

First insights into the oceanographic characteristics of a blue whale feeding ground in northern Patagonia, Chile

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ABSTRACT: Blue whales *Balaenoptera musculus* select highly productive feeding habitats where dense and abundant euphausiid aggregations dependably arise. This study seeks to understand the oceanographic characteristics that provide suitable foraging conditions for endangered blue whales in northern Chilean Patagonia (NCP). We present the first *in situ* oceanographic data (temperature, salinity and oxygen profiles, nutrients and chl *a*, mesozooplankton abundance, euphausiid species and size structure) associated with sightings of foraging blue whales collected during 3 austral summer campaigns and 1 winter campaign (2011 to 2013) at 2 feeding sites in the southeast Corcovado Gulf (~43° 53' S, 73° 19' W). Satellite data (MODIS) were also examined. 92% of all animals (n = 51) displayed foraging behavior, and sighting rates were higher in summer. The mesozooplankton was dominated by the euphausiid *Euphausia vallentini*. During summer 2012, significantly lower whale sightings coincided with significantly lower euphausiid abundance, chl *a* and silicate and observations of large localized salp blooms, compared to summer 2013. These conditions could be explained by changes in the inflow of oceanic and continental waters into the Corcovado Gulf leading up to summer 2012. A generalized linear model revealed that sightings of foraging blue whales during summer 2013 were significantly associated with a drop in chl *a*, most likely reflecting a synoptic succession pattern (days to weeks) of phytoplankton blooms–euphausiid aggregation–arrival of blue whales at a feeding site. Spatial variation suggests the important role of bathymetry in concentrating planktonic organisms. These findings are the first insights into the oceanographic factors that influence feeding conditions for endangered blue whales in Patagonia.

KEY WORDS: Foraging ecology · Blue whale · Euphausiid · Biological oceanography · Patagonia

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INTRODUCTION

Identifying the oceanographic processes that lead to prey availability is fundamental for understanding the ecology of marine predators and developing conservation strategies for critical feeding ground habitats. Blue whales are the largest animals on earth (Yochem & Leatherwood 1985) and are stenophagous feeders, preying exclusively on euphausiids (Nemoto 1970). In order to meet their energetic

demands, blue whales require 1120 ± 359 kg euphausiids $\text{ind.}^{-1} \text{d}^{-1}$ (Goldbogen et al. 2011) and foraging success relies not only on the abundance, but also on the density, of euphausiid aggregations (Goldbogen et al. 2011). Individuals concentrate foraging within relatively small areas, generally under 1 km^2 (Acevedo-Gutierrez et al. 2002). Blue whales worldwide select feeding habitats where high densities of euphausiids dependably arise (Croll et al. 1998, Branch et al. 2007), largely during the summer

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in seasonally productive mid- and high-latitude feeding grounds: the Indian Ocean (Samaran et al. 2010, Stafford et al. 2011, de Vos et al. 2014), the Southern Ocean (Mackintosh & Wheeler 1929), waters off Australia (Gill 2002, Gill et al. 2011), the Pacific coast of North America (e.g. Fiedler et al. 1998, Forney & Barlow 1998, Croll et al. 2005, Calambokidis et al. 2007), the St. Lawrence Estuary (Sears et al. 1990, Kingsley & Reeves 1998, Doniol-Valcroze et al. 2012) and northern Chilean Patagonia (NCP) off the southwest tip of South America (e.g. Hucke-Gaete et al. 2004).

The subantarctic feeding ground in NCP, also known as the Chiloense Ecoregion (41° 30'–47° 00' S) (Spalding et al. 2007), includes the Corcovado Gulf and the Pacific coast of Chiloé Island (Hucke-Gaete et al. 2004), the northwest of Chiloé Island (Cabrera et al. 2005, Galletti-Vernazzani et al. 2012) and the Inner Sea of Chiloé Island (Zamorano-Abramson & Gibbons 2010). An estimated 222 animals (CI 95% = 115–430) use the NCP feeding ground, based on surveys during February and March 2009 (Hucke-Gaete et al. 2010). Additionally, 303 animals (CI 95% = 176–625) have been estimated between north (18° S) and central Chile (38° S) (Williams et al. 2011). Both areas are most likely predominantly used by the southeast Pacific blue whale population numbering in the low thousands (Reilly et al. 2008). Buchan et al. (2015) found a seasonal peak in SEP blue whale songs in NCP between March and May, at the end of the austral summer.

NCP lies within the West Wind Drift Convergence zone. The bifurcation of the West Wind Drift reaches the Chilean coast between 40° and 45° S and then divides into the poleward Cape Horn Current and the equatorward Chile-Peru Current, part of the Humboldt Current System (Strub et al. 1998, Niklitschek et al. 2014). In NCP, the underlying oceanographic processes that explain the dependable occurrence of dense euphausiid aggregations and blue whale foraging success remain unknown. Chilean Patagonia is one of the largest estuarine systems in the world (Palma & Silva 2004), containing the topographically complex Patagonian Archipelago, an extensive network of islands, channels and fjords. This system receives oceanic water inputs from the Pacific Ocean and freshwater from mainland Chile (Silva & Guzmán 2006, Sievers & Silva 2008). This area has the highest levels of remote-sensed chlorophyll *a* (chl *a*) of the entire Chilean Patagonia region (>10 mg chl *a* m⁻³) (Montecino & Pizarro 2006), with spring/summer diatom blooms and the dominance of euphausiids (*Euphausia vallentini*) over the mesozooplankton community (González et al. 2010). Al-

though blue whale feeding behavior has been documented in NCP (Hucke-Gaete et al. 2004), no studies to date have examined the *in situ* oceanographic characteristics and mesozooplankton assemblage associated with foraging events. Harsh weather conditions and poor accessibility make *in situ* studies difficult in this remote area.

The Corcovado Gulf (~43° 37' S, 73° 26' W; see Fig. 1) is a large body of water within the Patagonian Archipelago of NCP, open to the Pacific Ocean and receiving winds predominantly from the west. The southeast Corcovado Gulf, located between the Guaitecas Archipelago and the mainland, is an area preferred by blue whales, based on satellite-tracking data and visual sightings (Hucke-Gaete 2004, Hucke-Gaete et al. 2010). This area has certain logistical advantages, such as proximity to the small port towns of Melinka (Guaitecas Archipelago) and Raul Marin Balmaceda (mainland Chile).

