2008, Silva & Guzman 2006, González et al. 2010). Likewise, higher salinities at the SC reflected more oceanic influences at this site.

Vertical profiles of temperature, salinity and oxygen were in line with reports by Silva & Guzman (2006) for Northern Patagonia. In particular, the low salinity surface layer is characteristic of Northern Patagonia (Silva & Guzman 2006). The T-S diagrams suggested the influence of Modified SAAW (MSAAW) at depth and EW in surface layers (Silva & Guzman 2006, Sievers & Silva 2008).

Nitrate concentrations were characteristic of oceanic influences, exceeding the ranges reported in the Corcovado Gulf during winter by González et al. (2010; 2.6 - 21.6 µM) and by Silva & Guzman (2006; 2.7-20.9 µM). González et al. (2010) found higher NO_3 in winter compared with spring, as observed in this study. Phosphate concentrations were within ranges reported by Gonzalez et al. (2010) and Silva & Guzman (2006).

Silicate concentrations were within the range reported by González et al. (2010) for the Corcovado Gulf and the Inner Sea of Chiloe (winter and spring, 9.0-30.0 µM approx.), and were within the range for the Corcovado Gulf and Moraleda Channel (winter: <8-20 µM approx.) reported by Silva & Guzman (2006). Silicate concentrations during summer 2012 fell within the very lower end of these previously reported ranges. Equally, Redfield ratios (N:Si:P = 16:15:1) (Redfield et al. 1963) were generally met, but silicate was well below Redfield during summer 2012 (N:Si:P ≈ 15:8:1) (Table 8; Fig. 12). In this estuarine system, high silicate concentrations are associated with freshwater inputs (Sievers & Silva 2008, Silva & Guzman 2006, González et al. 2010). None of the SiO_4 concentrations measured here were as high as the in land Reloncaví fjord, up to 126 µM (where salinities were as low as 2.6, González et al. 2010), or the Aysén fjord, up to 180 µM (with salinities around 2; Silva & Guzman 2006).

Summertime remote-sensed and *in situ* Chl-a concentrations were within the range of values observed in previous studies, i.e. 0-30 mgChl-a m^{-3} (Hucke-Gaete 2004, Montecino & Pizarro 2006, Iriarte et al. 2007). High variability in *in situ* Chl-a concentrations was also observed, as previously highlighted by Iriarte et al. (2007). Satellite images confirmed consistently high Chl-a concentrations and nFLH levels in the southeast Corcovado Gulf, and during spring and summer compared to winter. *In situ* Chl-a values in winter coincided with the findings of Iriarte et al. (2007) for this region (<1.0 mgChl-a m^{-3}) for the Inner Sea of Chiloe, but were higher (up to 15.08 mgChl-a m^{-3}) than these authors results for February-March (max. 8 mgChl-a m^{-3}), although these authors reported maximum values >30 mgChl-a m^{-3} during October (early spring). González et al. (2010) reported winter concentrations of 0.02-2.0 mgChl-a m^{-3}, slightly higher but within the same range as our wintertime measurements; and springtime concentrations of 22-30 mgChl-a m^{-3}, which are higher than our summertime measurements. This difference could be explained by our summer sampling period falling outside the reported springtime peak in primary production in Northern Patagonia (Iriarte et al. 2007, González et al. 2010).

Euphausiid densities were higher than densities reported further north (Comau Fjord; Sanchez et al. 2011) and were within the range of densities reported by Palma & Silva (2004) further south (46°S and 56°S). Palma & Silva (2004) presented no data on euphausiids in the Corcovado Gulf region but reported maximum densities in the Penas Gulf (47°S) of 1,400- 11,500 ind./1000m^3. This value is higher than our maximum reported densities, however we believe that our densities are likely underestimates due to the limitations of net sampling approaches (see Everson 2000 and references therein), particularly during daylight hours (which were conducted in order to carry out simultaneous cetacean survey effort), given the diel vertical migrations carried out by most euphausiids (Mauchline 1980), and *E. vallentini* in particular (Hamamé & Antezana 2010). Moreover, semi-diel migrations of zooplankton have recently been described in this region where zooplankton are closest to the surface during dusk and dawn, and remain at depth during daylight hours (Valle-Levinson et al. 2014).

Euphausia vallentini was by far the more abundant euphausiid, compared to the only other euphausiid species *N. megalops*. This is in line with previous reports that *E. vallentini* constitutes 98% of total euphausiid abundance between 46°S - 56°S (Palma & Silva 2004) and >90% of abundance the euphausiid abundance in our same study area (Gonzalez et al. 2010). We can therefore say with some certainty that this species is the main prey item for the blue whales that forage in the Corcovado Gulf.

The size structure of *E. vallentini* aggregations (Figs. 13 and 14) followed a normal distribution. However, there was a clear dominance of juvenile size classes during summer 2013, compared with summer 2012 and winter 2012. This suggest limited growth of the euphausiid population during summer 2012, and during winter 2012, which would be expected.

Intra-season timing of blue whale feeding events

Satellite and *in situ* data showed that nFLH and Chl-a fluctuated substantially on scale of days to weeks within a given season. Hucke-Gaete (2004) described satellite Chl-a fluctuations over 1-2 weeks in the Corcovado Gulf. The dynamics of marine primary productivity in estuarine systems is known to occur in pulses linked to freshwater inputs (Mallin et al. 1993) and tidal mixing (Cloern 1991, Gargett et al. 2003). Increased stratification due to salinity has also been found to increase primary productivity in estuaries (Cloern 1984, Masson & Peña 2009). In the Inner Sea of Chiloe, Castro et al. (2011) found that pulses of Chl-a were associated with tidal mixing and that zooplankton densities increased with the flood tide.

Our results reveal that often sightings of blue whales also occurred in bouts of several days interspaced by 1-3 weeks, especially during the summers of 2011 and 2013 when overall foraging conditions appeared to be more favorable for blue whales. During summer 2013, (when *in situ* oceanographic data is available), sightings of foraging blue whales coincided with a drop in nFLH levels and Chl-a concentrations, seen in both the *in situ* and the satellite data, and that this drop was preceded by a peak in nFLH and Chl-a approximately 10 days prior (Fig. 5 and 6). We hypothesize that at feeding sites in the southeast Corcovado Gulf, there is a time lag of approximately 10 days between a pulse in primary productivity and the formation of euphausiid aggregations at these productivity foci, which are targeted by foraging blue whales. The drop in Chl-a during blue whale feeding events can be explained by the grazing pressure of euphausiids on a phytoplankton bloom. We expected blue whale feeding events to overlap with higher euphausiid densities; however euphausiid densities were lower when blue whales were present, which could in turn reflect the predation pressure of blue whales on euphausiids.

Inter-annual changes in conditions for foraging blue whales

More blue whales were sighted per unit effort during summers 2011 and 2013 compared with summer 2012 and winter 2012. This observation is in line with the higher numbers of blue whales than usual reported off the coast of Valdivia (≈39°S), where the wind-driven coastal upwelling HCS dominates, during the summer of 2012 (Hucke-Gaete *unpublished*). This suggests a possible shift in blue whale preference from the Corcovado Gulf to feeding sites in the HCS during the summer of 2012.

The very high sighting rate (6.0 ind./day) during the summer of 2011 is noteworthy. However, it is unlikely that this high sighting rate would have been sustained throughout the entire summer season and is probably the result of our 5 observation effort days coinciding with the most important blue whale feeding events observed during our study period, accompanied by visual observations of large surface aggregations of euphausiids at the SC site.

We acknowledge that the lack of systematic abundance surveys for blue whales (e.g. line-transect surveys as per Williams et al. 2011) limits our conclusions about blue whale distribution between sites and between years. We were constrained by fieldwork logistics to carry out blue whale visual survey effort on-board the same research vessel as for the *in situ* oceanographic sampling. It was therefore not possible to determine, when working at one study site, whether blue whales were present at the other study site. An effort was made to rectify this by considering the number of days effort at each site when calculating sighting rates.

Compared with summers 2011 and 2013, there was a drop in remote-sensed nFLH and Chl-a levels (but not in SST) during February 2012 (Figs. 7-9). *In situ* data for 2012 compared with 2013 revealed lower surface temperatures, lower surface salinities, lower *in situ* Chl-a concentrations (in the same order of magnitude as winter 2012) (Tables 3-5; Figs. 10-11), markedly lower than Redfield ratio SiO_4 concentrations (N:Si:P ≈ 15:8:1 vs. Redfield N:Si:P = 16:15:1) (Table 8; Fig. 13) and a zooplankton community dominated by salps (vs. the euphausiid-dominated assemblage of summer 2013) (Table 9). This was particularly marked at the more oceanic SC feeding site.

A possible explanation for these changes during summer 2012 could be the increased inflow of SAAW through the Guafo Island entrance to the Corcovado Gulf: Giesecke et al. (2014), reported a massive intrusion of salps (*Ihlea magalhanica*) in the Inner Sea of Chiloe in 2010 explained by a change in the intensity of the Southern Annular Mode (SAM) and increased inflow of SAAW into the Inner Sea, transporting salps into this area. This was accompanied by a 1°C drop in SST and a weaker vertical thermohaline gradient. However, this does not explain why we recorded lower salinities during 2012. In the Southern Ocean, Antarctic krill (*Euphausia superba*) and salps (*Salpa thompsoni*) are both important macroherbivores but largely linked to different water masses (Pakhomov et al. 2002). Salps are favored by low-productivity (‘low-food’) conditions and higher water temperatures, and reproduce much faster than Antarctic krill (Voronina 1998, Atkinson et al. 2004, Smetacek & Nicol 2005).

Thus, during the summer of 2012, a salp intrusion associated with SAAW inflow could have exerted top-down control on phytoplankton and explained low Chl-a and nFLH during summer 2012. As an alternative to the salp intrusion hypothesis, increased salinities and lower silicate concentrations could also indicate a reduction in estuarine water inputs during the summer of 2012 into the southeast Corcovado Gulf. However, examination of daily average river discharge statistics (www.dga.cl) for three nearby rivers (Palena, Cisnes and Aysén; Annex 8.3) did not reveal any clear inter-annual reduction in discharge between 2010 and 2013.

From a bottom-up perspective, either increased SAAW or reduced continental water discharges could have modified growth conditions for phytoplankton in the Corcovado Gulf, and produced the low-food conditions which favor salps. Reduced density stratification (Cloern, 1984, Masson & Peña 2009) and/or reduced SiO_4 could have exerted bottom-up control on phytoplankton, particularly by limiting the growth of diatoms (e.g. Dugdale & Wilkerson 1998). The micro-zooplankton size fraction, which includes most diatoms, has been found to dominate in this northern part of Chilean Patagonia, associated with the highest levels of primary production of the entire region (Jacob 2012).

During summer 2012, silicate was well below a Redfield N:Si:P ratio of 16:15:1 (Redfield et al. (1963); additionally, nitrate was slightly below Redfield and phosphate was slight above Redfield (Table 8; Fig. 13). Deviations from Redfield for nitrate and phosphate were relatively small and may not have had a limiting effect in phytoplankton growth; however, the relatively important deviation from Redfield in Si may well have limited phytoplankton. In an inner Patagonian fjord, Torres et al. (2011) found that low silicate availability favored dinoflagellates over diatoms.

Whether caused by top-down (salps) or bottom-up control (growth conditions), limited development of diatom blooms could have limited the abundance of euphausiids. Letessier et al. (2009) found that numerical abundance of euphausiids in the oceanic waters of the Mid-Atlantic Ridge was significantly correlated with SiO_4 concentration among other variables, reflecting the association of euphausiids with diatom blooms. Iriarte et al. (2009) propose a conceptual model for Patagonian fjord ecosystems, where an increased Si:N ratio is associated with the dominance of euphausiids within the zooplankton community and a strengthening of the biological pump.

Apparently better conditions for foraging blue whales in the southeast Corcovado Gulf occurred during summers 2011 and 2013. We hypothesize that improved foraging conditions are, in some way, linked to increased estuarine water (silicate) inputs, which increases primary productivity during spring and summer in this open gulf area (where oceanic macronutrients are presumably non-limiting), and leads to increased euphausiid abundance.

Inter-site differences in conditions for foraging blue whales

Higher salinities at the SC are explained by its more oceanic location; lower salinities at the EC are explained by the influence of continental water runoff (the Palena River). Temperatures, salinities, *in situ* Chl-a and mesozooplankton densities (all groups) were consistently higher at the SC. Inter-site differences in foraging conditions were most evident during the summer of 2013 when the highest *in situ* Chl-a concentrations were registered at the SC, as well as higher euphausiid densities and the majority of blue whale sightings, compared with EC. Blue whale preference for the SC was previously observed using the satellite tracking of five blue whales during summer in the Corcovado Gulf, as well as based on visual sighting data (Hucke-Gaete 2004).

A possible explanation for this preference is the presence of a possible retention zone caused the Chonos Archipelago submarine canyon, as previously suggested by Hucke-Gaete (2004). The submarine canyon runs west-east from the Pacific Ocean at the Guafo Island entrance to the Gulf, along the northern edge of the Chonos Archipelago, and joins the entrance to the Moraleda Channel. At the SC site, where the canyon joins the Moraleda Channel, depths become much shallower and the site is surrounded by small islands. During sampling at the SC, total water column depths were as shallow as 70 m, compared to the EC, where 120 m was the minimum depth. We therefore hypothesize that the combination of the Guaitecas submarine canyon, island topography and shoaling depths leads to the retention of planktonic organisms, which under optimal conditions for primary production (e.g. nutrients, water column stability, sunlight) leads to particularly dense phytoplankton blooms and euphausiid aggregations.

Elsewhere, topography-driven retention zones have been found to provide dependable foraging conditions for blue whales, e.g. the Monterey Submarine Canyon off California (Croll et al. 2005) and the continental shelf break off southern Australia (Gill 2002, Gill et al. 2011). Croll et al. (2005) show the aggregation of blue whales along the edge of the Monterey Submarine Canyon, attributing this distribution to blue whales exploiting euphausiid swarms associated with the submarine canyon (rather than being driven by a direct response to changes in water temperature or currents).

Although the SC may be particularly suitable for blue whale foraging under optimal "productive" conditions, given its more oceanic locations, it may also be particularly susceptible to perturbations driven by oceanic dynamics. This could explain why the SC appears to have been more severely affected by the low-productivity conditions during summer 2012 compared with the EC (i.e. lower temperatures; low SiO_4 relative to Redfield; low *in situ* Chl-a; low euphausiid densities and low juvenile life stages; and almost no blue whales sightings). Moreover, if silicate is indeed a determining factor for primary productivity in this area, then sites closer to the continent, such as the EC, where continental water supply in direct and more consistent.

Foraging opportunities for blue whales in Chilean Patagonia

In terms of foraging opportunities for blue whales we can conceptually think of the Patagonian fjords and channels as an intricate spatial network of potentially productivity hotspots driven by the interaction between: a) a highly dynamic and tidally-influenced terrestrial-to-oceanic water mass gradient between the Chilean continent and the Pacific Ocean, which determines the balance of nutrients (e.g. SiO_4 and NO_3) for seasonal primary production, but also the distribution of frontal features, which retain planktonic organisms; and b) a complex and highly heterogeneous topography, which determines retention zones for planktonic organisms like euphausiids and the phytoplankton they feed on.

Dynamic natural inter-seasonal and inter-annual changes in oceanographic conditions may mean that this network of potential productive hotspots provides a diverse range of different feeding opportunities for blue whales, but also that their energetic demands may not always be met by the Corcovado Gulf feeding ground alone, driving them to exploit other productive systems, such as the HCS.

Conservation perspectives

The importance of freshwater and silicate inputs highlighted in this study are relevant in light of proposed hydroelectric damming projects throughout Chilean Patagonia. Dams are known to reduce the input of terrestrial nutrients, such as silicate into marine coastal systems (e.g. Ittekkot et al. 2010). Iriarte et al. (2009) put forward that a reduction of freshwater stream flow in Patagonian Fjords would reduce the effectiveness of the (euphausiid dominated) biological pump, relevant to carbon export. Low-productivity low-euphausiid conditions may not only affect foraging blue whales, but also fisheries resources (Neira et al. 2014a).

From an endangered species conservation perspective, blue whale feeding sites should be protected to ensure foraging success and species recovery. Fortunately, the EC has been protected since March 2014 as part of the Multiple-Use Marine Protected Area Pitipalena-Añihue and the Tic Toc National Marine Park (www.gob.cl). Priority should now be given to the SC site, north-northeast of the Chonos Archipelago and the entrance to the Moraleda Channel (S43°50’-S44°06’; W73°41’-W73°24), for which there are currently no protection measures and which lies in the path of an important marine shipping route with high levels of traffic.

Conclusions

Southeast Pacific blue whales remain one of the least understood populations of blue whales worldwide; and the same is true for the oceanography of their CER feeding ground habitat in Chilean Patagonia. Difficult access and adverse weather conditions have certainly not facilitated *in situ* sampling. This study provides the first *in situ* oceanographic data associated with sightings and foraging behavior data for blue whales, at relevant spatial and temporal scales for understanding blue whale foraging ecology in the Corcovado Gulf feeding ground. It has also provided the basis for testing the following hypotheses:

1) There is a time lag of approximately 10 days between a pulse in primary productivity and the formation of euphausiid aggregations at these productivity foci, which attract foraging blue whales;
2) Increased estuarine water (silicate) inputs, increases primary productivity during spring and summer in this open gulf area where oceanic macronutrients (nitrate) are presumably

non-limiting (or less limiting), and leads to increased euphausiid abundance and thereby foraging blue whale sightings.

3) The island topography in the Southern Corcovado and the Chonos Archipelago submarine canyon is a retention zone for planktonic organisms, increasing euphausiid density and thereby foraging blue whale sightings.

Undoubtedly, data with greater temporal and spatial coverage is required in order to draw firmer conclusions and bring our understanding of the Corcovado Gulf blue whale feeding ground up to speed with the current knowledge of other blue whale feeding grounds worldwide.

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Tables

Table 1 Blue whale sighting data 2011-2013. Date, time, location, number of individuals, behavior and availability of associated in situ oceanographic data

Sighting No.	**Date**	**Time**	**Study site**	**No. of individuals (including No. calves)**	**Behavior**	***In situ* oceanographic data**
1	22.02.2011	13:39	SC	1(0)	Lunges	No
2	22.02.2011	17:11	SC	3(0)	Lunges	No
3	25.02.2011	11:18	SC	2(0)	Lunges	No
4	25.02.2011	14:26	SC	2(0)	Lunges	No
5	03.03.2011	17:33	SC	2(0)	Lunges	No
6	04.03.2011	16:00	SC	2(0)	Lunges	No
7	04.03.2011	16:26	SC	2(0)	Lunges	No
8	04.03.2011	16:27	SC	2(0)	Lunges	No
9	05.03.2011	13:52	SC	1(0)	Lunges	No
10	05.03.2011	14:15	SC	1(0)	Lunges	No
11	05.03.2011	14:25	SC	2(0)	Lunges	No
12	05.03.2011	14:26	SC	1(0)	Lunges	No
13	05.03.2011	19:03	SC	3(0)	Lunges	No
14	18.02.2012	12:04	EC	1(0)	Undetermined	No
15	20.02.2012	13:36	SC	1(0)	Undetermined	No
16	20.02.2012	14:01	SC	1(0)	Undetermined	No
17	29.02.2012	15:37	SC	1(0)	Lunges	Yes
18	17.03.2012	16:11	EC	3(0)	Lunges	Yes
19	19.03.2012	18:07	EC	2(0)	Lunges	Yes
20	07.06.2012	10:48	EC	1(0)	Deep dives	Yes
21	07.06.2012	14:40	EC	2(0)	Deep dives Lunges	Yes
22	07.06.2012	15:15	SC	1(0)	Transit	Yes
23	09.02.2013	13:05	SC	1(0)	Deep dives Lunges	Yes
24	16.02.2013	9:11	SC	1(0)	Deep dives	Yes
25	16.02.2013	9:44	SC	2(1)	Deep dives	Yes
26	17.02.2013	16:05	EC	1(0)	Deep dives	Yes
27	17.02.2013	17:26	EC	1(0)	Deep dives	Yes
28	18.02.2013	9:57	SC	1(0)	Deep dives	Yes
29	18.02.2013	9:59	SC	1(0)	Deep dives Lunges	Yes
30	18.02.2013	10:26	SC	1(0)	Deep dives	Yes
31	18.02.2013	10:58	SC	1(0)	Deep dives	Yes
32	18.02.2013	13:16	SC	1(0)	Lunges	Yes
33	18.02.2013	14:18	SC	1(0)	Lunges	Yes
34	21.02.2013	10:29	SC	1(0)	Deep dives	Yes
35	14.03.2013	11:15	SC	1(0)	Deep dives	Yes

Table 2 Sighting rates (ind./day effort) of foraging blue whales at Southern Corcovado, Eastern Corcovado and both sites combined during summer 2011, summer 2012, winter 2012 and summer 2013. Note: that a value of 0.0o was obtained during winter 2012 at the SC because no whales were sighted at that sites, not because of lack of sighting effort; on the other hand a value of 0.00 was obtained during summer 2011 at the EC because no sighting effort was carried out at that site.

	SC	**EC**	**Overall**
Summer 2011	6.00	0.00 (no effort)	6.00
Summer 2012	0.14	0.71	0.43
Winter 2012	0.00 (no whales)	0.80	0.33
Summer 2013	0.85	0.28	0.65

Table 3 Average SST (°C) conditions (2m depth) in the Southern and the Eastern Corcovado study sites for summer 2012, winter 2012 and summer 2013.

	Southern Corcovado			**Eastern Corcovado**		
SST (°C)	**Summer 2012**	**Winter 2012**	**Summer 2013**	**Summer 2012**	**Winter 2012**	**Summer 2013**
Average	13.49	9.82	14.17	13.14	9.99	13.48
s.d.	0.94	0.26	1.29	0.45	0.19	1.27
Min	11.95	9.49	12.10	12.67	9.75	11.80
Max	14.88	10.05	17.32	13.88	10.28	16.20
n	9	4	33	8	7	21

Table 4 Average salinity conditions (2m depth) in the Southern and the Eastern Corcovado study sites for summer 2012, winter 2012 and summer 2013.

	Southern Corcovado			**Eastern Corcovado**		
Salinity	**Summer 2012**	**Winter 2012**	**Summer 2013**	**Summer 2012**	**Winter 2012**	**Summer 2013**
Average	31.60	32.97	30.63	28.82	30.96	30.08
s.d.	0.72	0.29	0.61	1.97	2.44	2.68
Min	30.80	32.53	29.47	25.04	27.30	22.70
Max	32.88	33.18	31.98	31.04	33.77	32.60
n	9	4	33	8	7	21

Table 5 Average Chlorophyll-a (mgChl-a m^{-3}) concentrations (2m depth) in the Southern and the Eastern Corcovado study sites for summer 2012, winter 2012 and summer 2013.

	Southern Corcovado			**Eastern Corcovado**		
Chl-a (mgChlam^{-3})	**Summer 2012**	**Winter 2012**	**Summer 2013**	**Summer 2012**	**Winter 2012**	**Summer 2013**
Average	0.75	0.7	3.25	0.79	0.45	2.21
s.d.	0.2	0.16	3.92	0.3	0.13	2.34
Min	0.39	0.52	0.38	0.31	0.26	0.19
Max	1.27	0.99	15.08	1.42	0.67	9.97
n	20	11	37	28	17	22

Table 6 Nutrient concentrations (µM) at 2m depth in the Southern and the Eastern Corcovado study sites for summer 2012, winter 2012 and summer 2013. Values reported ± standard deviations and *n*=sample size.

		Southern Corcovado			Eastern Corcovado		
		Summer 2012	**Winter 2012**	**Summer 2013**	**Summer 2012**	**Winter 2012**	**Summer 2013**
NO_3 (µM) at 2m	**Average ± sd (*n*)**	14.19 ± 4.65 (*n*= 18)	24.30 ± 5.26 (*n*=11)	16.58 ± 4.51 (*n*=35)	13.43 ± 3.92 (*n*=29)	26.87 ± 4.32 (*n*=17)	16.11 ± 3.28 (*n*=22)
	Min-Max	8.19-24.79	18.31-31.17	10.04-28.35	6.24-21.65	18.79-32.71	10.91-24.55
NO_2 (µM) at 2m	**Average ± sd (*n*)**	0.68 ± 0.19 (*n*=18)	0.36 ± 0.12 (*n*=11)	0.53 ±0.38 (*n*=35)	0.52 ± 0.21 (*n*=31)	0.32 ± 0.20 (*n*=17)	1.11 ± 0.60 (*n*=22)
	Min-Max	0.26-0.99	0.17-0.55	0.01-1.47	0.05-0.99	0.00-0.68	0.31-2.78
SiO_4 (µM) at 2m	**Average ± sd (*n*)**	7.97 ± 2.93 (*n*=19)	15.51 ± 2.09 (*n*=11)	18.42 ± 6.81 (*n*=35)	9.08 ± 6.09 (*n*=31)	20.00 ± 7.41 (*n*=17)	17.79 ± 6.43 (*n*=22)
	Min-Max	3.32-12.15	12.62-19.39	10.42-39.05	0.82-29.08	11.77-43.87	9.06-31.14
PO_4 (µM) at 2m	**Average ± sd (*n*)**	1.14 ± 0.32 (*n*=17)	0.76 ± 0.07 (*n*=11)	0.49 ± 0.39 (*n*=34)	1.02 ± 0.40 (*n*= 29)	0.66 ± 0.18 (*n*=17)	0.63 ± 0.46 (*n*=22)
	Min-Max	0.15-1-50	0.69-0.94	0.06-1.67	0.04-1.62	0.31-1.14	0.13-2.27

Table 7 Nutrient concentrations (µM) at 50m depth in the Southern and the Eastern Corcovado study sites for summer 2012, winter 2012 and summer 2013. Values reported ± standard deviations and n=sample size.

		Southern Corcovado			Eastern Corcovado		
		Summer 2012	**Winter 2012**	**Summer 2013**	**Summer 2012**	**Winter 2012**	**Summer 2013**
NO_3 (µM) at 50m	**Average ± sd (*n*)**	19.77 ± 4.79 (*n*=20)	26.55 ± 7.72 (*n*=11)	20.66 ± 4.60 (*n*=33)	20.71 ± 5.56 (*n*=24)	29.23 ± 4.15 (*n*=16)	19.03 ± 4.26 (*n*=22)
	Min-Max	6.13-25.41	17.91-40.43	14.36-32.13	11.44-32.88	23.51-36.79	10.10-25.71
NO_2 (µM) at 50m	**Average ± sd (*n*)**	0.46 ± 0.26 (*n*=20)	0.26 ±0.07 (*n*=11)	0.86 ± 0.56 (*n*=33)	0.45 ± 0.35 (*n*=22)	0.22 ± 0.12 (*n*=16)	0.85 ± 0.38 (*n*=22)
	Min-Max	0.02-1.03	0.20-0.37	0.04-2.60	0.01-1.27	0.00-0.46	0.37-1.95
SiO_4 (µM) at 50m	**Average ± sd (*n*)**	7.20 ± 4.15 (*n*= 20)	12.18 ± 1.38 (*n*=11)	17.33 ± 5.75 (*n*=33)	8.89 ± 2.80 (*n*=23.00)	12.56 ± 2.43 (*n*=16)	16.78 ± 5.94 (*n*=22)
	Min-Max	0.09-19.62	10.13-14.27	10.13-33.23	2.16-13.09	9.29-20.05	7.70-31.54
PO_4 (µM) at 50m	**Average ± sd (*n*)**	1.43 ± 0.36 (*n*=20)	0.79±0.04 (*n*=11)	0.71 ± 0.34 (*n*=33)	1.30 ± 0.55 (*n*=24)	0.67 ± 0.14 (*n*=16)	0.68 ± 0.38 (*n*=22)
	Min-Max	0.57-2.04	0.74-0.89	0.19-1.45	0.00-2.07	0.41-0.88	0.30-1.90

Table 8 Redfield ratio of elemental nutrient concentrations (µM) at 2m and 50m depth in the Southern and the Eastern Corcovado study sites for summer 2012, winter 2012 and summer 2013. Note: reference Redfield ratio N:Si:P=16:15:1.

	Redfield Ratio	Southern Corcovado			Eastern Corcovado		
		Summer 2012	**Winter 2012**	**Summer 2013**	**Summer 2012**	**Winter 2012**	**Summer 2013**
N: Si: P (2m)	**16: 15: 1N:Si:P (2m)**	14.87: 7.97: 1.14	24.66: 15.51: 0.76	17.11: 18.42: 0.68	13.95: 9.08: 1.02	27.19: 20.00: 0.66	17.22: 17.79: 0.63
N: Si: P (2m)	**16: 15: 1**	20.23: 7.20: 1.43	26.81: 12.18: 0.79	21.52: 17.33: 0.71	21.16: 8.89: 1.30	29.45: 12.56: 0.67	19.88: 16.78: 0.68

Table 9 Zooplankton assemblage data: average densities of the main species of mesozooplankton (ind. 1000m^{-3} ± standard deviation) counted from bongo net trawls in the Southern and Eastern Corcovado during summer 2012, winter 2012 and summer 2013. *n*=sample size.

Mesozooplankton densities (ind./1000m^3 ± sd)	**Southern Corcovado**			**Eastern Corcovado**		
	Summer 2012 (*n*=11)	**Winter 2012 (*n*=6)**	**Summer 2013 (*n*=36)**	**Summer 2012 (*n*=13)**	**Winter 2012 (*n*=12)**	**Summer 2013 (*n*=14)**
Adult *Euphausia vallentini*	850 ±1.37	10 ±0.02	330 ±1.35	130 ±0.21	10 ±0.01	460 ±0.72
Adult *Nematocelis megalops*	60 ±0.08	10 ±0.02	60 ±0.12	3 ±0.01	10 ±0.01	50 ±0.04
Euphausiid calyptopis	10 ±0.02	0±0.00	1,980 ±4.53	0 ±0.00	0 ±0.00	340 ±0.94
Euphausiid furcilia	10 ±0.03	10 ±0.02	3,280 ±5.98	10 ±0.01	0 ±0.00	140 ±0.30
Amphipods	880 ±1.93	40 ±0.07	390 ±0.61	40 ±0.09	10 ±0.01	80 ±0.12
Ctenophores	30±0.05	0±0.00	0 ±0.01	20 ±0.02	0 ±0.00	3 ±0.01
Salps	6,100 ±17.79	0±0.00	50 ±0.14	5,270 ±17.33	0 ±0.00	80 ±0.22
Siphonophores	20 ±0.04	0 ±0.00	2,980 ±4.73	10 ±0.01	0 ±0.00	10±0.02

Figures

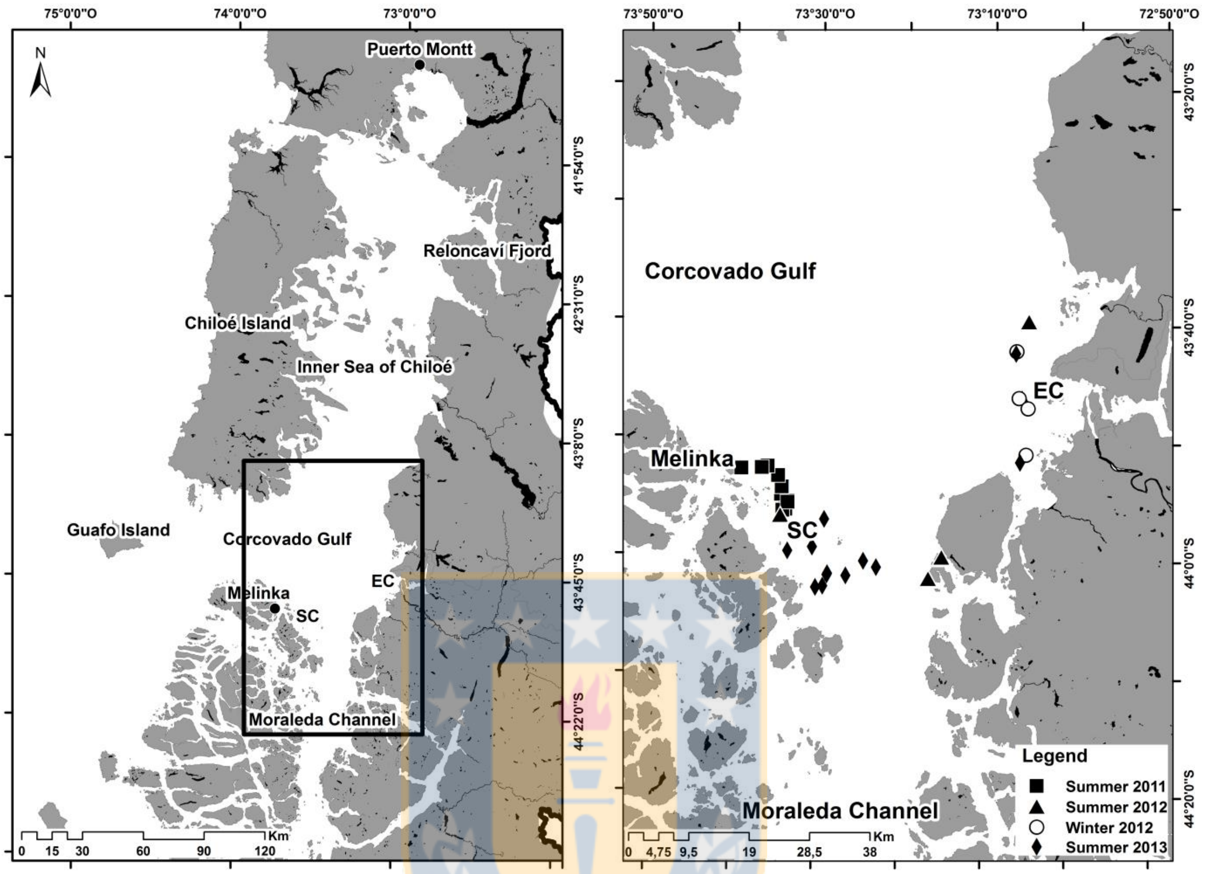


Figure 1 Map of study area with blue whale sighting data. SC: Southern Corcovado Gulf feeding sites. EC: Eastern Corcovado Gulf feeding site.