In this study, we seek to achieve an understanding of the oceanographic characteristics that provide suitable foraging conditions for endangered blue whales in the southeast Corcovado Gulf. Based on *in situ* and remote-sensed environmental data associated with sightings of foraging blue whales at 2 study sites over 4 sampling campaigns (2011–2013), we aim to (1) confirm blue whale feeding sites; (2) characterize the general environmental conditions (oceanographic variables, mesozooplankton assemblage, euphausiid species) at feeding sites; (3) examine the temporal and spatial variation in sighting rates of foraging blue whales and environmental conditions (within and between campaigns; between sites); and (4) determine the oceanographic variables associated with the sighting of foraging blue whales.

MATERIALS AND METHODS

Study area and sampling approach

Two study sites (<50 km²), which we operationally call 'feeding sites', were selected in the southeast Corcovado Gulf (Fig. 1): (1) the south Corcovado (SC) feeding site, located between the Guaitecas Archipelago and the entrance to the Moraleda Channel (~S 43° 50'–43° 59'; W 73° 36'–73° 29'), closer to the Pacific Ocean; and (2) the eastern Corcovado (EC), closer to the Chilean mainland, including Raul Marin Bay, which receives direct discharge from the Palena River, and Tic Toc Bay just north of Raul Marin Bay (~S 43° 42'–43° 49'; W 73° 09'–73° 03'). Each study site was divided up into 12 fixed stations, approximately

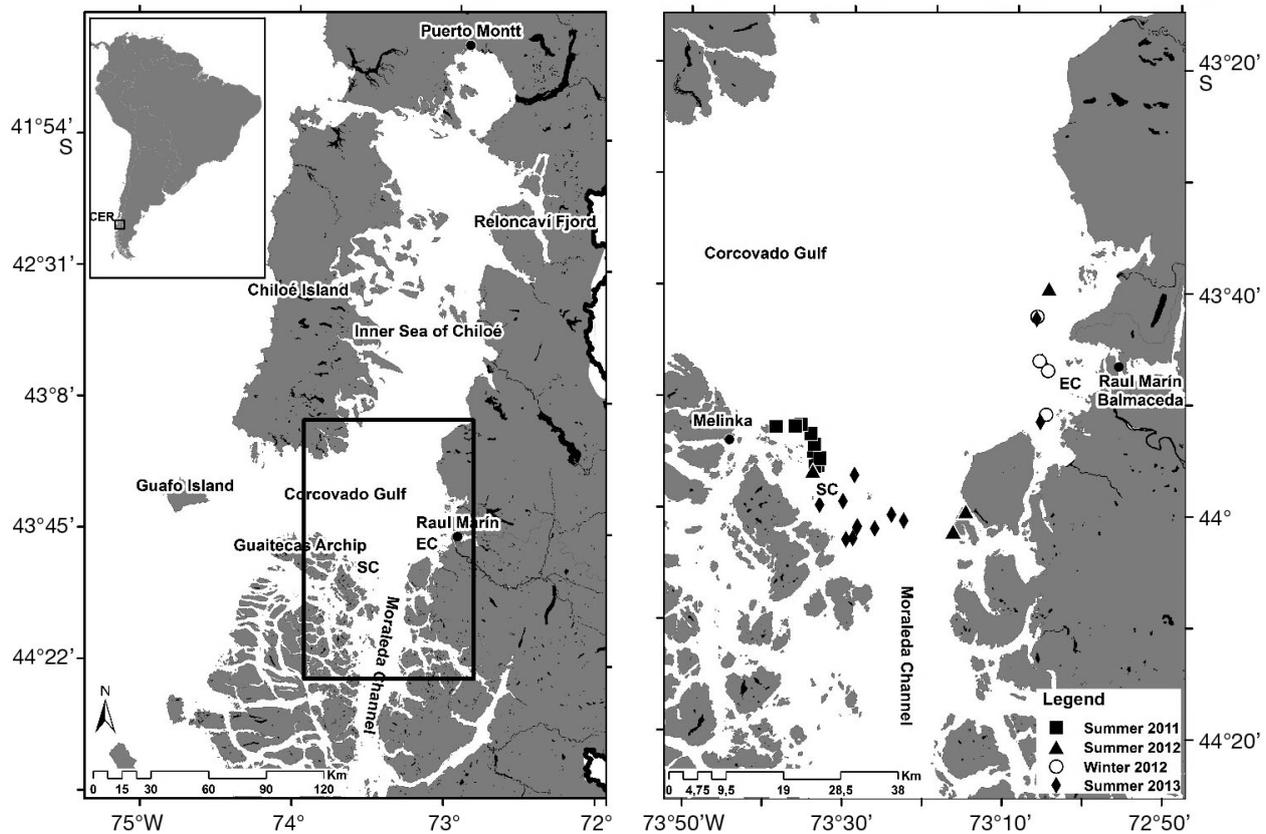


Fig. 1. Study area in the southeast Corcovado Gulf with sightings of foraging blue whales *Balaenoptera musculus* per sampling campaign (summer 2011, summer 2012, winter 2012, summer 2013). SC: southern Corcovado Gulf feeding site. EC: eastern Corcovado Gulf feeding site. CER: Chiloense Ecoregion. Note: SC and EC contained 12 fixed sampling stations each, which are not shown here

2–4 km apart (not shown in Fig. 1). Total water column depths at sampling stations ranged between 70 and 230 m.

Boat-based blue whale sighting data were collected at study sites during the summers of 2011 (February), 2012 (February–April), and 2013 (February–March); and winter 2012 (May–June). *In situ* oceanographic data (temperature, salinity, oxygen, nutrients, chl *a*, mesozooplankton) were collected during the summers in 2012, 2013 and winter 2012, associated with sightings of blue whale foraging behavior at the SC and the EC study sites. No *in situ* oceanographic data were collected during 2011, which was largely an exploratory campaign. When foraging blue whales were sighted, focal individuals were followed and *in situ* oceanographic sampling was carried out every time and at the exact location where foraging behavior was observed. Thus, for one sighting, several oceanographic data points were obtained during the focal follow. When blue whales were absent, oceanographic sampling was carried out at the fixed sampling stations at SC and EC. Sighting and *in 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 sampling equipment was manually deployed, providing that the weather conditions were suitable for the safe deployment of instruments. In addition to *in situ* measurements, remote-sensed oceanographic data (sea surface temperature, chl *a*, fluorescence) were obtained for the entire study period (2011 to 2013) (see 'Materials and methods: Oceanographic data').