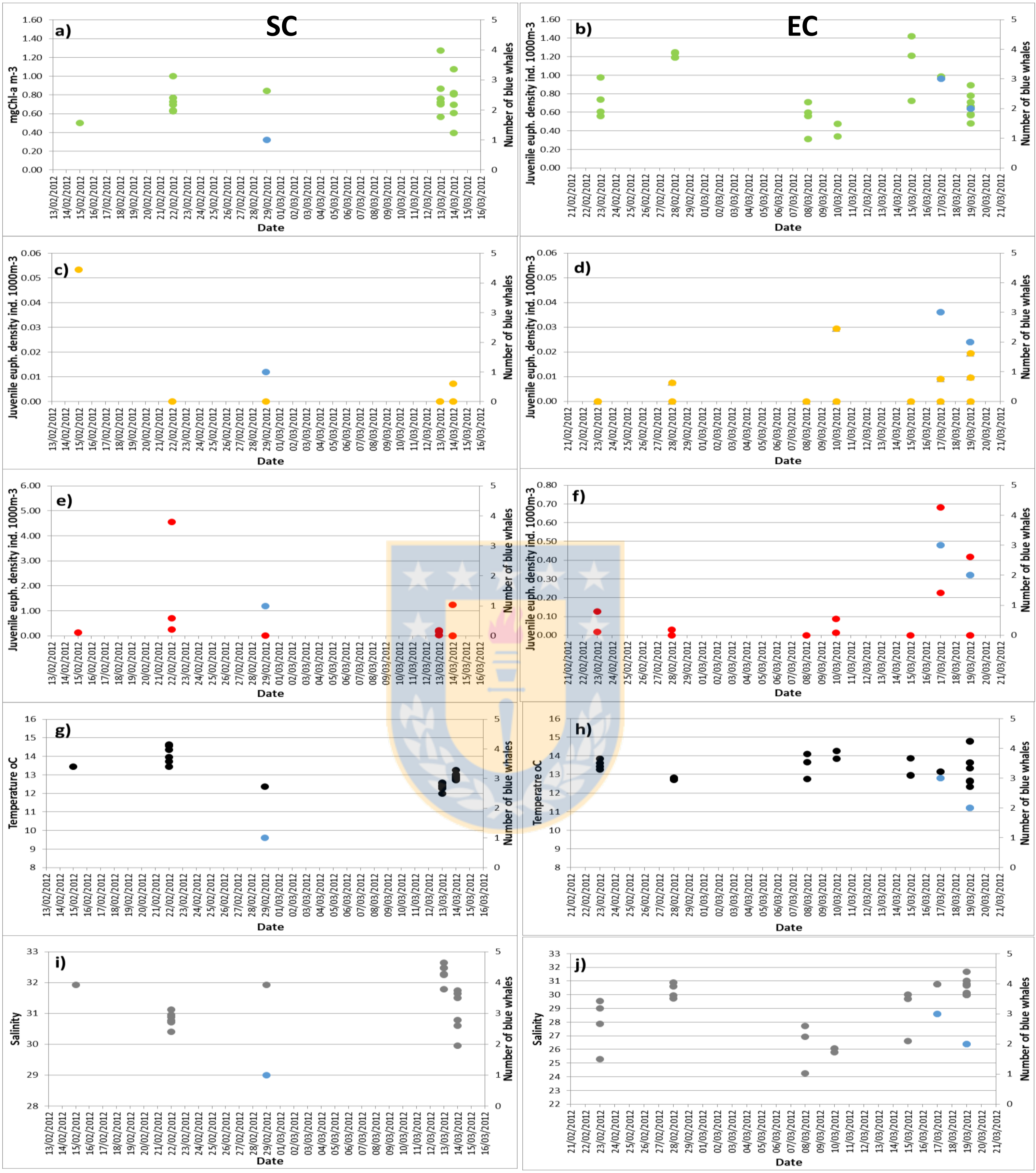


Figure 2 Temporal variation of blue whales sightings (blue circles) and oceanographic variables during summer 2012: a) Chl-a at SC; b) Chl-a at EC; c) juvenile euphausiid densities at SC; juvenile euphausiid densities at EC; d) adult euphausiid densities at SC; f) adult euphausiid densities at EC; g) SST at SC; h) SST at EC; i) Salinity at SC; j) salinity at EC.

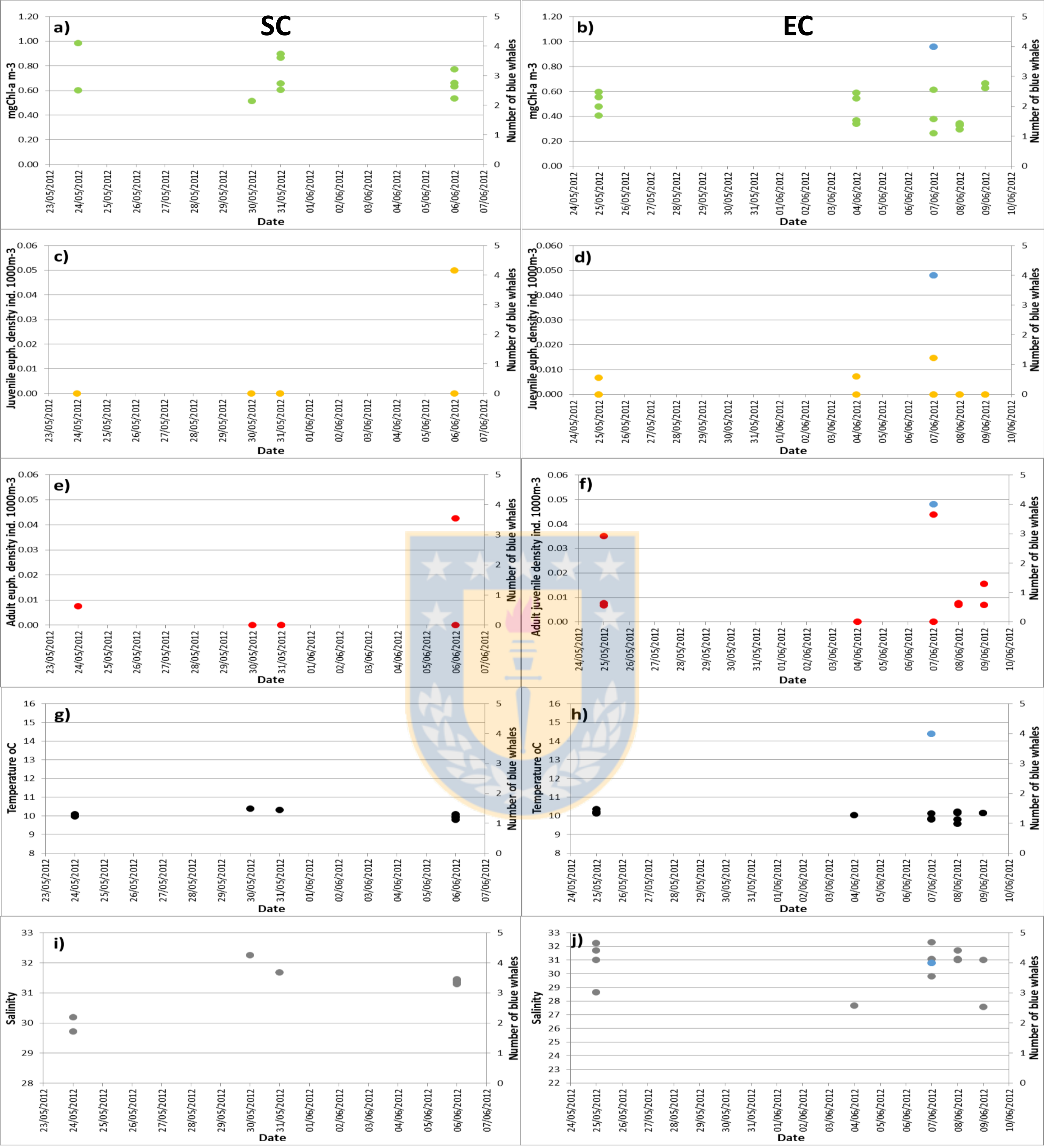


Figure 3 Temporal variation of blue whales sightings (blue circles) and oceanographic variables during winter 2012: a) Chl-a at SC; b) Chl-a at EC; c) juvenile euphausiid densities at SC; juvenile euphausiid densities at EC; d) adult euphausiid densities at SC; f) adult euphausiid densities at EC; g) SST at SC; h) SST at EC; i) Salinity at SC; j) salinity at EC.

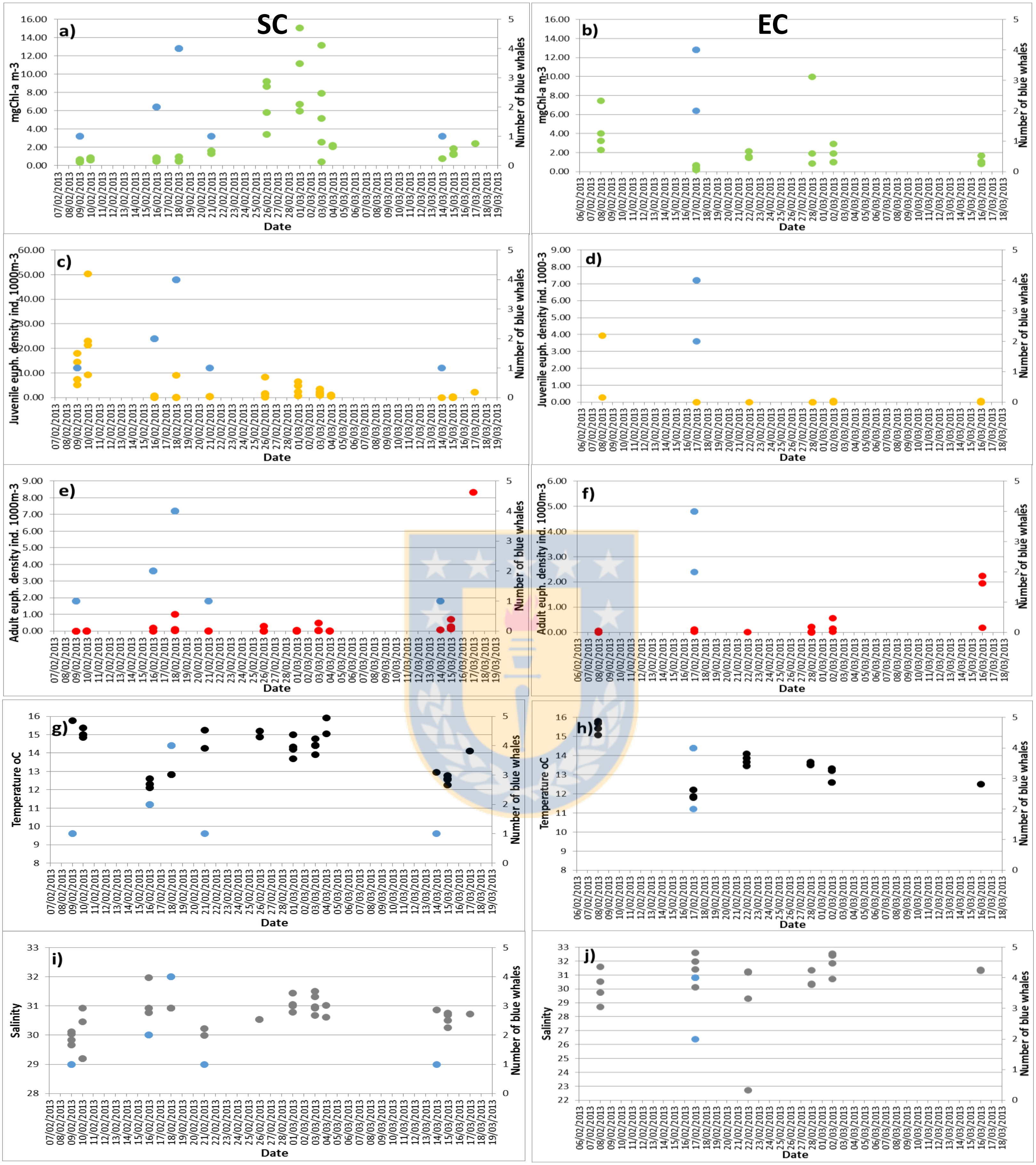


Figure 4 Temporal variation of blue whales sightings (blue circles) and oceanographic variable during summer 2013: a) Chl-a at SC; b) Chl-a at EC; c) juvenile euphausiid densities at SC; juvenile euphausiid densities at EC; d) adult euphausiid densities at SC; f) adult euphausiid densities at EC; g) SST at SC; h) SST at EC; i) Salinity at SC; j) salinity at EC.

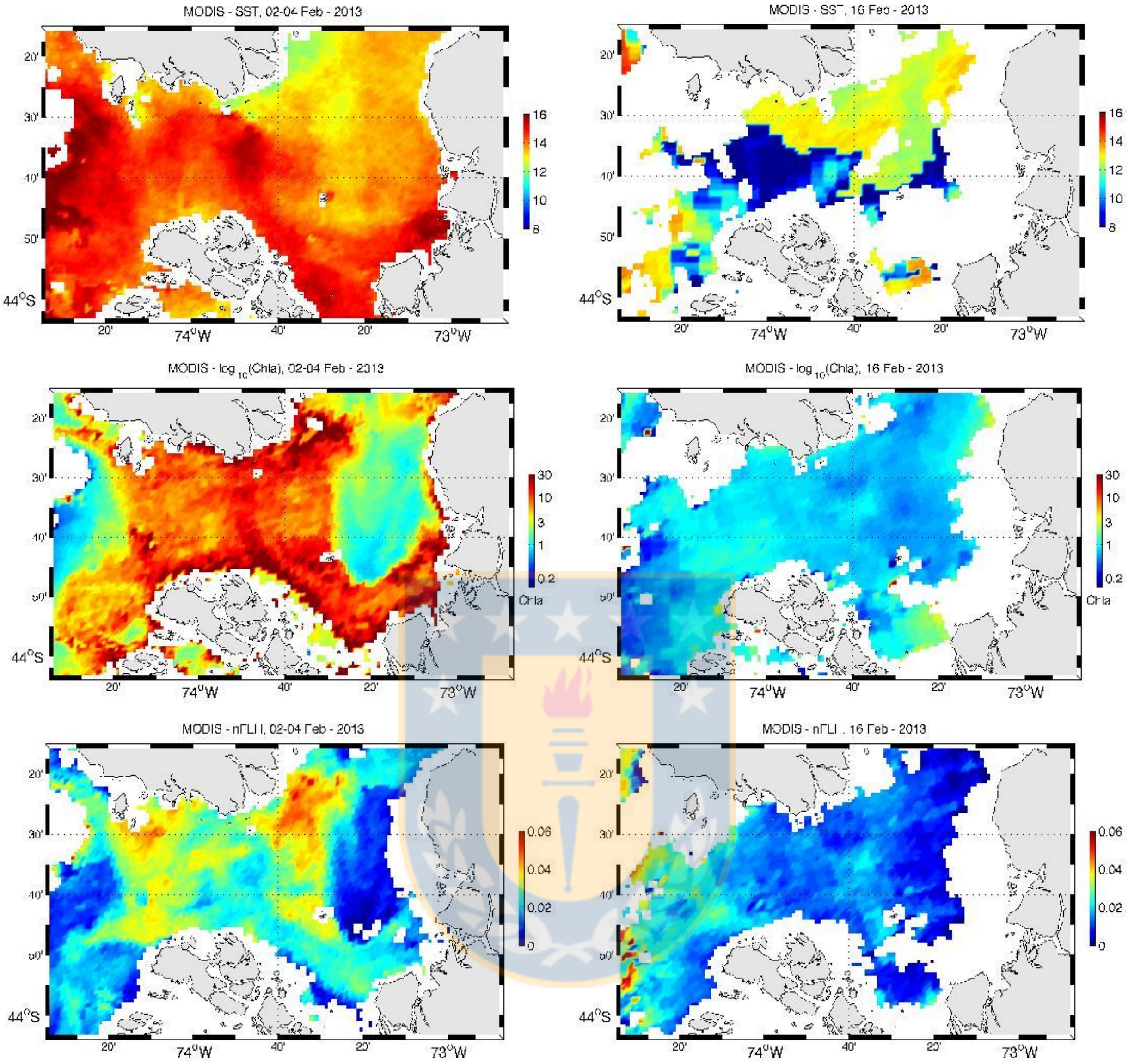


Figure 5 Satellite images of SST (top row), Chl-a (middle row) and nFLH (bottom row) on the 2-4 February 2013 (left hand column) and the 16 February 2013 (right hand column). Three blue whales were sighted on the 16 February 2013 in the Southern Corcovado.

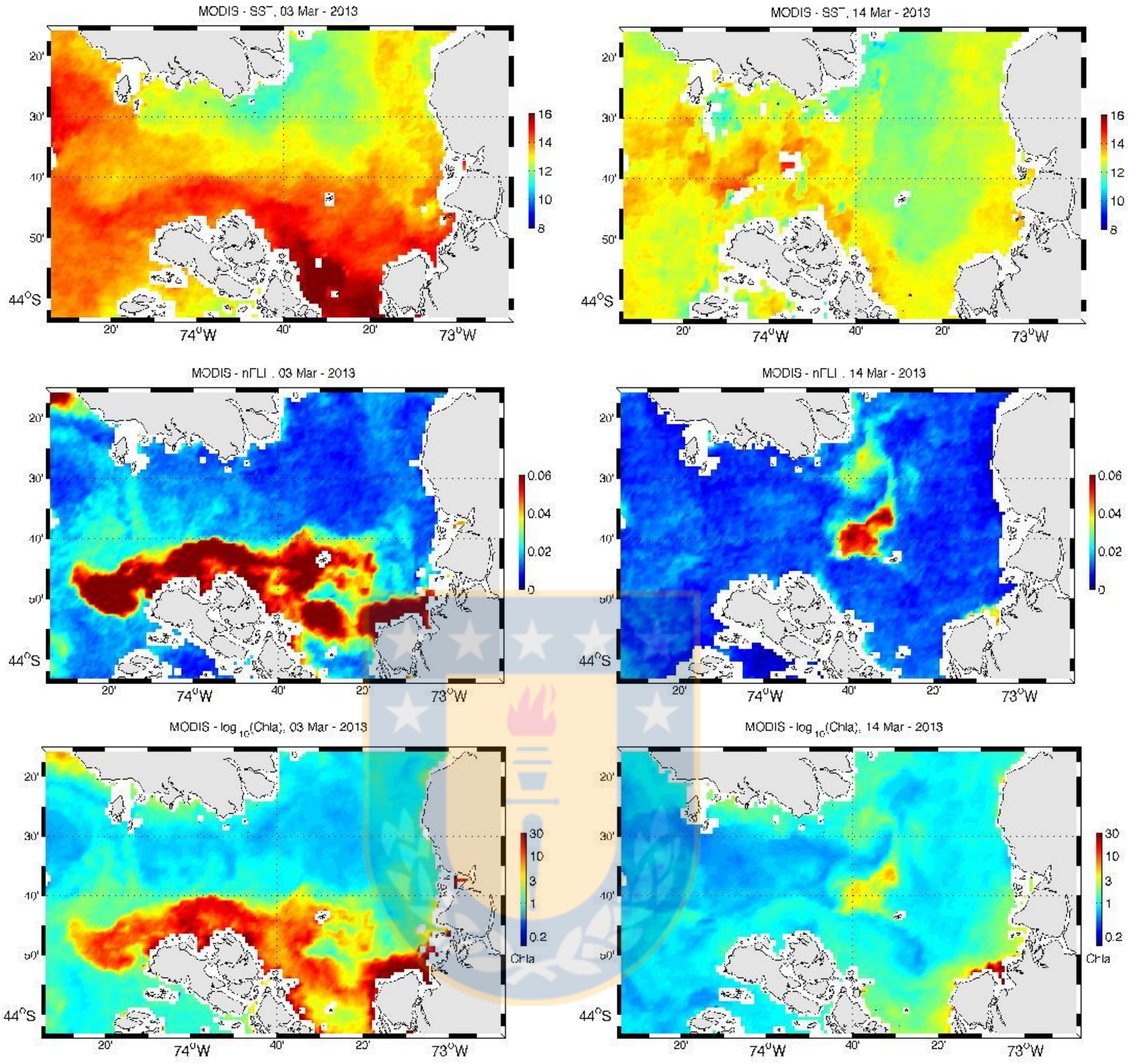


Figure 6 Satellite images of SST (top row), Chl-a (middle row) and nFLH (bottom row) on the 3 March 2013 (left hand column) and the 14 March 2013 (right hand column). One blue whale was sighted on the 14 March 2013 in the Southern Corcovado.

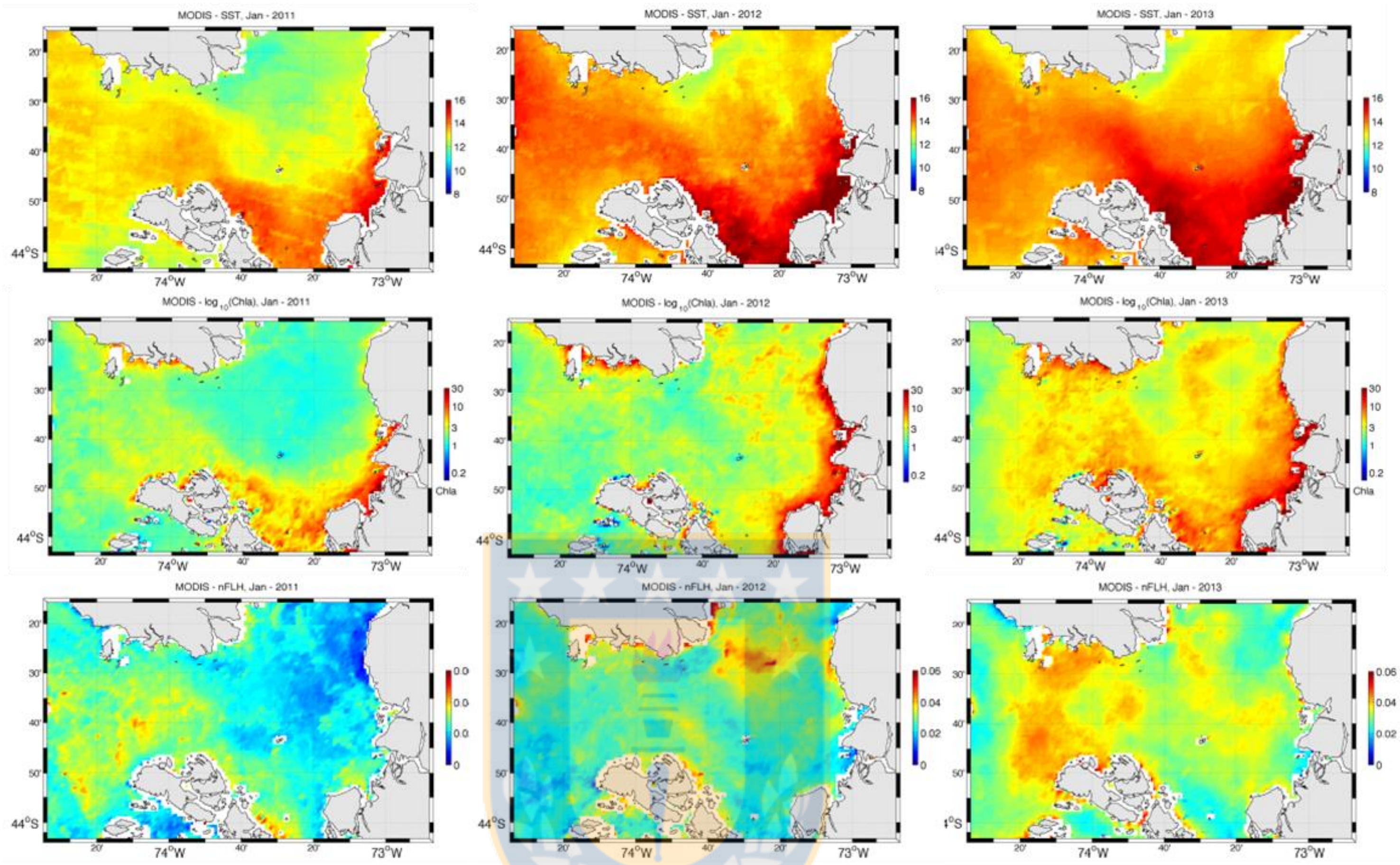


Figure 7 Monthly average satellite data of SST (top row), Chl-a (middle row) and nFLH (bottom row) for January 2011 (left hand column), 2012 (middle column), and 2013 (right hand column).

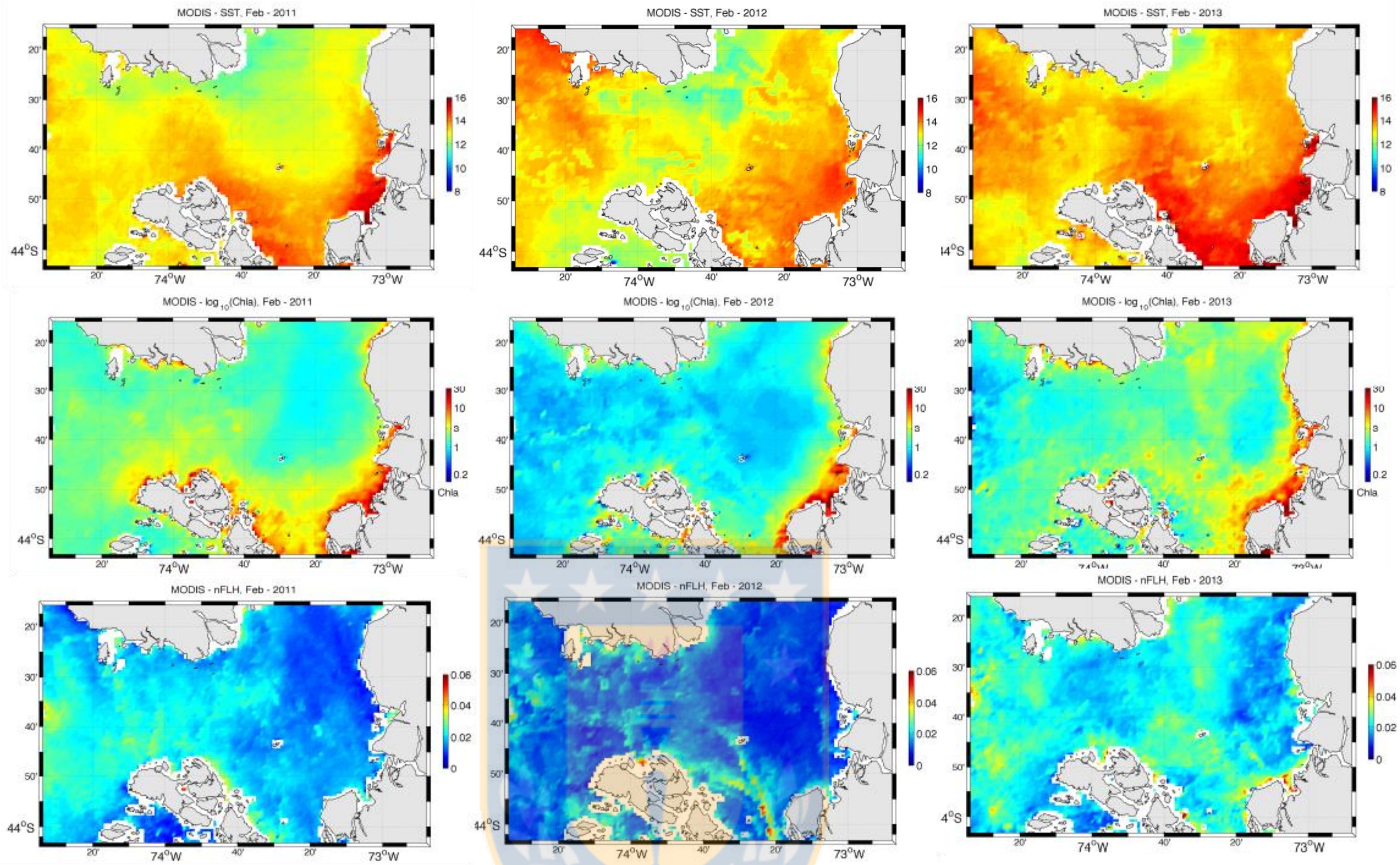


Figure 8 Monthly average satellite data of SST (top row), Chl-a (middle row) and nFLH (bottom row) for February 2011 (left hand column), 2012 (middle column), and 2013 (right hand column).

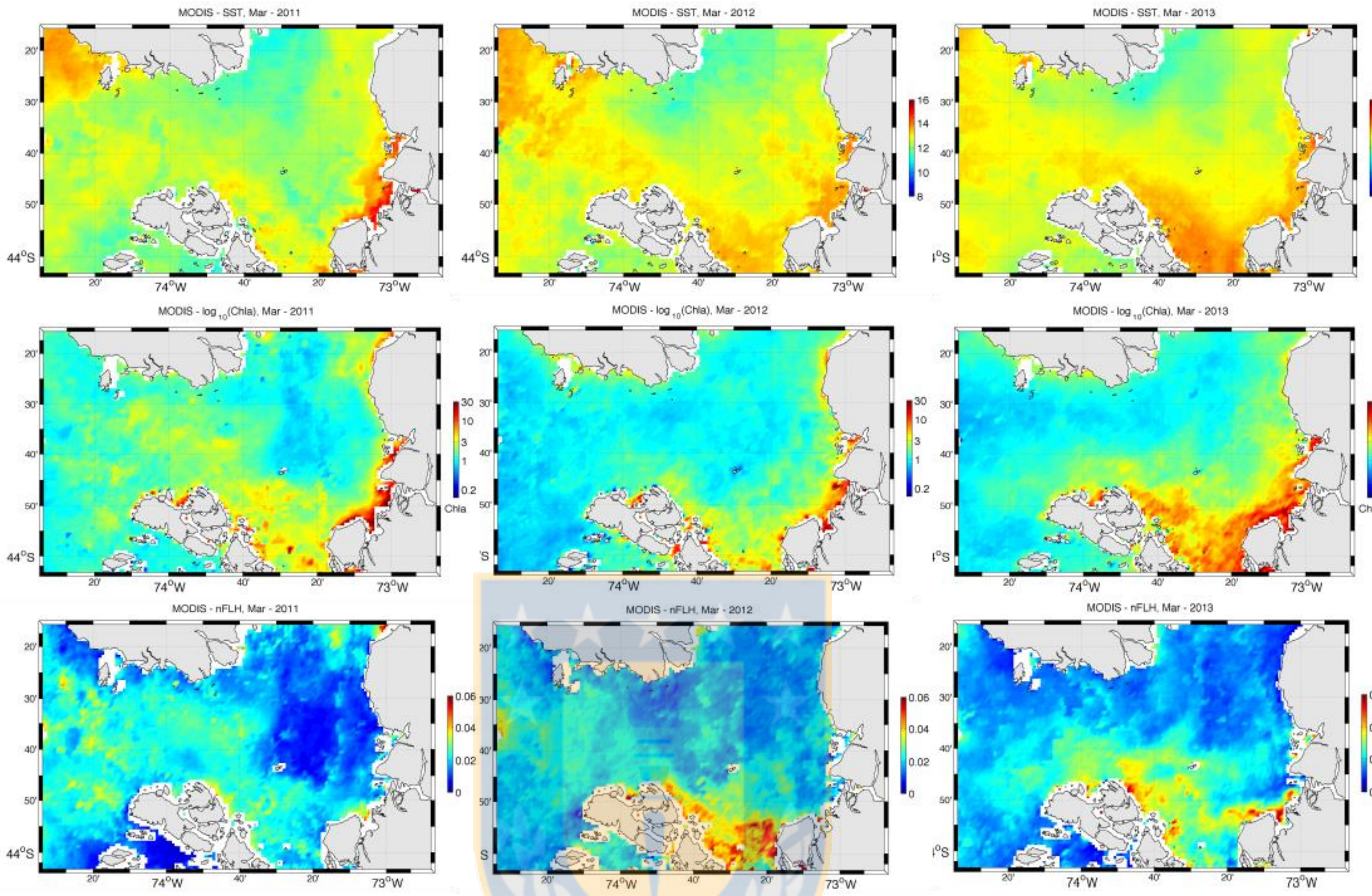


Figure 9 Monthly average satellite data of SST (top row), Chl-a (middle row) and nFLH (bottom row) for March 2011 (left hand column), 2012 (middle column), and 2013 (right hand column).

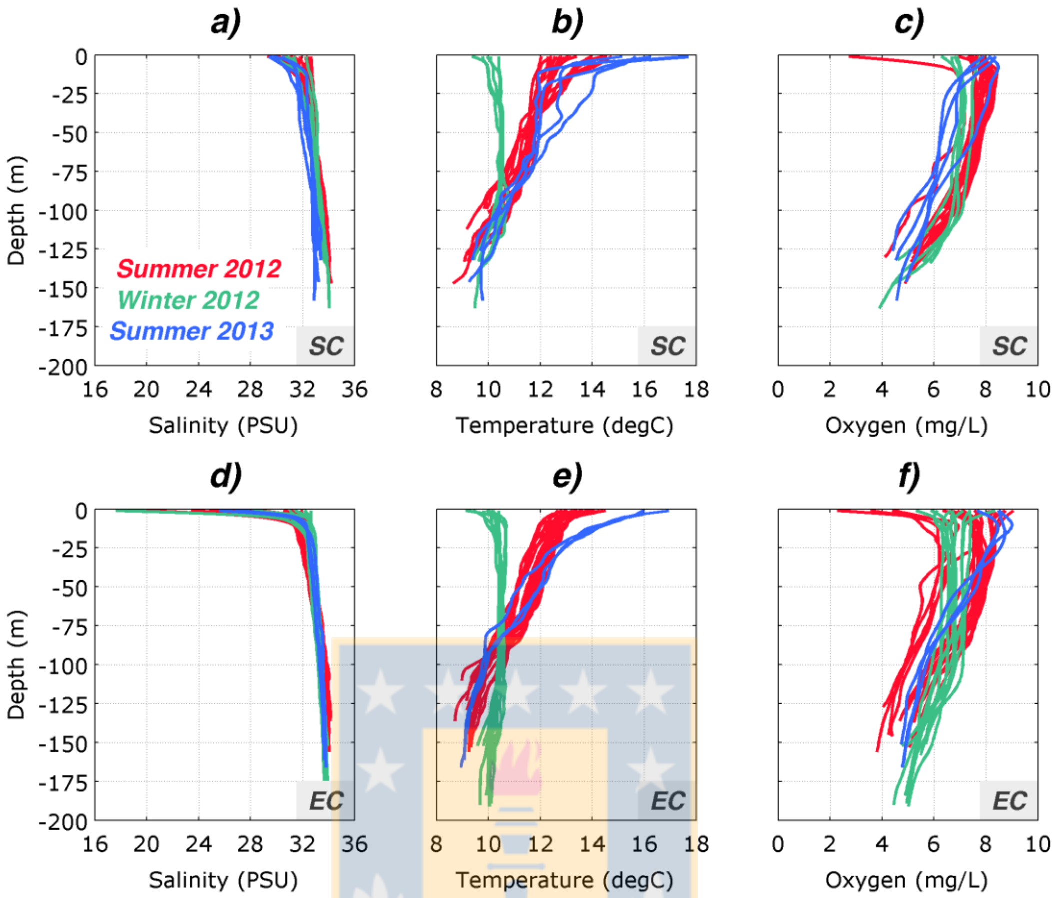


Figure 10 Salinity (a, d), Temperature (b, e) and Oxygen (c, f) vertical profiles at the SC and the EC during summer 2012, winter 2012 and summer 2013.

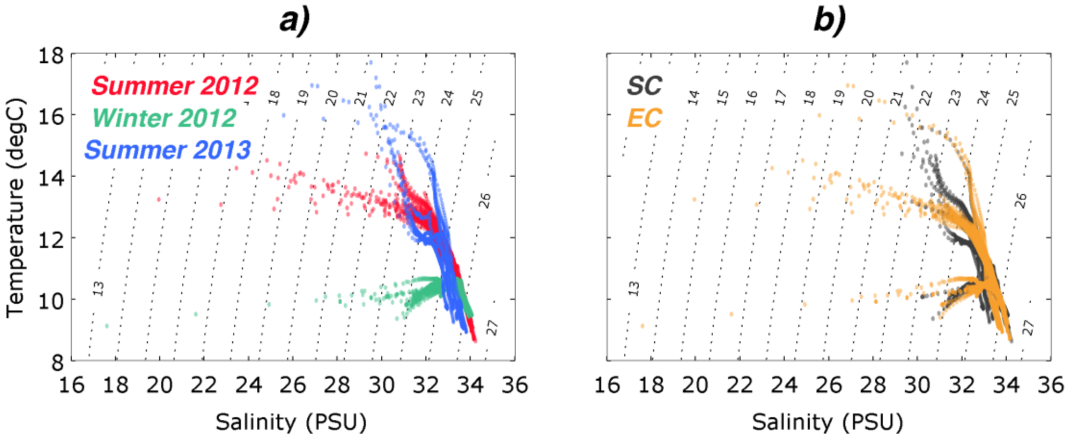


Figure 11 Temperature and salinity diagrams for a) summer 2012, winter 2012 and summer 2013; and b) SC and EC feeding sites. Dotted lines: isopycnals.