Blue whale sighting data

Observation effort was carried out continuously at sea by an experienced observer who recorded the following: date, time, GPS position, species, number of calves and behavior of each blue whale sighting. Behavior was classified 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 with a circular movement track). Photographic evidence was also taken of foraging behavior. Lunges and deep dives can be considered indicative of foraging behavior in blue whales, either feeding on subsurface or deep aggregations of euphausiids (Fiedler et al. 1998, Goldbogen et al. 2011, 2013), or possibly searching for euphausiid aggregations at depth. Sighting rates of foraging blue whales (excluding whales in transit or with unidentified behavior) were calculated as the number of foraging individuals sighted divided by the number of days of observation effort.

Oceanographic data

Vertical profiles for salinity, temperature (0.000°C) and oxygen (mg l^{-1}) down to 200 m were taken at sampling stations measured with a CTD-O (SAIV A/S, model SD204). In addition, sea surface temperature (SST; 0.000°C) and surface salinity readings were taken at 2 m depth with a multiparameter probe (YSI 650 MDS). The CTD-O was calibrated before and after the field season; no drift in calibration was detected. However, on 11 February 2013, the CTD-O was irreparably damaged due to bad weather conditions and no data were available after this date. The CTD-O data were cleaned and processed by removing values with a negative sigma-t value and the 'upcast' data. Vertical profiles with vertically smoothed data (1 m resolution) and temperature–salinity (T–S) diagrams were plotted. For the T–S diagrams, salinity criteria were taken from Sievers & Silva (2008) and Pérez-Santos et al. (2014): estuarine freshwater (EFW) = 11–21; estuarine saline water (ESW) = 21–31; modified subantarctic water (MSAAW) = 31–33; subantarctic water (SAAW) > 33.

Seawater samples for nutrient analysis were collected at 2 m using a Niskin bottle. 100 ml of seawater from each sample was then filtered through a Millipore glass fiber filter of 25 mm diameter and 0.7 μm pore size to eliminate particulate material, and the filtrate was frozen until laboratory analysis. Concentrations of nitrate (NO_3^-), nitrite (NO_2^-), silicate (SiO_4^{4-}) and phosphate (PO_4^{3-}) to 0.00 μM were determined at the Laboratory of Geochemistry of the University of Concepción using standard techniques (Hansen & Koroleff 2007). The $\text{SiO}_4^{4-}:\text{NO}_3^-$ ratio was determined for comparison with the Redfield ratio of Si:N:P = 15:16:1 (Redfield et al. 1963).

Seawater samples for determining chl *a* concentrations were collected at 2 m depth using a Niskin bottle. 500 ml of seawater were filtered through a GF

Millipore filter (47 mm diameter; 0.7 μm nominal pore size) that was then wrapped in aluminum foil and frozen until laboratory analysis. The chl *a* concentration to 0.00 mg chl a m^{-3} of each water sample was determined in accordance with Holm-Hansen et al. (1965).

Mesozooplankton samples were collected with oblique tows down to 100 m depth, or at 15 m from the maximum depth in shallower areas, with a bongo net (250 μm mesh net; 0.71 m mouth diameter) during approximately 20 min at 2 knots (start and end time taken when mouth of net entered and exited the water). A General Oceanics flowmeter (model 2030R) was used to estimate the volume of water filtered. Sampling was conducted during daylight hours to coincide with blue whale visual surveys. Samples were stored in 500 ml plastic containers and fixed with 5% formaldehyde until laboratory analysis. In the laboratory, all organisms were counted and identified to order level; the most abundant orders were reported. Euphausiid counts were subdivided by life stage: adults and juveniles (i.e. calyptopis and furcilia). Adults were identified to species level. For juveniles, species-level identification was not possible. The abundance of mesozooplankton groups were calculated as ind. 1000 m^{-3} filtered water. The size structure of euphausiids was determined by measuring the body length (tip of rostrum to tip of telson) to 0.000 mm, in accordance with Melo & Antezana (1980). When samples contained over 100 individuals, a random sub-sample of 100 ind. was taken for size structure analysis, using a Folsom splitter and counting chamber.

Monthly and daily (or several days depending on data availability) average satellite images for SST, normalized fluorescence line height (nFLH) and chl *a* were obtained with a resolution of 1 km from the moderate resolution imaging spectroradiometer (MODIS) database (<http://modis.gsfc.nasa.gov/data>) for the area between 43° 15'–44° 04' S and 74° 39'–72° 47' W. Ocean color remote sensing data from MODIS 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 S 43° 15' to S 44° 04' and W 74° 39' to W 72° 47') were processed for chl *a* and nFLH outputs. The near-infrared and shortwave infrared combined atmospheric correction algorithm (NIR-SWIR) 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 pro-

jected outputs at 1 km resolution. Synoptic average (1–3 d, depending on cloud cover) composites were processed, coinciding with *in situ* sampling days. Monthly average composites were computed for January–March 2011, 2012, 2013 and May–June 2012, coinciding with *in situ* sampling campaigns.

Statistical analyses

We performed statistical analyses on data from summer 2012 and summer 2013 because the summer season is when most foraging activity occurs, and these were the only 2 summers with complete sighting and environmental data that allowed for robust comparison. We excluded winter 2012, because we had no other winter season to compare it with.

To examine inter-annual differences, the non-parametric exact Wilcoxon signed-rank test (Gibbons & Chakraborti 2003, Hollander et al. 2014) was conducted under the null hypothesis that there was no difference in sighting rates (ind. per day effort) and selected oceanographic variables (euphausiid and salp abundance; chl *a*, NO₃, PO₄, SiO₄ concentrations; SiO₄:NO₃ ratio; temperature and salinity) between the summers 2012 and 2013. Salps and euphausiids were the 2 mesozooplankton groups included in this analysis given their dominance over the community during summers 2012 and 2013, respectively. To examine inter-site differences, the null hypothesis was that there was no difference in sighting rates (ind. per day effort) and oceanographic variables between sites was tested. The Wilcoxon's *W* statistic was calculated using R (v.3.0.2 R Development Core Team 2005,) and the package 'exactRank-Tests' (Hothorn & Hornik, 2015).