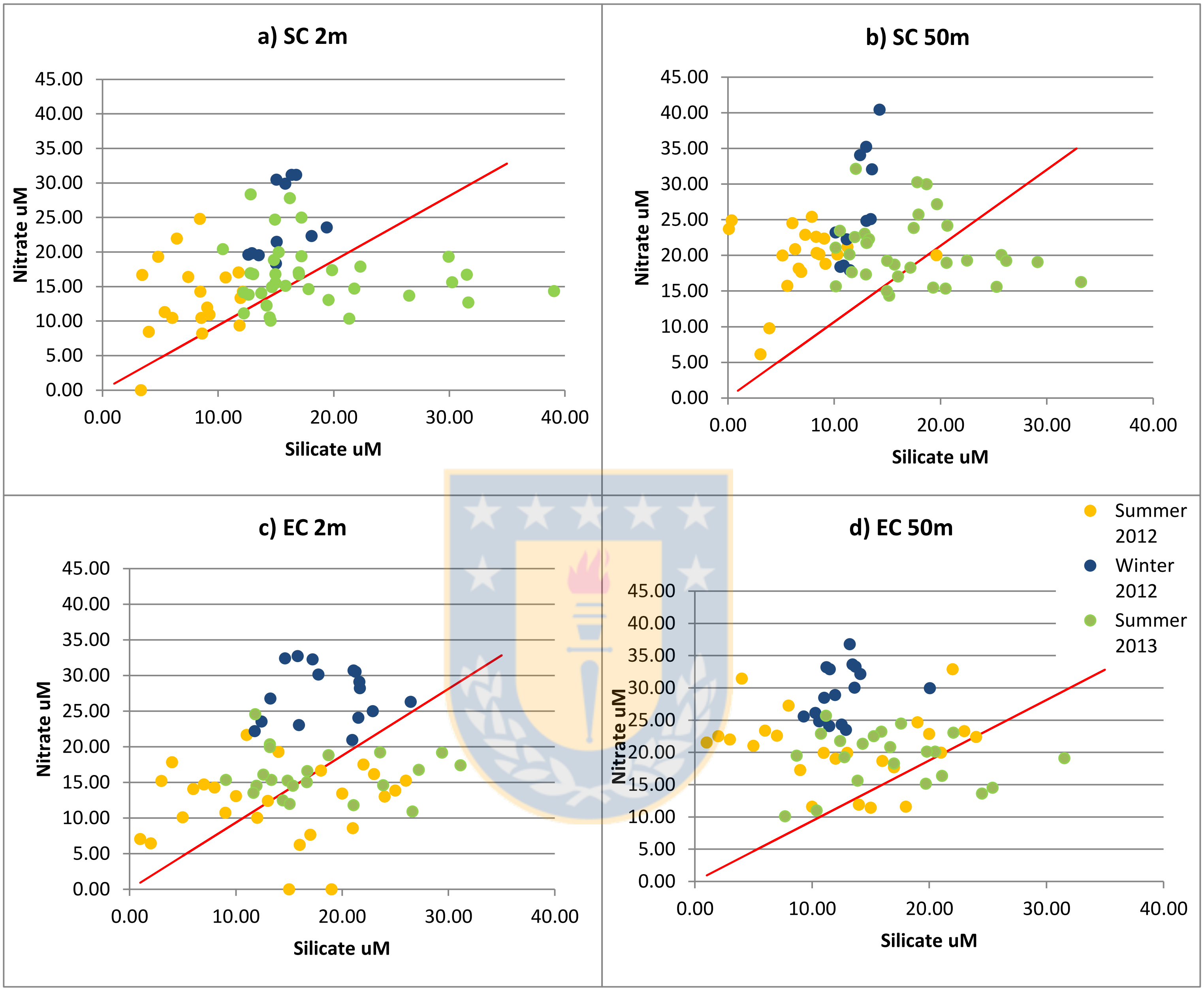


Figure 12 Scatter plots of NO_3 vs. SiO_4 during summer 2012, winter 2012 and summer 2013 at the a) Southern Corcovado 2 m depth; b) Southern Corcovado 50 m depth; c) Eastern Corcovado 2 m depth; and d) Eastern Corcovado 50 m depth. Elemental Redfield ratio N:Si = 16:15 marked by red line.

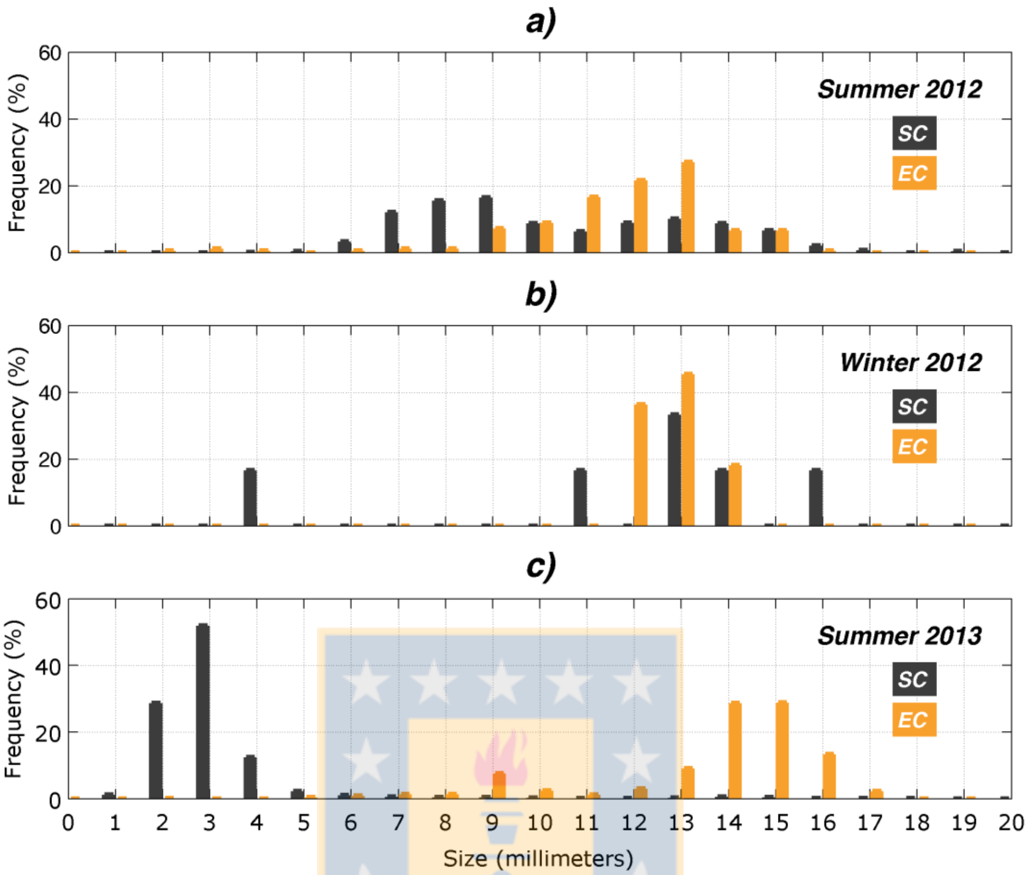


Figure 13 *Euphausia vallentini* size structure histograms for all sampling days grouped in the Southern (SC) and Eastern Corcovado (EC) Gulf during a) summer 2012, b) winter 2012 and c) summer 2013.

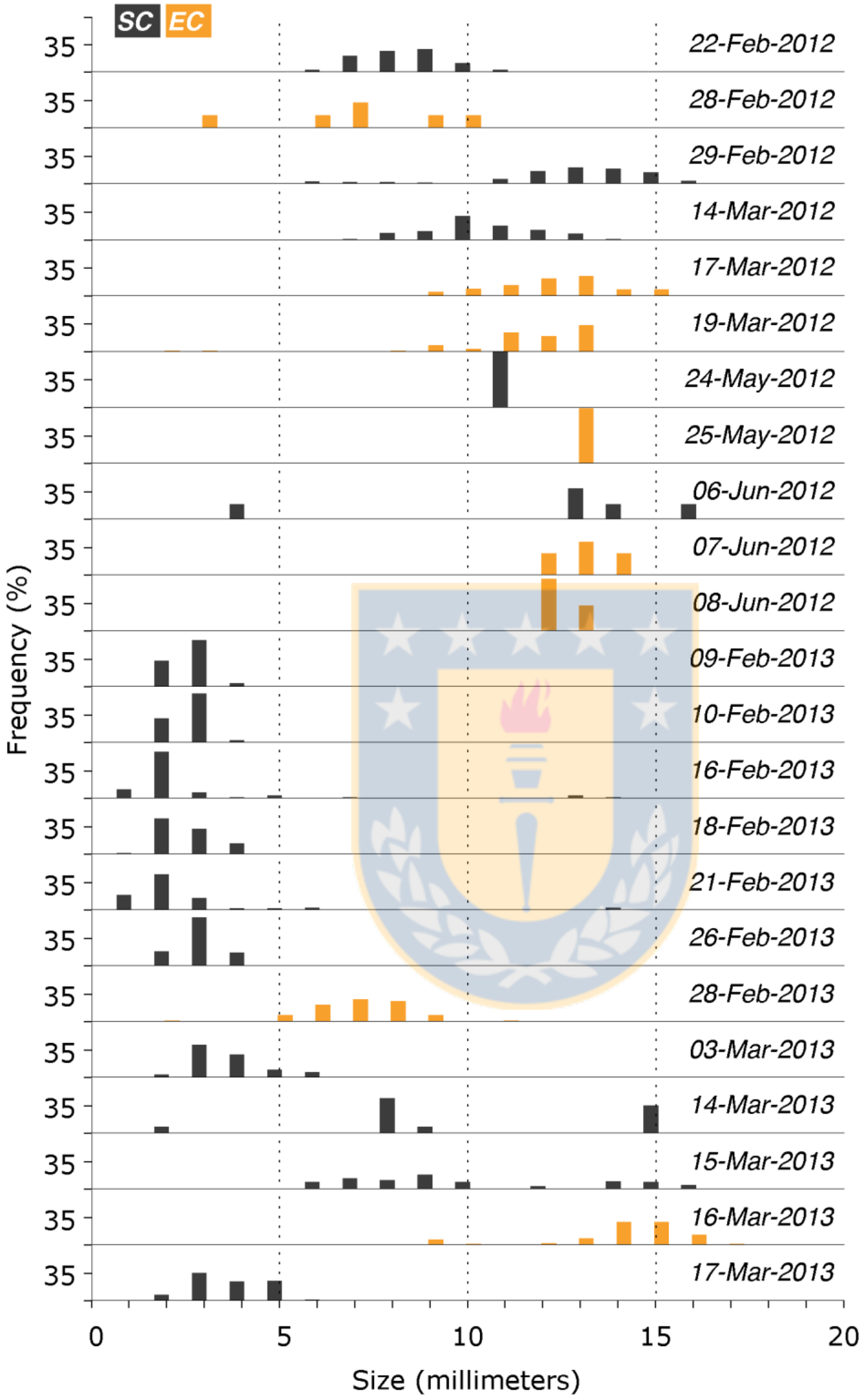


Figure 14 *Euphausia vallentini* size structure histograms for each sampling day separately in the Southern (SC) and Eastern Corcovado (EC) Gulf during summer 2012, winter 2012 and summer 2013.

5. DISCUSIÓN

5.1 Identidad acústica y patrones de desplazamiento estacional de ballenas azules en el Pacífico Suroriental

Caracterización de cantos de ballenas azules en la ecorregión Chiloense y un nexo acústico con el Pacífico Tropical Oriental

El primero estudio de acústica de ballenas azules en esta zona fue realizado por Cummings & Thompson (1971) en el año 1970. Esta tesis (Buchan et al. 2014, Capítulo 1) es el segundo en examinar los cantos regionales de ballenas azules en el golfo Corcovado (en la ecorregión Chiloense) con el fin de caracterizar el o los cantos regionales y entender la identidad acústica de las ballenas azules del PSO, además de los posibles nexos acústicos con otras regiones.

El análisis de las grabaciones con hidrófono móvil en esta tesis detecto dos cantos distintos, uno que he llamado SEP1 (“Southeast Pacific” 1) que es igual que el canto descrito por Cummings & Thompson (1971), y un segundo canto, llamado SEP2 que no había sido registrado anteriormente para las ballenas azules del golfo Corcovado. Se realizó una comparación de ambos cantos, SEP1 y SEP2, con registros acústicos de otras regiones (Océano Austral, Širović et al. 2009; Pacífico Norte, Stafford et al. 2009; PTO, Stafford et al. 1999b). Ambos cantos produjeron un calce con los registros de Stafford et al. (1999b) de un hidrófono autónomo anclado aproximadamente a 500 mn al suroeste de Galápagos, reafirmando el nexo acústico establecido para SEP1 por estos autores y estableciendo un nexo nuevo para SEP2 entre el golfo Corcovado y el PTO (Buchan et al. 2014). En consecuencia, los resultados obtenidos validan la **Hipótesis 1.** Este nexo acústico sugiere una migración de ballenas azules entre el golfo Corcovado y el PTO, coincidiendo con las especulaciones de Stafford et al. (1999b).

La identidad acústica característica de las ballenas azules del PSO concuerda con estudios anteriores que apoyan a la clasificación de las ballenas azules chilenas como un nueva subespecie de *Balaenoptera musculus* (ej. Clarke et al. 1978; Branch et al. 2007a, b; Torres-Florez et al. 2014b).

Presencia estacional de cantos SEP en la ecorregión Chiloense

Los resultados del Monitoreo Acústico Pasivo fijo en la ERC y en el PTO (Buchan et al. *en prensa,* Capítulo 2), evidenciaron la tendencia temporal de presencia de cantos en cada sitio de monitoreo. En la ERC, se observó un fuerte patrón estacional en las detecciones SEP1 y SEP2 evidenciando un aumento durante el mes de enero, con una máxima entre marzo y mayo, y luego una disminución fuerte en junio/julio. No hubo detecciones entre los meses de septiembre y noviembre. Por lo tanto los resultados de la presente Tesis rechazan la **Hipótesis 2**, ya que la máxima estacional ocurrió en entre marzo y mayo, y no en enero-marzo como había sido planteado.

Este patrón de presencia estacional coincide con avistamientos registrados entre enero y julio (ej. Findlay et al. 1998; Hucke-Gaete et al. 2003, 2010; Försterra & Häussermann 2012). Esta máxima durante el verano austral tardío y el principio del otoño podría coincidir con la máxima anual de eufáusidos, lo cual fue postulado anteriormente por Burtenshaw et al. (2004) en base a la misma tendencia temporal de cantos de ballenas azules al final del verano en el Pacífico Noreste. En el mar interior de Chiloé, González et al. (2010) registraron una abundancia de *E. vallentini* dos veces mayor durante la primavera respecto al invierno, y aunque estos autores no muestrearon en otoño, es plausible que la abundancia de eufáusidos a fin del verano podría ser aún mayor que durante la primavera.

Sin duda, será necesario obtener más registros acústicos y oceanográficos de largo plazo para dilucidar como la distribución espacial-temporal, anual y estacional, de ballenas azules está asociada a factores ambiental en el área de alimentación del ERC.

Desplazamiento estacional hacia el Pacífico Suroriental

En el PTO, abarcando siete años de registros acústicos, se detectaron cantos SEP2 durante todos los meses del año, evidenciando una presencia anual de ballenas azules en esta zona, y un patrón estacional mucho menos marcado que el de la ERC (Buchan et al. *en prensa* y Capítulo 2). Sin embargo, hubo mayores detecciones alrededor del mes de julio, sugiriendo una mayor presencia durante el invierno austral. Así, se rechaza la **Hipótesis 3**, precisando que la máxima estacional ocurrió alrededor del mes de junio, y no entre los meses de junio y septiembre como se había anteriormente planteado.

Esta variación temporal coincide con la disminución de cantos SEP durante julio en la ERC. Desafortunadamente, los datos del PTO y los de la ERC fueron tomados con una década de desfase, lo cual puede introducir una variación inter-anual. Cualquier cambio en las condiciones ambientales a escala decadal podría haber modificado el patrón temporal de presencia de ballenas. A pesar de esta limitación, los datos acústicos dan más peso al nexo acústico previamente demostrado entre la ERC y el PTO (Buchan et al. 2014, Capítulo 1), e indican una residencia estacional en verano en la ERC y en invierno en el PTO. Estas observaciones sugieren un desplazamiento estacional desde la ERC hacia el PTO durante el otoño austral. Este desplazamiento se refleja también en avistamientos y capturas históricas (Clarke 1980; Donovan 1984; Reilly & Thayer 1990; Capella et al. 1999; Palacios 1999; Branch et al. 2007b; Felix et al. 2007), estudios bioacústicos anteriores (Stafford et al. 1999b), y el rastreo satelital de ballenas azules (Hucke-Gaete 2004).

5.2 Condiciones oceanográficas intra-estacionales para el forrajeo óptimo de ballenas azules en el suroriente del Golf Corcovado

Condiciones oceanográficas generales del sector suroriental del golfo Corcovado

Los valores de salinidad y temperaturas registradas durante el muestreo oceanográfico en el sector suroriental del golfo Corcovado (sitios CS y CO) reflejaron el gradiente de condiciones estuarinas presentes en los fiordos y canales de la Patagonia Norte (Sievers & Silva 2008). Las mediciones de temperatura y salinidad estuvieron dentro del rango de valores reportados anteriormente para el golfo Corcovado (Silva & Guzmán 2006; González et al. 2010). Las salinidades más bajas detectadas en el CO reflejaron la influencia de la desembocadura del río Palena. La estructura vertical observada es característica del sistema megaestuarino de la Patagonia Norte, con una capa de baja salinidad en superficie (Silva y Guzmán 2006). Los diagramas T-S sugieran la influencia de Agua Sunantartica Modificada (ASAAM) y Agua Estuarina (AE) (Silva & Guzman 2006; Sievers & Silva 2008).