To verify possible associations between sightings of foraging blue whales and environmental variables on a synoptic scale, we carried out generalized linear model (GLM) analyses (Zuur et al. 2009, Hilbe 2014). Due to the unbalanced structure of the database, which means there was not always a corresponding sample of zooplankton data for every single record of physical-chemical variables, 2 sets of GLMs were done for physical-chemical variables and zooplankton separately. The first set of GLMs included the physical-chemical variables: chl *a*, NO₃⁻, NO₂⁻, PO₄³⁻, SiO₄⁴⁻ concentrations; SiO₄⁴⁻:NO₃⁻ ratio; temperature and salinity for summer 2012 (58 observations), summer 2013 (81 observations) separately, and summers 2012 and 2013 combined (139 observations). Chl *a* concentration data and SiO₄⁴⁻:NO₃⁻ ratio were considered as factors with 2 levels each:

0–1 and >1 mg chl *a* m⁻³, and 0–0.6 and >0.6 μM SiO₄⁴⁻:NO₃⁻ ratio. In the second set of GLMs, due to the relatively low number of observations, only euphausiids (*Euphausia vallentini* adults and juvenile euphausiids) were included in the model as factors, with 2 levels: 0 to <0.2 and >0.2 ind. 1000 m⁻³. Summer 2012 (30 observations), summer 2013 (67 observations) and the summers of 2012 and 2013 combined (97 observations) were analysed independently. For all GLMs, whale presence (1) or absence (0) was the response variable following a binomial distribution (Bernoulli) (Zuur et al. 2009).

A Mann-Kendall non-parametric test (Hipel & McLeod, 1994) was used for trend detection on river discharge time series data (2010 to 2013) obtained from the General Water Administration (www.dga.cl) and passed through a Lowess filter, to test whether any significant changes in fresh water inputs had taken place during the study period. Unfortunately, data for the Palena River near our study site was too incomplete to serve for this analysis. Therefore, we used data for the nearest river with sufficient data for analysis, which was the Aysén River, located further south of the study area (45° 24' S, 72° 43' W).

RESULTS

Thirty-five sightings of a total of 51 blue whale individuals were recorded (Table 1) on 17 separate days out of a total of 45 boat days. The majority of blue whales (92%; 47 ind.) displayed foraging behavior, i.e. lunge feeding (Fig. 2a) or diving (Fig. 2b). Associated *in situ* mesozooplankton and oceanographic data were collected for almost all foraging events during 2012 and 2013, except when highly adverse weather conditions prevented sampling. Blue whales sightings were not evenly spread throughout the study period; numerous sightings tended to occur within the space of 1 to 3 consecutive days at a given site (Table 1). Between sites across all sampling seasons, sighting rates of foraging individuals (Table 2) were higher at SC (1.42 ind. d⁻¹) compared with EC (0.53 ind. d⁻¹), and statistically significant ($p < 0.05$). Between seasons at both sites, sighting rates showed that foraging blue whales were mostly sighted during summer 2011 (4.80 ind. d⁻¹), followed by summer 2013 (0.78 ind. d⁻¹), summer 2012 (0.46 ind. d⁻¹) and finally winter 2012 (0.33 ind. d⁻¹). The Wilcoxon signed rank test revealed significant differences between summer 2012 and summer 2013 in sighting rates ($p < 0.05$), as well as almost all of the environmental variables, as summarized in Table 3.

Table 1. Blue whale *Balaenoptera musculus* sighting data 2011–2013, showing date, time, location, number of individuals, behavior, and availability of associated *in situ* oceanographic data. SC: south Corcovado feeding site; EC: eastern Corcovado feeding site

Sighting no.	Date	Time	Study site	No. of individuals (no. of calves)	Behavior	<i>In situ</i> 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	Yes
22	07.06.2012	15:15	SC	1 (0)	Transit	Yes
23	09.02.2013	13:05	SC	1 (0)	Deep dives	Yes
24	16.02.2013	9:11	SC	1 (0)	Lunges	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,	Yes
30	18.02.2013	10:26	SC	1 (0)	Lunges	Yes
31	18.02.2013	10:58	SC	1 (0)	Deep dives	Yes
32	18.02.2013	13:16	SC	1 (0)	Deep dives	Yes
33	18.02.2013	14:18	SC	1 (0)	Lunges	Yes
34	21.02.2013	10:29	SC	1 (0)	Lunges	Yes
35	14.03.2013	11:15	SC	1 (0)	Deep dives	Yes

The mesozooplankton assemblage—averaged across all sites and seasons ($n = 113$; Fig. 3a)—was dominated by euphausiids, with 41 % of total numerical abundance; salps (28%), siphonophores (19%) and amphipods (5%) were also present. Ctenophores, mysids, megalopa, isopods, chaetognaths, cnidarians, sygnathidea and fish larvae made up the remaining 7% of the mesozooplankton. Euphausiids (92%) and amphipods (84%) were present in most samples; siphonophores in 55% of samples, salps in 40% (data not shown). Abundances of all groups

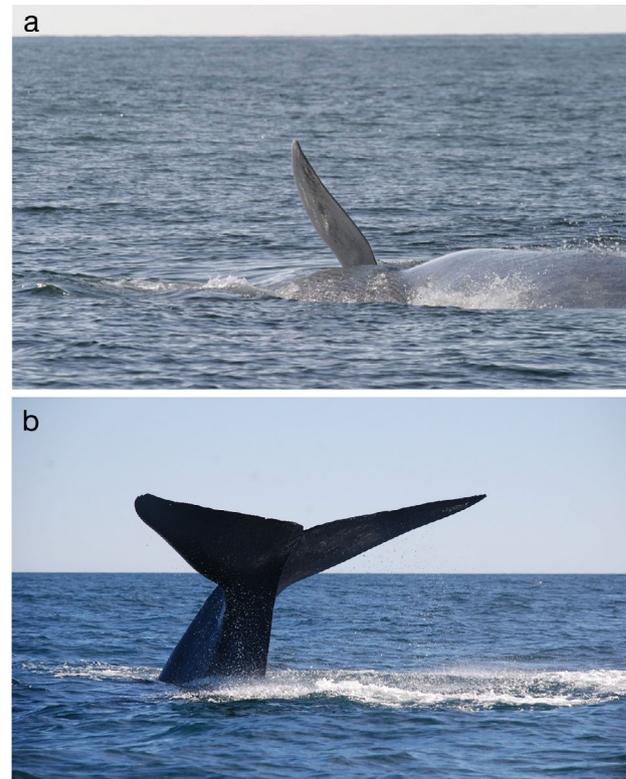


Fig. 2. Photographic evidence of blue whale foraging behavior at the southern Corcovado feeding site: (a) a lateral lunge revealing pectoral fin and ventral grooves (summer 2011); (b) a deep dive showing tail fluke (summer 2013)