Las concentraciones de nitrato observadas en el sector suroriental del golfo Corcovado son características de aguas estuarinas y oceánicas (6,24-32,71 µM a 2m), superando los valores reportados por González et al. (2010) (0-20 µM) en el golfo Corcovado. Las concentraciones mayores de nitrato fueron detectadas en invierno en comparación con el verano, lo que es similar a lo reportado por González et al. (2010). El silicato estaba en el rango reportando para el Mar

Interior de Chiloé, el golfo Corcovado y el canal Moraleda (0-30 µM; Silva & Guzmán 2006; González et al. 2010). En el sector norte de la Patagonia chilena, las mayores concentraciones de silicato (<120 µM) están asociadas a aportes de agua dulce registradas en zonas más cerca del continente, ej. el fiordo Reloncaví (González et al. 2010) y el fiordo Aysén (Silva & Guzmán 2006). La clorofila *in situ* y satelital se encuentran en el rango de valores reportados en estudios previos para el golfo Corcovado (Hucke-Gaete 2004; Montecino & Pizarro 2006; Iriarte et al. 2007; González et al. 2010) y destacaron el sector suroriente de golfo Corcovado como un área de alta Cl-a.

Las densidades de eufáusidos en el sector suroriental del golfo fueron más altas que los reportes existentes para el fiordo Comau y dentro del rango reportado por Palma & Silva (2004) para la región más al sur (46°S - 56°S). Sin embargo no se registraron valores tan altos como el máximo registrado en el golfo de Penas por Palma & Silva (2004) que alcanzó valores de 1.400-11.500 ind./1000m^3. *Euphausia vallentini* fue mucho más abundante que la otra especie de eufáusido registrada, *N. megalops,* lo cual coincide con lo observado por Palma & Silva (2004), quienes encontraron que *E. vallentini* constituía 98% de la abundancia total de eufáusidos en esta zona. La estructura de tamaños de las agregaciones de *E. vallentini* fue normal; sin embargo, durante el verano 2012, se notó una clara ausencia de estadios juveniles, comparando con el verano 2013. Durante el verano 2013, se apreció una sucesión de juveniles a adultos durante febrero y marzo 2013. Esto apunta a una máxima biomasa de eufáusidos a fin del verano.

Variación temporal intra-estacional en avistamientos de ballenas azules y variables oceanográficas

Cuando se analizaron los eventos de forrajeo de ballenas azules en función de variables ambientales, (T, S, Cl-a, densidad de eufáusidos juveniles y *E. vallentini* adultos) se observó en el verano de 2013 un desfase temporal de aproximadamente 10 días entre una máxima intra-estacional de clorofila-a y avistamientos de ballenas azules alimentándose en el sector suroriente del golfo Corcovado. Es decir, los eventos de alimentación coincidieron con un periodo de baja Cl-a; y no se vio un patrón claro para las densidades de eufáusidos. Esto conduce a rechazar la **Hipótesis 4** que los eventos de alimentación de ballenas azules ocurren durante periodos de alta abundancia de eufáusidos y altas concentraciones de Cl-a. Estos resultados podrían explicarse por la alta presión de pastoreo por parte de los eufáusidos sobre el fitoplancton, lo cual produciría bajas concentraciones de Cl-a cuando las densidades de eufáusidos son mayores (*i.e.* durante eventos de forrajeo de ballenas azules); sin embargo, esto no se vio reflejado en los datos de densidad de eufáusidos. Una posible razón es la presión de depredación sobre los eufáusidos por parte de las ballenas. Una explicación alternativa es el error conocido asociado al muestreo de eufáusidos con redes (Everson 2000) y sobre todo durante el día (para coincidir con el esfuerzo de avistamiento de ballenas azules) dado la migración vertical realizada por los eufáusidos en general (Mauchline 1980), y por *E. vallentini* (Hamamé & Antezana 2010) en particular.

Cambios inter-anuales en condiciones de forrajeo para ballenas azules

Se avistaron más ballenas azules durante los veranos 2011 y 2013, comparado con el verano 2012, en el sector suroriental del golfo Corcovado. Esto coincide con mayores avistamientos de ballenas azules en la costa de Valdivia (≈39°S) durante el verano de 2012 (Hucke-Gaete *no publicado*), sugiriendo un posible cambio de preferencia de zona de alimentación durante dicho periodo.

Durante el verano 2012, comparando con los veranos de 2011 (sin datos *in situ*) y 2013, hubo una baja en la salinidad, una baja en TSS y Cl-a *in situ*, una baja en nFLH y Cl-a satelital, una marcada baja en SiO_4 (por debajo de la razón Redfield: ej. N:Si:P ≈15:8:1 vs. Redfield 16:15:1) y una comunidad zooplanctónica dominada por salpas (comparado con el verano de 2013 cuando dominaban los eufáusidos). Estas tendencias se observaron de manera más marcada en el CS, es decir el sitio más cerca del océano Pacífico. Esto valida la **Hipótesis 5,** en cuanto a que las diferencias inter-anuales e inter-sitio en avistamientos de forrajeo de ballenas azules son generadas por variaciones en la abundancia local de eufáusidos.

Una de las explicaciones posibles para los cambios observados durante el verano 2012 es la mayor entrada de ASAA al golfo Corcovado. En 2010, Gieseke et al. (2014) reportaron un afloramiento masivo de salpas (*Ihlea magalhanica*) en el Mar Interior de Chiloé, explicado por un cambio en la intensidad del Modo Anular del Sur (SAM por sus siglas en ingles) y una mayor entrada de ASAA al Mar Interior, lo cual fue acompañado por una disminución de 1°C en TSS y un menor gradiente termohalino vertical. Sin embargo, esto no explicaría la baja en salinidad observada en 2012. En el Océano Austral, el krill antártico (*Euphausia superba*) y las salpas (*Salpa thompsoni*) son macro-herbívoros importantes generalmente asociadas a masas de aguas distintas (Pakhomov et al. 2002). Las salpas son favorecidas por condiciones de baja productividad (poco alimento) y temperaturas más altas, y se reproducen más rápidamente que el krill antártico (Voronina, 1998; Atkinson et al. 2004; Smetacek & Nicol 2005). Por otra parte, las salinidades más altas y el silicato más bajo durante el verano 2012 podría también sugerir una reducción en la cantidad de aguas estuarinas en el sector suroriental del golfo Corcovado, afectando particularmente el sitio más oceánico, es decir el CS. Efectivamente, la dinámica (pulsos) de productividad primaria en sistemas estuarinos ha sido asociada a los aportes de aguas continentales (Mallin et al. 1993). Una reducción en el ingreso aguas continentales, y por tanto en suministro de silicato, podría haber limitado la producción primaria y en particular la formación de afloramientos de diatomeas (ej. Dugdale & Wilkerson 1998). En un fiordo patagónico, Torres et al. (2011) encontraron que las bajas concentraciones de silicato favorecían la dominancia de dinoflagelados en desmedro de las diatomeas. A su vez, la limitación de florecimientos de diatomeas podría haber causado las condiciones de baja productividad que favorecen las salpas. Sin embargo, las estadísticas de caudal medio diario de la Dirección General de Aguas (www.dga.cl/) disponibles para el río Cisnes, el río Aysén, y el río Palena durante 2010-2013, no registraron un cambio notorio en los caudales diarios (Anexo 8.3) que hubiese podido demostrar una reducción en la llegada de aguas continentales al golfo Corcovado.

Un factor importante considerar en estudios futuros es la influencia de la marea, ya que la productividad primaria en sistemas estuarinos también ha sido ligada a el efecto de mezcla de las mareas (Cloern 1991; Gargett et al. 2003).

Diferencias entre sitios en las condiciones para el forrajeo de ballenas azules

El sitio SC presenta de forma consistente, mayores salinidades, temperaturas, concentraciones de Cl-a y densidades de organismos planctónicos. Las diferencias entre los dos sitios de estudio, el CS y el CO, fueron más evidentes durante el verano de 2013 cuando hubo una mayor concentración de Cl-a *in situ*, mayor abundancia de eufáusidos y más avistamientos de ballenas azules en el CS comparado con el CO. La aparente preferencia por el CS por parte de las ballenas y la mayor productividad primaria podría explicarse por las concentraciones de nutrientes (particularmente el SiO_4, como se ha mencionado anteriormente) y la presencia de una zona de retención de organismos planctónicos debido a la topografía de islas y el cañón submarino al norte del Archipiélago de los Chonos. Una preferencia por el CS por parte de las también se ha demostrado por rastreo satelital de cinco ballenas azules durante el verano y otoño 2004 (Hucke-Gaete 2004). Esta zona de retención podría ayudar en la formación de agregaciones densas de eufáusidos en el CS (Hucke-Gaete 2004) y así proveer condiciones ideales para el forrajeo de ballenas azules. En California, Croll et al. (2005) observo una preferencia por parte de ballenas azules por el cañón submarino de la bahía de Monterey, en donde también encontraron densidades más altas de zooplancton determinado mediante métodos hidroacústicos.

5.3 Lo que sabemos (y lo que sabemos que no sabemos) sobre la distribución estacional de las ballenas azules del Pacífico Suroriental

Distribución a escala anual y de cuenca oceánica

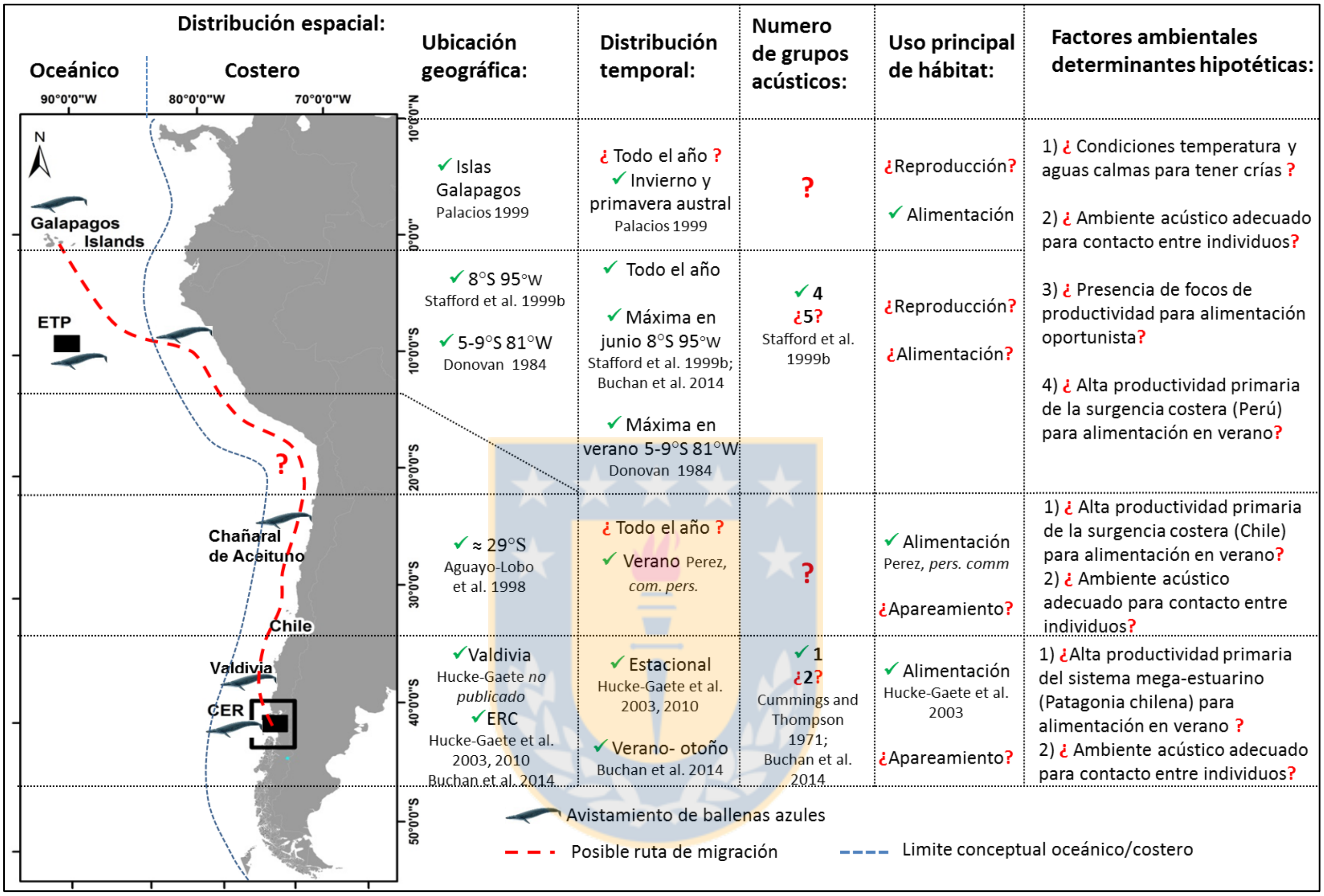
La Figura 5.1 resume esquemáticamente el estado actual del conocimiento sobre la distribución espacio-temporal de ballenas azules del PSO, complementado con datos de avistamientos y presencia acústica, el número de grupos acústicos presentes en la región (incluyendo grupos acústicos descritas para otras regiones), el uso principal del hábitat, y algunas especulaciones sobre los principales factores ambientales que podrían determinar la distribución espacio-temporal.

Como se puede apreciar, “lo que no sabemos” es mayor que “lo que sabemos”. No obstante, emerge el patrón de un grupo o población de ballenas azules del PSO que se desplaza a lo largo de la costa de Sudamérica, entre zonas de alimentación costeras hacia el sur en latitudes intermedias, como la ecorregión Chiloense, y una posible zona de nacimiento desconocida hacia el ecuador, probablemente en aguas más oceánicas. Las zonas de alimentación se caracterizan por sus altos niveles de productividad primaria y disponibilidad de alimento (Norris 1967; Laws 1985; Tynan 1998; Croll et al. 2005; Gill et al. 2011). Desafortunadamente, existe un gran desconocimiento respecto a la ubicación y de cómo las ballenas azules seleccionan sus áreas de nacimiento y apareamiento. Los factores determinantes podrían estar relacionados a las condiciones ambientales adecuadas para tener crías, es decir aguas calmas y cálidas (ej. Norris 1967; Whitehead & Moore 1982; Clapham 1996), o a lugares con menor riesgo de ataque por orcas (*Orcinus orca*) (Corkeron & Connor 1999).

Durante la migración de ballenas azules del PSO entre la ERC y el PTO, existen numerosas oportunidades de alimentación a lo largo de la costa de Sudamérica durante la estación productiva en latitudes intermedias. Estás áreas estarían sostenidos por las características de sistema megaestuarino de la ERC (44°S), y del sistema de surgencia de la Corriente Humboldt (≈42°S - 5°S). Es probable que en estas áreas, la actividad principal es la alimentación y que no ocurra el nacimiento de crías en estas regiones; sin embargo no es imposible pensar que el apareamiento podría ocurrir en zonas de alimentación, en donde individuos adultos se concentran en focos de alta productividad. Esto podría explicar el alto nivel de cantos de ballenas azules registrados durante los meses de verano y otoño, no solo en la ERC (Buchan et al. 2014) sino también en otras zonas de alimentación a nivel global (ej. Burtenshaw et al 2004; Gavrilov & McCauley 2013). Desafortunadamente, a nivel mundial los sitios de apareamiento de ballenas azules permanecen desconocidos.

Una vez que las ballenas entran en aguas más tropicales es también posible que su actividad principal sea el nacimiento de crias. Sin embargo, dado los importante costos energéticos de una ballena azul (Reilly et al. 2004; Goldbogen et al. 2011), es plausible que las ballenas aprovechen focos de productividad dentro de sus posibles zonas de nacimiento y apareamiento. Un ejemplo de esto serían las Islas Galápagos, (≈10°S - 0°S), donde Palacios (1999) observo ballenas azules alimentándose de agregaciones de *Nyctiphanes simplex*.

La disponibilidad de estos focos de productividad (ej. islas Galápagos) durante todo el año para el forrajeo de ballenas azules podría explicar la presencia de cantos SEP durante todo el año en el PTO, aunque a niveles muchos más bajos que en la ERC. Es posible pensar que un individuo podría optar no migrar durante un verano si la disponibilidad de alimento es suficiente. Por otro lado, existe la hipótesis de la existencia una población residente en el PTO durante el año completo, llamado el “Galapagos biostock” (Berzin 1978) o ‘población tropical’ (Donovan 1984). La presencia de por lo menos 4 grupos acústicos de ballenas azules en el sitio de estudio del PTO (8°S, 95°W) descritos por Stafford et al. (1999b), es decir los cantos regionales del Océano Austral y del PSO principalmente, pero también del Pacífico Noroeste y Noreste, indica que varias poblaciones de ballenas azules podrían coincidir en esta región. Por último, los resultados de un estudio genético de ballenas azules en el golfo Corcovado por Torres-Florez et al. (2014a) apoya la hipótesis que las ballenas azules del ERC serian parte de una población más grande que se separaría en varias sub-poblaciones durante la época de alimentación del verano austral. Evidentemente, la estructura de la población de ballenas azules del PSO y PTO sigue siendo muy poco entendida.



Ubicación geográfica:	Distribución temporal:	Numero de grupos acústicos:	Uso principal de hábitat:	Factores ambientales determinantes hipotéticas:
✓ Islas Galapagos Palacios 1999	¿ Todo el año ? ✓ Invierno y primavera austral Palacios 1999	?	¿Reproducción? ✓ Alimentación	1) ¿ Condiciones temperatura y aguas calmas para tener crías ? 2) ¿ Ambiente acústico adecuado para contacto entre individuos?
✓ 8°S 95°W Stafford et al. 1999b ✓ 5-9°S 81°W Donovan 1984	✓ Todo el año ✓ Máxima en junio 8°S 95°W Stafford et al. 1999b; Buchan et al. 2014 ✓ Máxima en verano 5-9°S 81°W Donovan 1984	✓ 4 ¿5? Stafford et al. 1999b	¿Reproducción? ¿Alimentación?	3) ¿ Presencia de focos de productividad para alimentación oportunista? 4) ¿ Alta productividad primaria de la surgencia costera (Perú) para alimentación en verano?
✓ ≈ 29°S Aguayo-Lobo et al. 1998	¿ Todo el año ? ✓ Verano Perez, *com. pers.*	?	✓ Alimentación Perez, *pers. comm* ¿Apareamiento?	1) ¿ Alta productividad primaria de la surgencia costera (Chile) para alimentación en verano? 2) ¿ Ambiente acústico adecuado para contacto entre individuos?
✓Valdivia Hucke-Gaete *no publicado* ✓ERC Hucke-Gaete et al. 2003, 2010 Buchan et al. 2014	✓ Estacional Hucke-Gaete et al. 2003, 2010 ✓ Verano- otoño Buchan et al. 2014	✓ 1 ¿2? Cummings and Thompson 1971; Buchan et al. 2014	✓ Alimentación Hucke-Gaete et al. 2003 ¿Apareamiento?	1) ¿Alta productividad primaria del sistema mega-estuarino (Patagonia chilena) para alimentación en verano ? 2) ¿ Ambiente acústico adecuado para contacto entre individuos?

Avistamiento de ballenas azules

Posible ruta de migración

Limite conceptual oceánico/costero

Figura 5.1 Resumen del estado actual de conocimiento sobre la distribución estacional espacio-temporal de las ballenas azules del Pacífico Suroriental. Incluye también información sobre la cantidad de grupos acústicos en una región en particular, en donde las ballenas del PSO se consideran un solo grupo. Se presentan algunas hipótesis sobre el uso del hábitat y los factores ambientales determinantes de la distribución observada.

Distribución a escala intra-estacional y de área de alimentación

Para entender de mejor manera la distribución espacial intra-estacional de ballenas azules dentro de su área de alimentación de la ERC, es necesario referirse al marco teórico de Stern (2002), el cual categoriza los movimientos realizados por ballenas dentro de su rango de hogar. Este marco teórico fue utilizado por Hucke-Gaete (2004) para ilustrar las categorías de desplazamiento realizadas por ballenas azules dentro de la ecorregión Chiloense (Anexo 8.4).

He adaptado esta figura conceptual al contexto geográfico del PSO y del golfo Corcovado (Fig. 5.2), para ilustrar la jerarquía espacial de las *áreas*, *zonas* y *parches* de alimentación.

A partir de este marco teórico, se puede considerar que los sitios CS y CO son dos *parches* de alimentación, separados por aprox. 25 mn (≈46 km) de distancia, en una misma *zona*. La escala del *parche* se relacionaría a que las ballenas azules tienden a alimentarse en áreas chicas de ≈1 km^2 (Acevedo-Gutierrez et al. 2002); la escala de la *zona* de alimentación se relacionaría a que las ballenas azules pueden desplazarse ≈100km/día durante época de alimentación (Mate et al. 1999). Sin duda existen otras *zonas* de alimentación dentro de esta misma *área* de alimentación, como por ejemplo, la zona al norte de la Isla Guafo (Hucke-Gaete 2004; Hucke-Gaete et al. 2010). Además, los avistamientos de ballenas azules en la costa de Valdivia (Hucke-Gaete *no publicado*) y en Chañaral de Aceituno (Moraga *no publicado*) sustenta la presencia de otras áreas de alimentación, conteniendo cada una zonas y parches de alimentación.

En términos de las condiciones oceanográficas, Stern (2002) modificado por Hucke-Gaete (Anexo 8.4) plantea que los *parches* de alimentación adyacentes tendrían las mismas

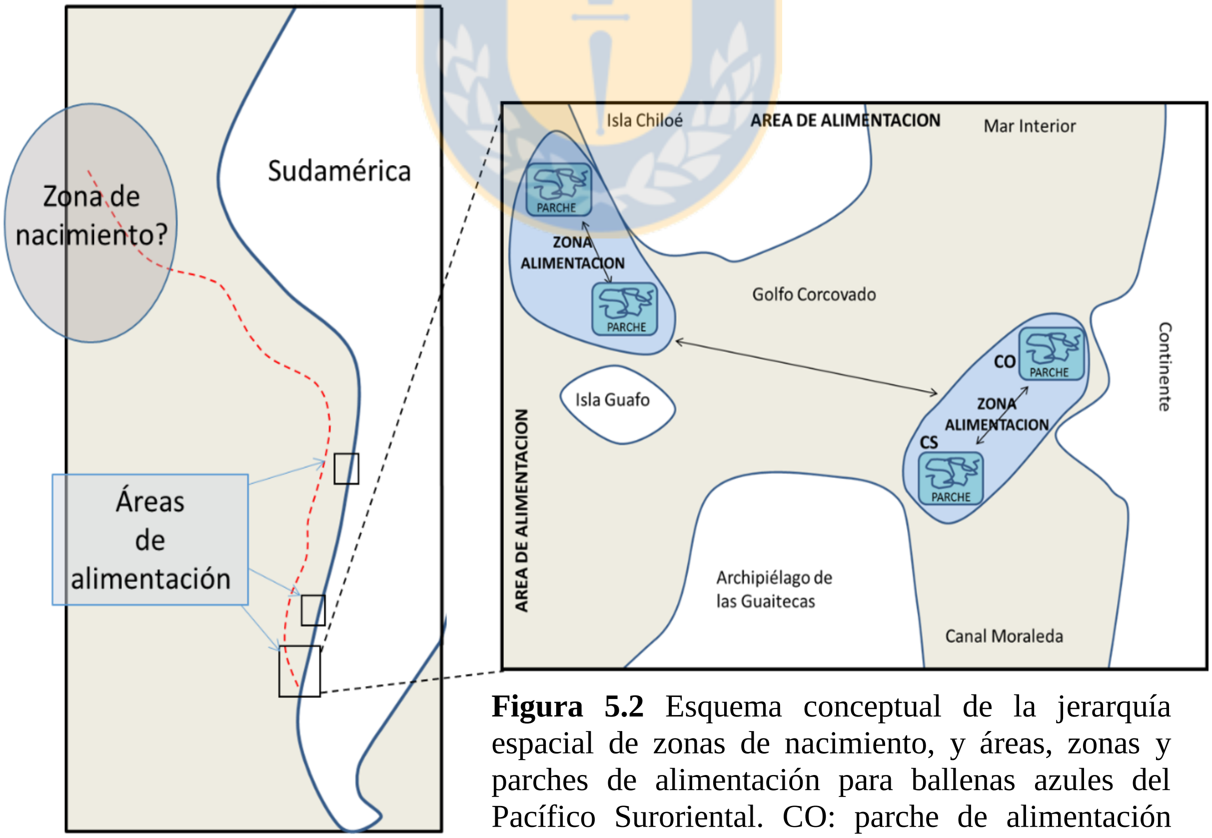


Figura 5.2 Esquema conceptual de la jerarquía espacial de zonas de nacimiento, y áreas, zonas y parches de alimentación para ballenas azules del Pacífico Suroriental. CO: parche de alimentación Corcovado Oriente; CS: parche de alimentación

condiciones oceanográficas, pero que las condiciones oceanográficas entre *zonas* de alimentación serían distintas. Es cierto que las condiciones oceanográficas entre las posibles zonas de alimentación en la costa de Valdivia o Chañaral de Aceituno (Sistema de Corriente Humboldt) difieren claramente de las de la ecorregión Chiloense (sistema mega-estuarino); y en relación al contexto oceanográfico del Pacífico Suroriental, las zonas de alimentación en la ERC son similares. En efecto, en la descripción de ecorregiones marinas, Spalding et al. (2007) especifica que los factores ambientales forzantes que definen las ecorregiones incluyen fenómenos tales como la surgencia costera, los suministros de nutrientes, el aporte de aguas continentales, y la topografía, entre otros. Sin embargo, los resultados del muestreo oceanográfico realizado en el presente estudio indican que existen también diferencias a pequeña escala entre las condiciones oceanográficas de parches (CS y CO), debido a la importante heterogeneidad ambiental de este sistema megaestuarino de fiordos y canales Patagónicos.

Se entiende que la distribución de ballenas azules a escala intra-estacional, dentro de sus áreas de alimentación, estaría ligada a la distribución espacio-temporal de parches de

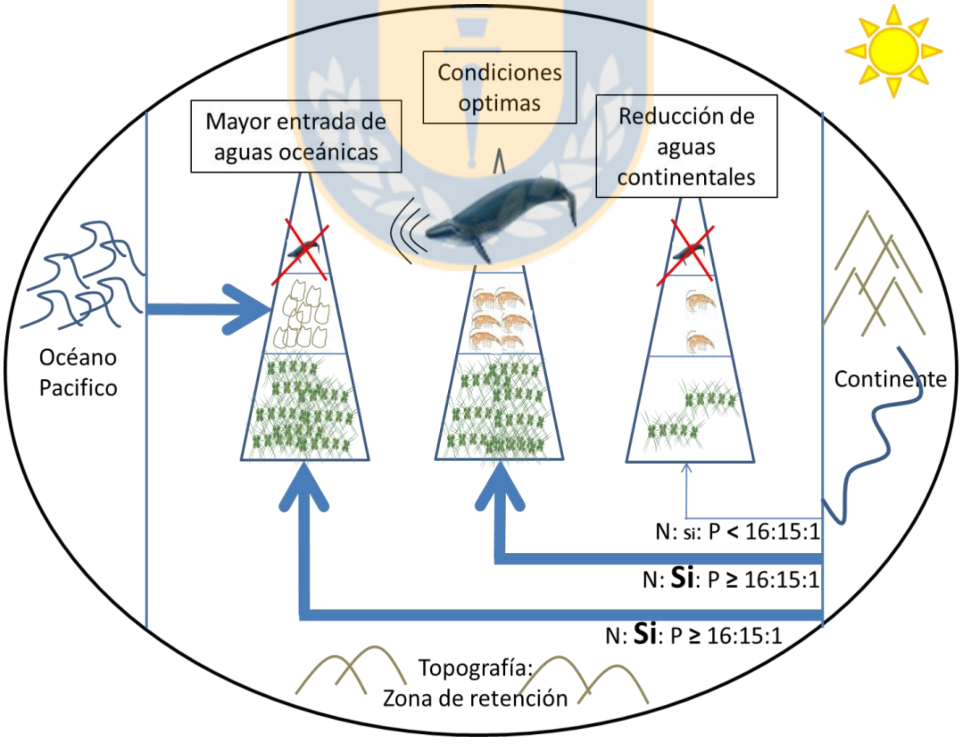


Figura 5.3 Esquema conceptual de configuraciones oceanográficas de condiciones óptimas y no favorables para el forrajeo de ballenas azules en el golfo Corcovado. Los grupos de organismos representados en las cadenas tróficas: las diatomeas, los eufáusidos o las salpas, y las ballenas azules.

alimentación (Croll et al. 1998, 2005). El análisis de las diferencias entre el CS y el CO nos ofrece algunas pistas sobre las condiciones oceanográficas que configuran los parches de alimentación dentro de la ECR. La Figura 5.3 resume tres ejemplos de configuraciones oceanográficas distintas que afectarían el forrajeo de ballenas azules, y propone que la presencia de parches dentro de la ECR estaría asociado principalmente a la topografía y zonas de retención de organismos planctónicos, y a los cambios en el suministro de aguas continentales (conteniendo SiO_4) e intrusión de aguas oceánicas. Cambios en la llegada de estas masas de agua distintas podrían explicar una variación temporal intra-estacional en la presencia de ballenas azules en un parche de alimentación. A futuro, será necesario obtener series de tiempo más extensas de presencia de ballenas azules (acústica o visual) y variables oceanográficas, para poner a prueba estas hipótesis.

6. CONCLUSIONES

1) La caracterización detallada de los cantos producidos (SEP1 y SEP2) por ballenas azules que se alimentan en el golfo Corcovado, Patagonia chilena (Capítulo 1; Buchan et al. 2014), detectó un nuevo canto para este grupo (SEP2). Esta caracterización permitirá monitorear la distribución espacio-temporal de este grupo de ballenas azules a futuro.
2) Se estableció un nexo acústico entre la Patagonia chilena y el Pacífico Oriental Tropical para los cantos regionales SEP1 y SEP2 (Capítulo 1; Buchan et al. 2014), así validando la **Hipótesis 1**.
3) La presencia estacional de cantos regionales de ballenas azules en la Patagonia chilena (más abundantes y fuertemente estacional con una máxima en marzo-mayo) y el Pacífico Oriental Tropical (menos abundantes, presencia durante todo el año con una máxima alrededor de junio), conduce a rechazar las **Hipótesis 2 y 3**. Estos resultados sugieren una migración entre la Patagonia chilena y el PTO (Capítulo 2; Buchan et al. *en prensa*), representando un avance en nuestro entendimiento sobre la distribución anual de las ballenas azules del Pacífico Suroriental.
4) Las diferencias interanuales en la presencia de cantos de ballenas azules en un registro acústico de 7 años en el Pacífico Oriental Tropical, estaría posiblemente vinculado a fenómenos oceanográficos tales como El Niño (Capítulo 2; Buchan et al. *en prensa*);
5) En términos de la ecología de forrajeo de ballenas azules, hubo un desfase temporal de aproximadamente 10 días entre un máximo intra-estacional de clorofila-a y avistamientos de ballenas azules alimentándose en el sector suroriente del golfo Corcovado; en consecuencia se rechaza la **Hipótesis 5**.
6) La disminución interanual en avistamientos durante el verano 2012 (vs. 2011 y 2013) coincide con salinidades más elevadas, una baja dramática en concentraciones de silicato por debajo de la razón Redfield, una baja en clorofila a (*in situ* y satelital) y fluorescencia (satelital), densidades más bajas de *E. vallentini*, una ausencia de estadios juveniles de eufáusidos y la dominancia de salpas en el mesozooplancton. Esto valida la **Hipótesis 4** y sugiere que una disminución en el ingreso de aguas continentales y/o un aumento en aguas oceánicas en la zona de estudio podrían haber tenido un efecto negativo sobre la producción

primaria y la producción segundaria de eufáusidos, así reduciendo la presencia de ballenas azules en sector suroriente del golfo Corcovado;

7) El sitio Corcovado Sur presentó concentraciones de clorofila-a, densidades de eufáusidos y avistamientos de ballenas azules más altos en comparación con el sitio Corcovado Oriente, lo cual podría estar asociado a la topografía de las islas y al cañón submarino del Archipiélago de los Chonos, los cuales generarían una zona de retención de eufáusidos.
8) La intrusión de aguas oceánicas y el ingreso de aguas continentales en la zona costera son procesos importantes que influencian la productividad primaria y, por consiguiente, contribuyen a generar las condiciones adecuadas para la existencia de una abundancia suficiente de eufáusidos para el forrajeo de ballenas azules del Pacífico Suroriental en el sistema megaestuarino de la Patagonia chilena.
9) Esta tesis ha demostrado que la aplicación del Monitoreo Acústico Pasivo acoplado con la oceanografía *in situ* e satelital es factible, relevante y debería ser una prioridad en materia de investigación en la Patagonia chilena para entender los cambios intra-estacionales e inter-anuales en la distribución de ballenas azules y su asociación con las condiciones oceanográficas.
10) Este trabajo completa algunos vacíos de conocimiento relevante para generar e implementar estrategias integrales de manejo y conservación para las amenazadas ballenas azules en la Patagonia chilena y su hábitat de alimentación.

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8. ANEXOS

Anexo 8.1 Promedios diarios de TSM, Cl-a y nFLH satelital verano 2012.

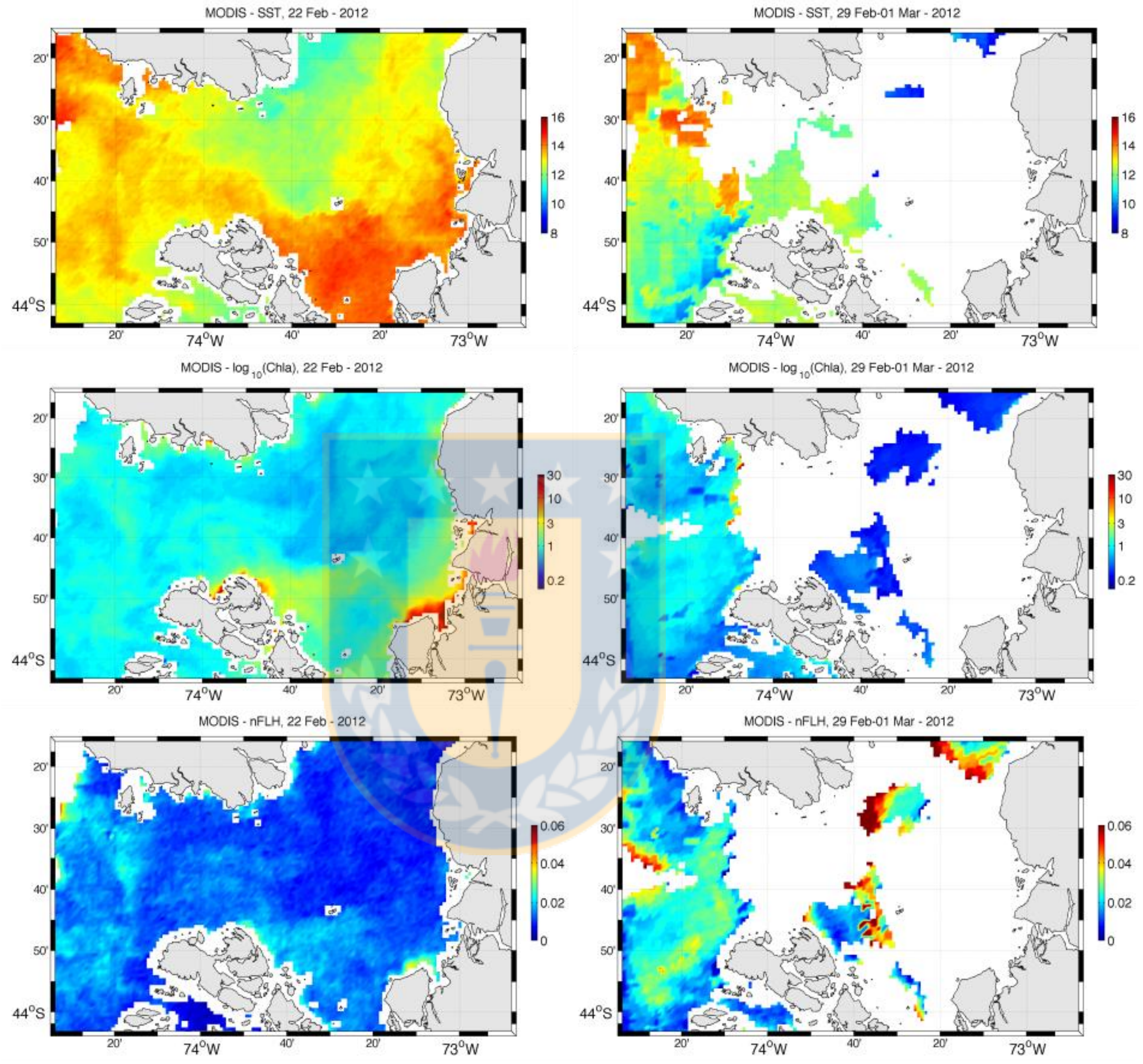


Figura 8.1a Imágenes satelitales de TSM, Cl-a y nFLH el 22 febrero 2012 (izquierda) y el 29 febereo-01 marzo 2012 (derecha). Ballenas azules fueron avistados el 20 y 29 de febrero en el sitio Corcovado Sur.