Table 2. Sighting rates (ind. per day effort) and effort (no. of days) of foraging blue whales at southern Corcovado (SC), eastern Corcovado (EC) and both sites combined during summer 2011, summer 2012, winter 2012, and summer 2013

Season	SC		EC		Both sites	
	Rate	Effort	Rate	Effort	Rate	Effort
Summer 2011	4.80	5	0.00	0	4.80	5
Summer 2012	0.20	5	0.63	8	0.46	13
Winter 2012	0.00	4	0.60	5	0.33	9
Summer 2013	1.00	12	0.33	6	0.78	18
All seasons	1.42	26	0.53	19	1.13	45

were higher in summer compared with winter (Fig. 4b–e). Community composition between 2012 and 2013 was dramatically different, with salps dominating in 2012 and euphausiids in 2013 (Figs. 3b,d). Wilcoxon tests revealed significant differences between summers 2012 and 2013 for euphausiid ($p < 0.001$) but not for salp ($p > 0.05$) abundance (Table 3). Between sites, abundances of all mesozooplankton groups were higher at SC compared with EC (Fig 4b–e); with significant differences for euphausiids ($p < 0.05$) and salps ($p < 0.001$).

Table 3. Summary of summertime blue whale sighting rates and environmental conditions during 2012 and 2013. Wilcoxon signed ranked test results (where applicable) are displayed to determine significant differences between both summer seasons. SAAW: subantarctic water; MSAAW: modified subantarctic water. Arrows pointing up: increase in relative influence; arrows pointing down: decrease in relative influence. *significant at $p < 0.05$; NA: not applicable

	Summer 2012	Summer 2013	Wilcoxon test results (p-value)
Blue whales			
Sighting rate of foraging animals (ind. d ⁻¹)	0.46	0.78	0.0096*
Euphausiids			
Abundance (ind. 1000 m ⁻³) ± SD	0.01 ± 0.03 (n = 31)	3.44 ± 7.72 (n = 59)	0.0000*
As % of total mesozooplankton abundance	<1%	57%	NA
Size structure	Dominance of adults	Dominance of juveniles	NA
Salps			
Abundance (ind. 1000 m ⁻³) ± SD	2.64 ± 12.28 (n = 31)	0.06 ± 0.16 (n = 59)	0.3702
As % of total mesozooplankton abundance	84%	8%	NA
Surface chl a			
Concentration (mg chl a m ⁻³) ± SD	0.78 ± 0.25 (n = 45)	2.24 ± 3.09 (n = 57)	0.0287*
Surface nutrients			
NO ₃ ⁻ (µM) ± SD	13.88 ± 4.11 (n = 45)	16.32 ± 3.95 (n = 57)	0.0027*
PO ₄ ³⁻ (µM) ± SD	1.05 ± 0.36 (n = 45)	0.73 ± 1.09 (n = 57)	0.0000*
SiO ₄ ⁴⁻ (µM) ± SD	8.50 ± 5.00 (n = 45)	18.15 ± 6.64 (n = 57)	0.0000*
SiO ₄ ⁴⁻ :NO ₃ ⁻ ± SD	0.72 ± 0.53 (n = 45)	1.18 ± 0.54 (n = 57)	0.0000*
Physical variables			
Temperature at 2 m depth ± SD	13.26 ± 0.68 (n = 45)	13.51 ± 1.34 (n = 57)	0.9545
Salinity at 2 m depth ± SD	30.41 ± 1.70 (n = 45)	30.79 ± 1.22 (n = 57)	0.0317*
Relative influence of waters masses	↑SAAW ↓MSAAW	↑MSAAW ↓SAAW	NA

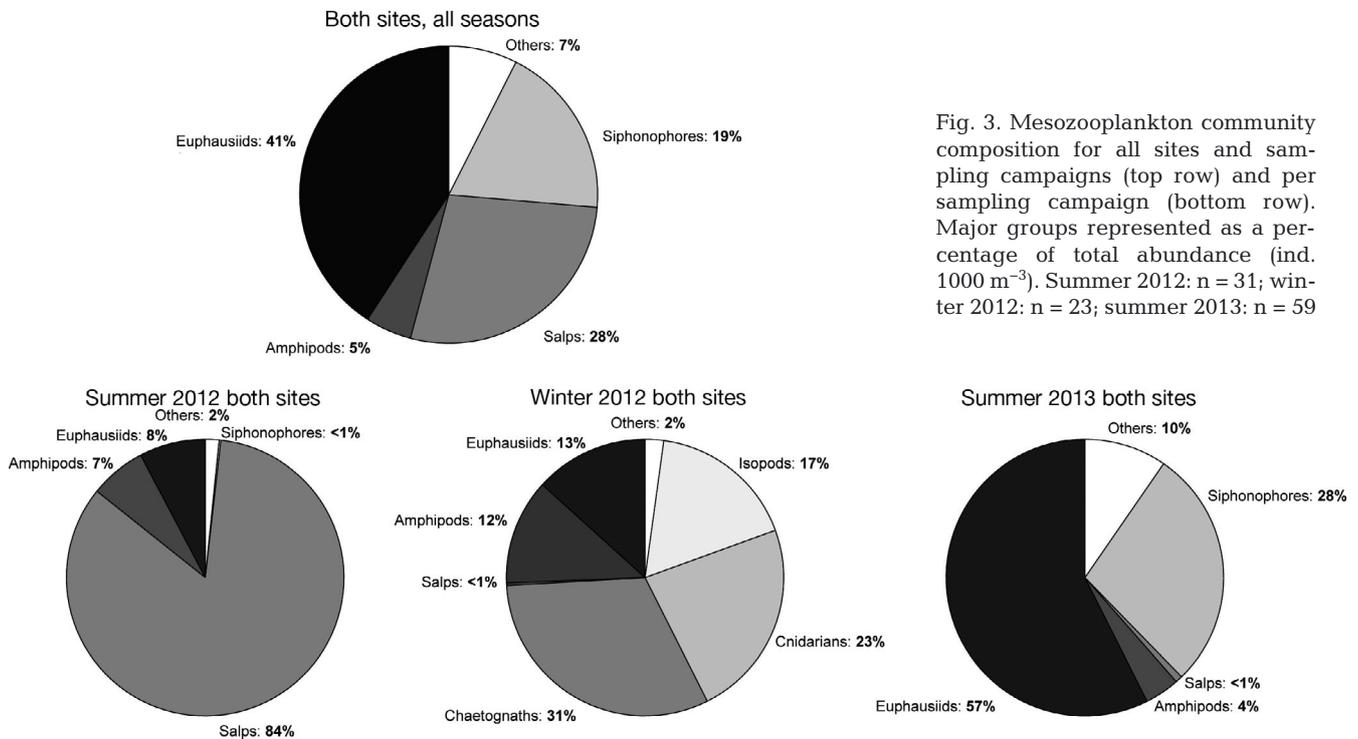


Fig. 3. Mesozooplankton community composition for all sites and sampling campaigns (top row) and per sampling campaign (bottom row). Major groups represented as a percentage of total abundance (ind. 1000 m⁻³). Summer 2012: n = 31; winter 2012: n = 23; summer 2013: n = 59

Two species of euphausiid were identified: *Euphausia vallentini* and *Nematocelis megalops*. *E. vallentini* accounted for 90.3% of adult euphausiid abundance. Size structure histograms for *E. vallen-*

tini per season and site showed size structures centered around 9 mm (juveniles) and 13 mm (adults) during summer 2012 (bimodal, Fig. 5a); 13 mm (adults) during winter 2012 (unimodal, Fig. 5b); and

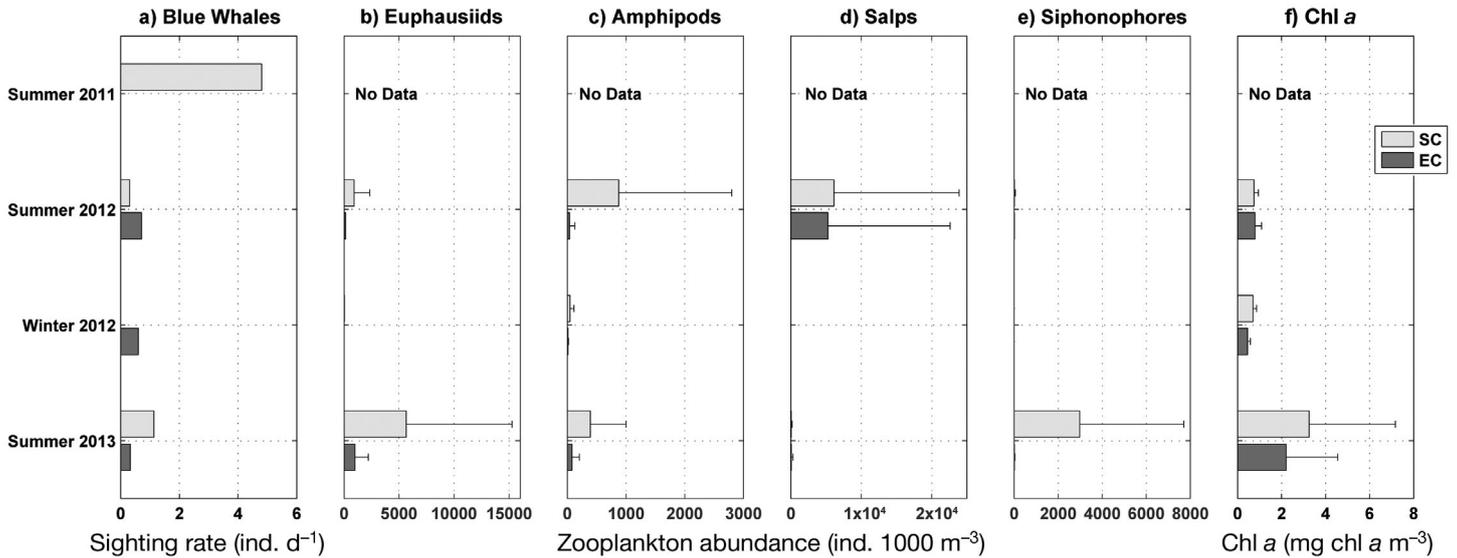


Fig. 4. (a) Sighting rates of foraging blue whales (ind. d⁻¹); (b–e) average abundance (ind. 1000 m⁻³) of major mesozooplankton groups (n = 113): (b) euphausiids, (c) amphipods, (d) salps, (e) siphonophores; (f) *in situ* chl a concentrations (mg m⁻³; n = 130) per sampling campaign at the southern Corcovado (SC) and eastern Corcovado (EC) study sites. Data are mean + SD for mesozooplankton abundance and chl a concentration

3 mm (juveniles), 9 mm (juveniles) and 15 mm (adults) during summer 2013 (trimodal, Fig. 5c). Summer 2013 was the only season when the smallest juveniles (mode around 3 mm) were present.

In situ surface chl a concentrations (n = 130; Fig. 4) were highest during summer 2013 (in the order of 10.00 to 15.00 mg chl a m⁻³; n = 57) and lowest in winter 2012 (in the order of 0.5 mg chl a m⁻³; n = 28). Chl a concentrations were significantly higher at SC

compared with EC (p < 0.001, data not shown). Surface nitrate ranged from 6.24 to 32.71 μM and was highly variable (n = 130; Fig. 6), and was higher in winter compared with both summers. Surface nitrite ranged from 0.00 to 2.60 μM (n = 130; data not shown) across all sampling sites and seasons, and was lower in winter compared to summer, and highest during summer 2013. Surface phosphate ranged from 0.00 to 2.04 μM (n = 130; data not shown) and