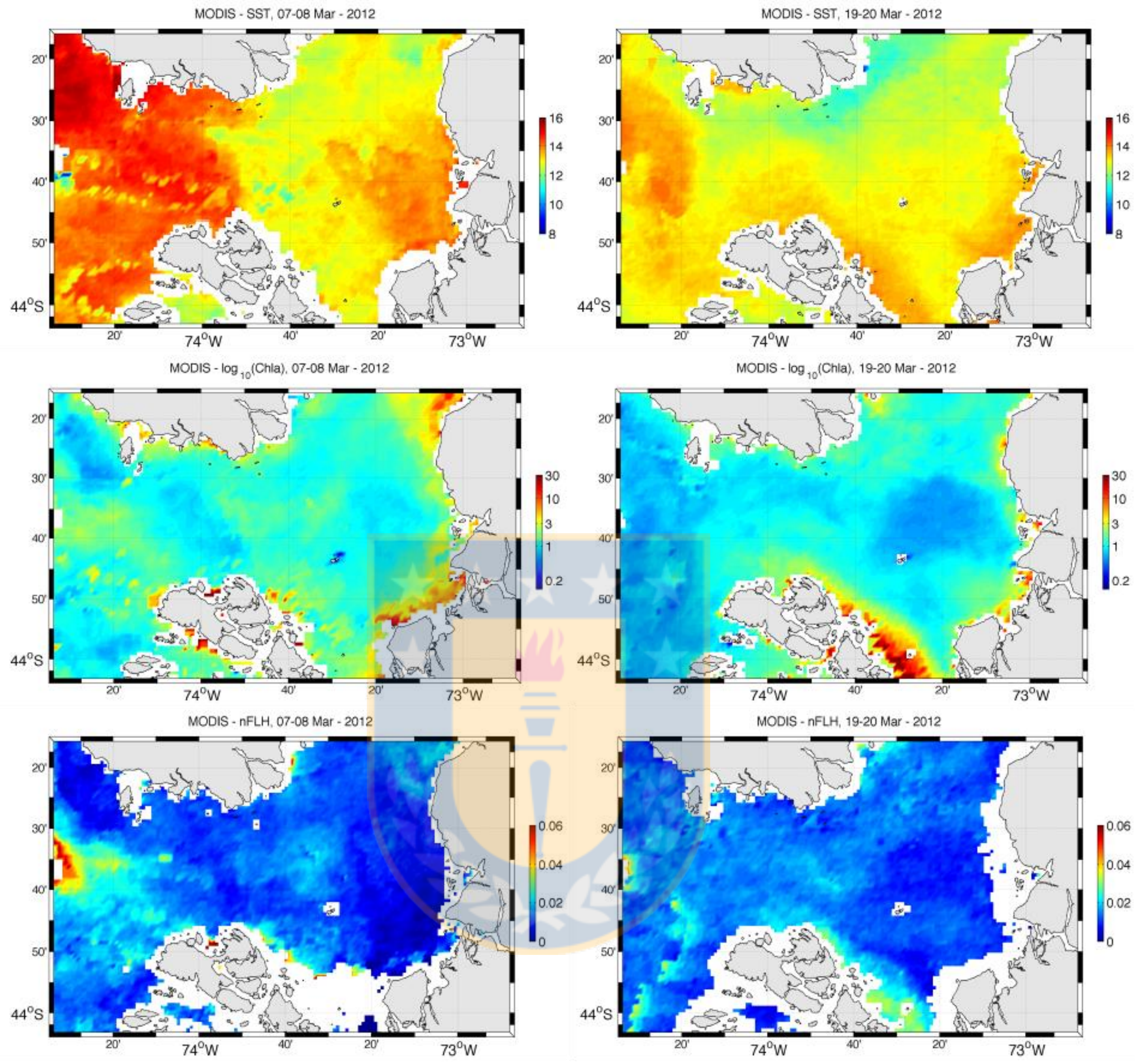


Figura 8.1b Imágenes satelitales de TSM, Cl-a y nFLH el 7-8 marzo 2012 (izquierda) y el 19-20 marzo 2012 (derecha). Ballenas azules fueron avistados el 17 y 19 marzo en el sitio Corcovado Oriente.

Anexo 8.2 Promedios diarios de TSM, Cl-a y nFLH satelital invierno 2012.

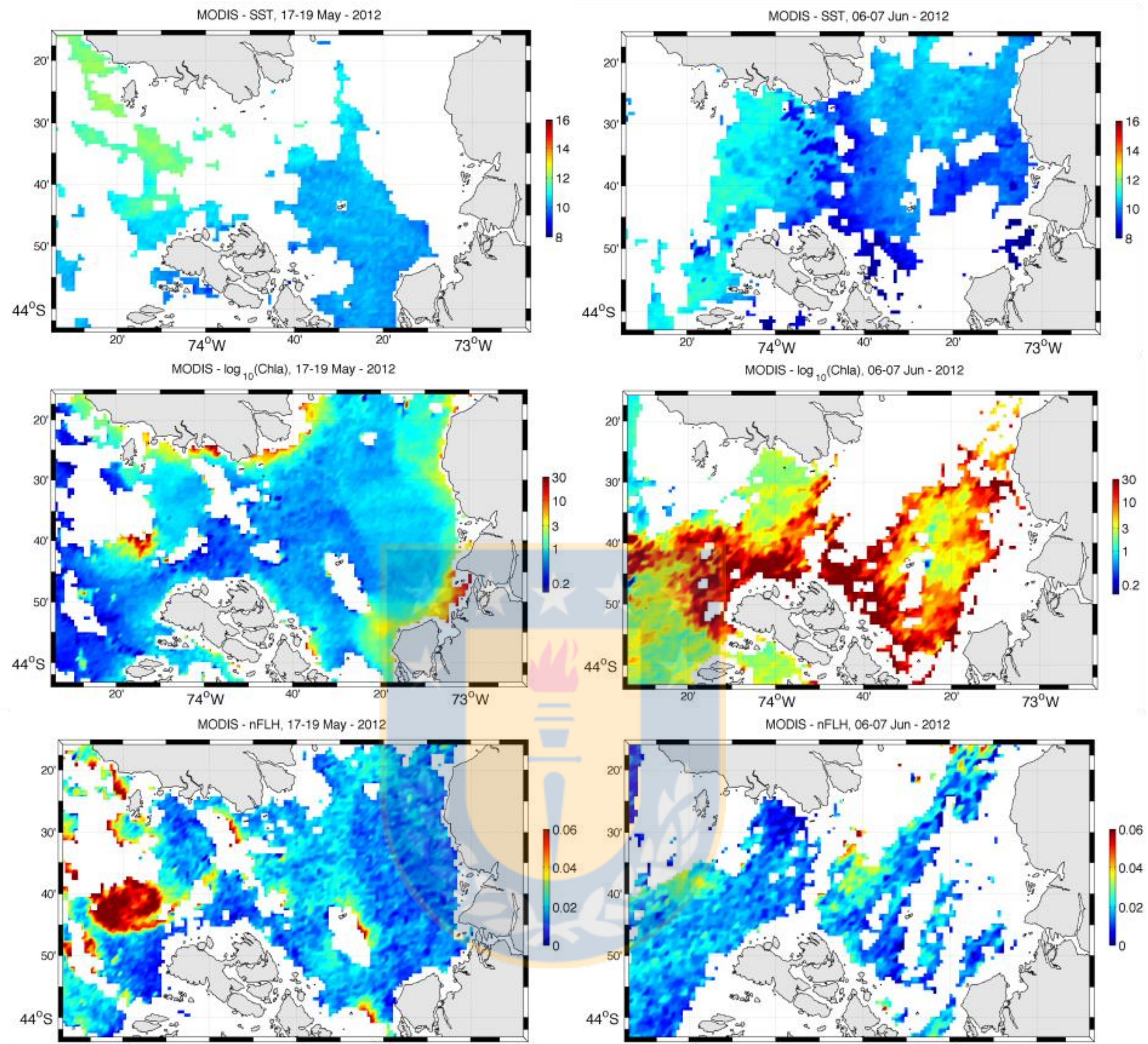
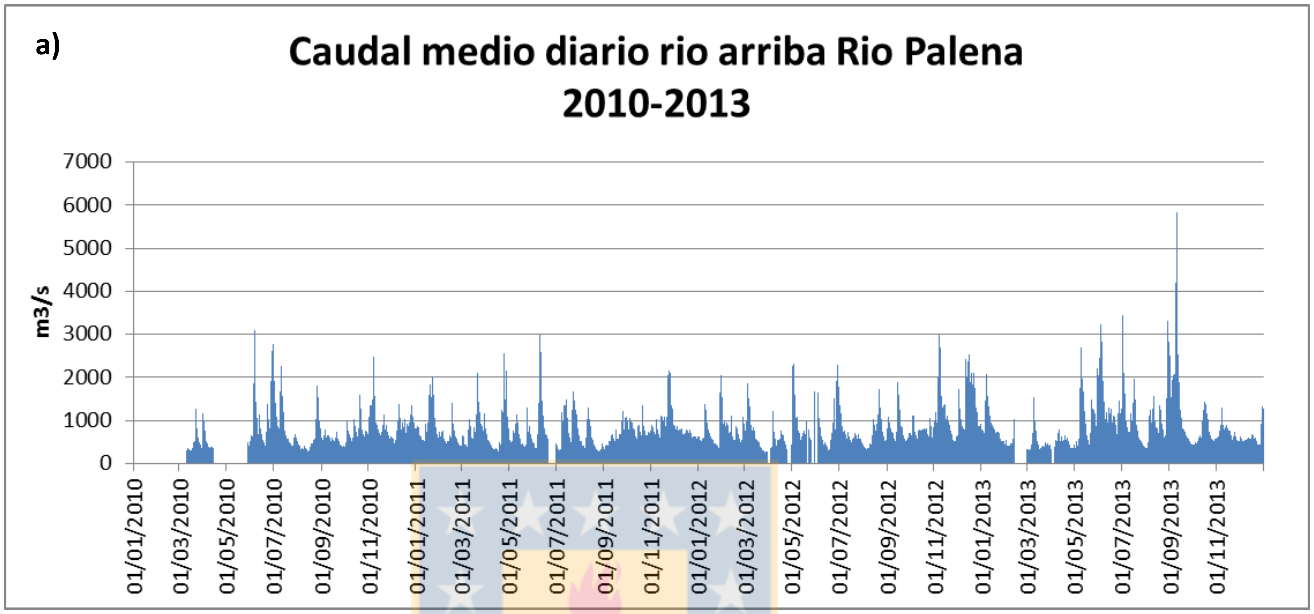
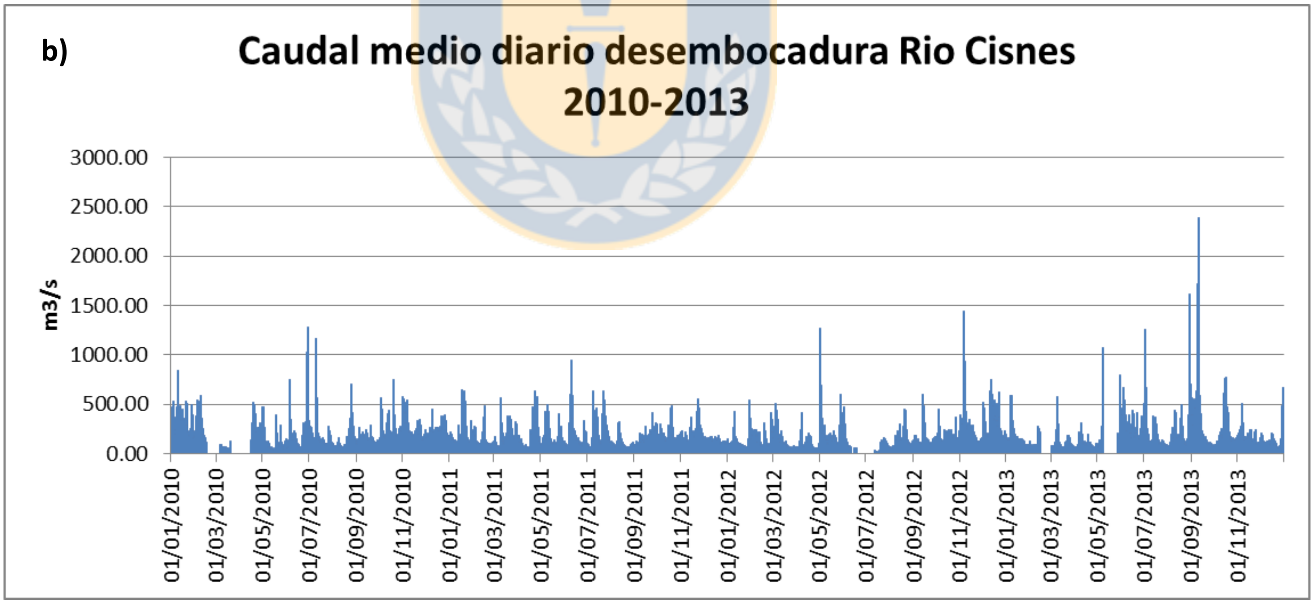
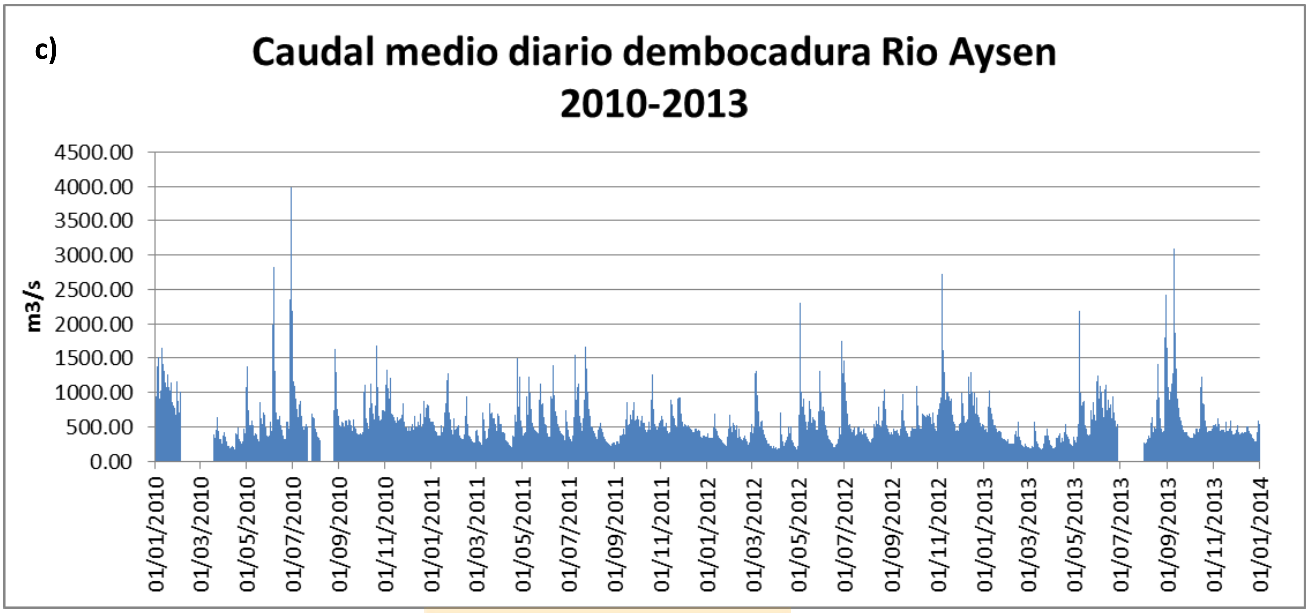


Figura 8.2 Imágenes satelitales de TSM, Cl-a, nFLH el 17-19 mayo 2012 (izquierda) y 6-7 junio 2012 (derecha). Ballenas azules fueron avistadas el 7 junio 2012 en el Corcovado Oriente.

Anexo 8.3. Caudales medios diarios de (a) río Palena (S43° 49' 08", W72° 23' 00"), (b) desembocadura río Cisnes (S44° 45' 00", W72° 43' 00") y (c) desembocadura río Aysén (S45° 24' 21",W72° 37' 23"); datos obtenidos de la Dirección General de Aguas (www.dga.cl)






c)
Caudal medio diario dembocadura Rio Aysen
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Anexo 8.4. Esquema de los tres tipos de desplazamiento de ballenas azules dentro de su rango de hogar. Extraído de Hucke-Gaete (2004) quien modificó la figura de Stern (2002).