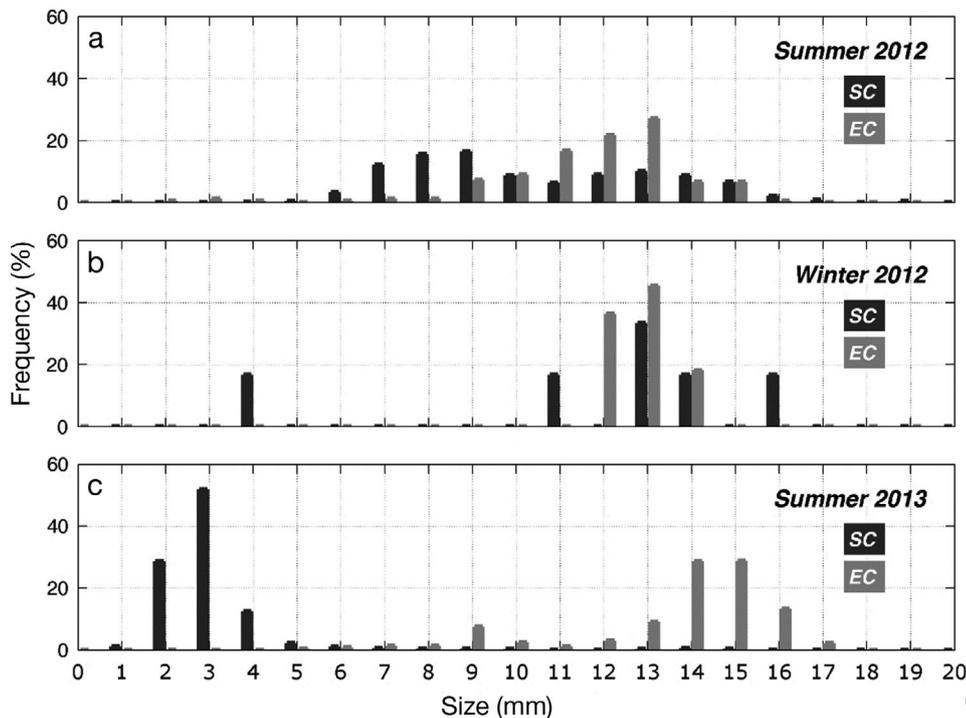


Fig. 5. *Euphausia vallentini* size structure histograms for all samples grouped for the southern Corcovado (SC) and eastern Corcovado (EC) study sites per sampling campaign: (a) summer 2012 (n = 31); (b) winter 2012 (n = 31); (c) summer 2013 (n = 59)

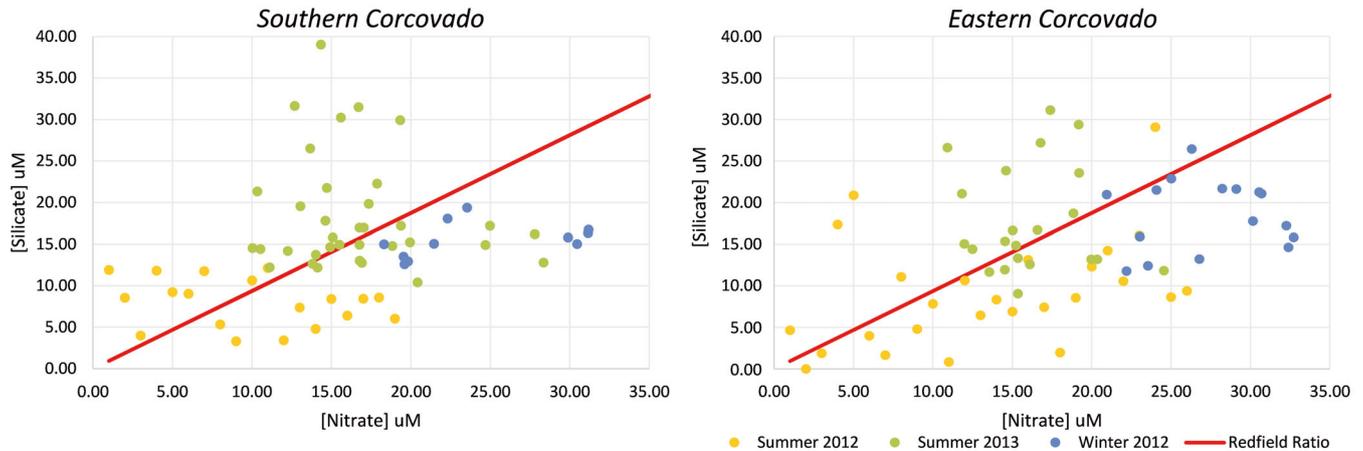


Fig. 6. Scatter plot of silicate vs. nitrate concentrations at 2 m depth in the southern and eastern Corcovado study sites per sampling season: summer 2012 ($n = 45$), winter 2012 ($n = 28$), summer 2013 ($n = 57$). The red line indicates an elemental Redfield ratio, Si:N = 15:16

was higher during summer 2012, compared to winter 2012 and summer 2013. Surface silicate ranged between 0.09 and 33.32 μM ($n = 130$; Fig. 6) across all samples, and, similar to NO_3^- , was highly variable. Significant differences between the summers 2012 and 2013 were detected for all 4 nutrients (Table 3). NO_3^- was significantly higher at EC, and PO_4^{3-} and SiO_4^{4-} were significantly higher at SC ($p < 0.001$). $\text{SiO}_4^{4-}:\text{NO}_3^-$ values were highest in winter 2012 and lowest in summer 2013 (Fig. 6). SiO_4^{4-} was markedly below the Redfield ratio during summer 2012, which

explained the significant differences in $\text{SiO}_4^{4-}:\text{NO}_3^-$ from summer 2013 ($p < 0.001$; Table 3). $\text{SiO}_4^{4-}:\text{NO}_3^-$ was significantly higher at SC compared with EC ($p < 0.05$).

Vertical profiles for temperature, salinity and oxygen (Fig. 7) showed a warmer, less saline, well-oxygenated surface layer (ca. 0–10 m depth) overlying a more saline, cooler, less-oxygenated layer (Fig. 7a,c, d,f). The water column was more homogenous in winter than in summer, with a slight temperature inversion (Fig. 7b,e). Wilcoxon tests revealed sig-

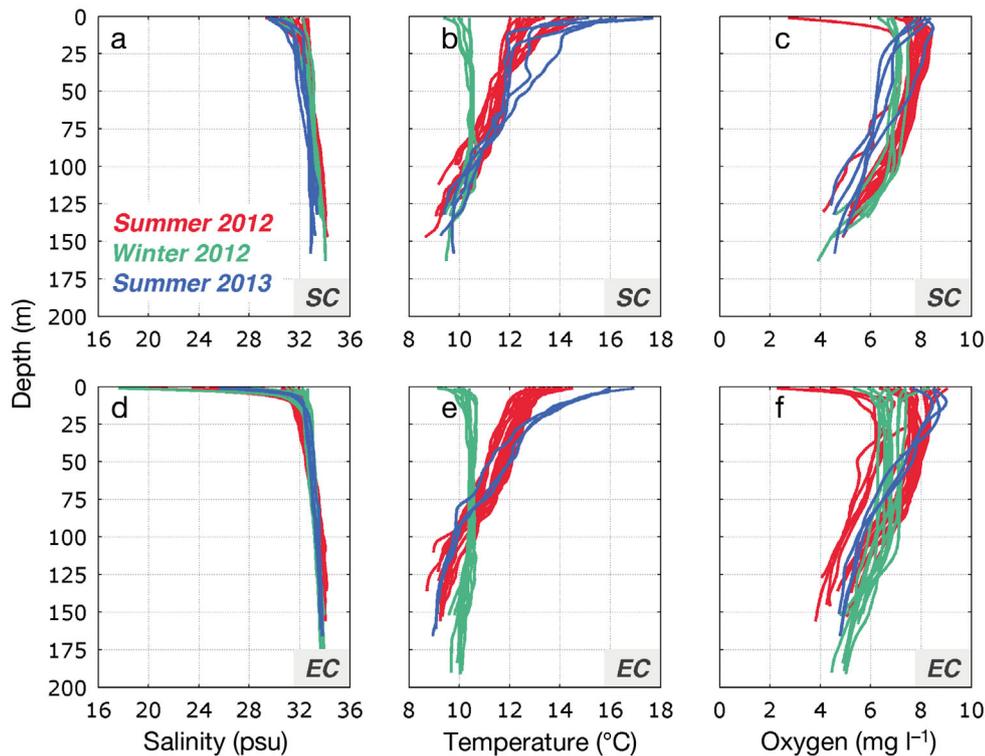


Fig. 7. Vertical profiles of (a,d) salinity, (b,e) temperature, and (c,f) oxygen concentration at the (a–c) southern Corcovado (SC) and (d–f) eastern Corcovado (EC) sampling sites per sampling campaign (summer 2012, winter 2012, and summer 2013)

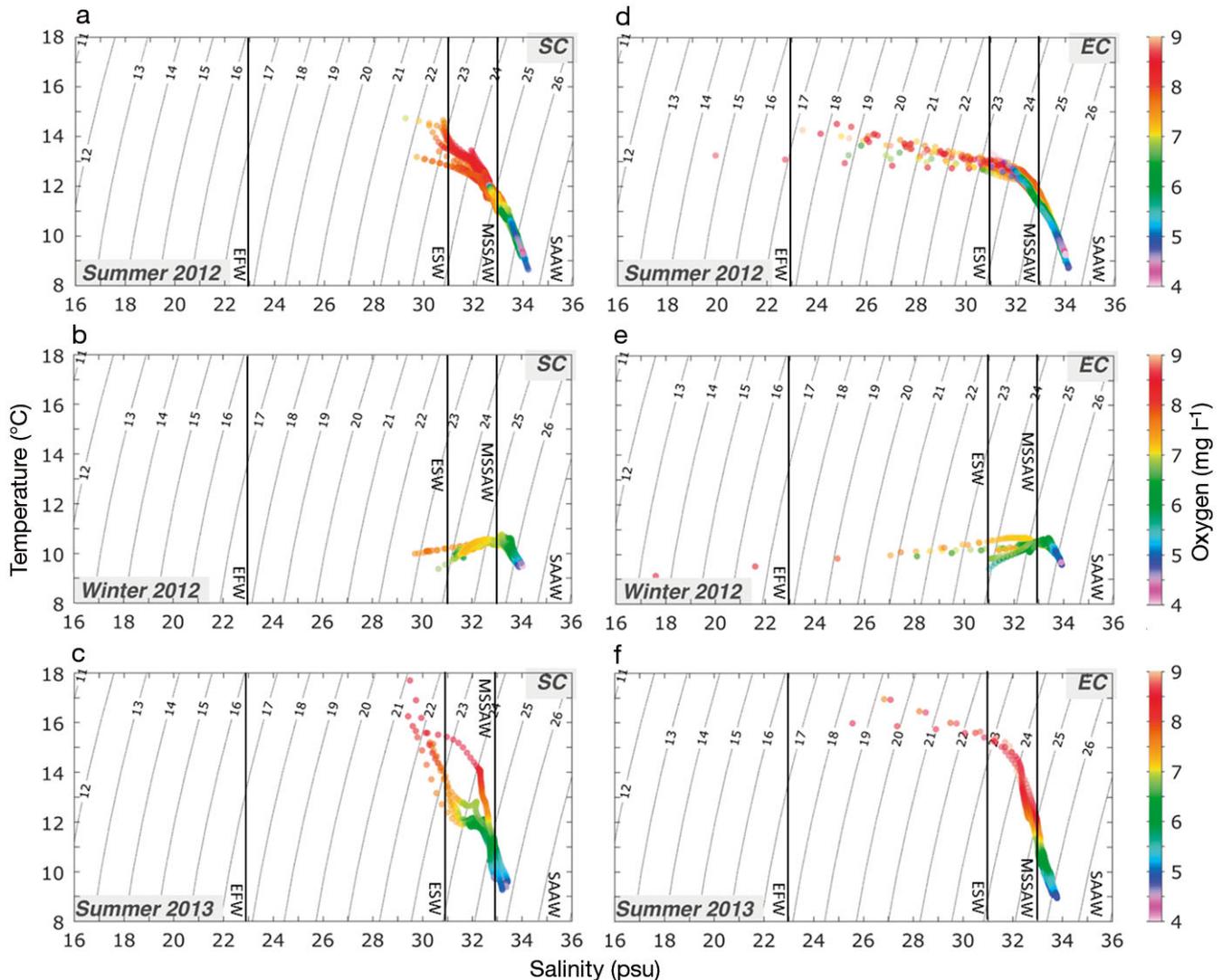


Fig. 8. Temperature–salinity diagrams for (a,d) summer 2012, (b,e) winter 2012, and (c,f) summer 2013 at the (a–c) southern Corcovado (SC) and (d–e) eastern Corcovado (EC) sampling sites. Vertical black lines delimit salinity criteria according to Sievers & Silva (2008) and Pérez-Santos et al. (2014): EFW = estuarine freshwater (11–21); ESW = estuarine saline water (21–31); MSAAW = modified subantarctic water (31–33); SAAW = subantarctic water (>33)

nificant differences between the summers of 2012 and 2013 in surface salinity but not temperature (Table 3). Both temperature and salinity were significantly higher at SC compared with EC ($p < 0.001$). Oxygen concentrations mostly ranged between 4 and 8 mg l^{-1} and were slightly lower during winter vs. summer (Fig. 7c,f).

Temperature–salinity diagrams per site and sampling season (Fig. 8) show the influence of the water masses ESW, MSAAW, and SAAW. EC (near the Palena River mouth) had greater low-salinity surface ESW influences. SAAW had greater influence at maximum depths, MSAAW at intermediate depths, and ESW in surface waters. Comparing between

summers, SAAW had more influence during 2012 at intermediate and maximum depths (Fig. 8a,d), compared with 2013 when MSAAW had a stronger influence throughout the water column (Fig. 8c,f).

Satellite images of monthly averages for January (data not shown), February (Fig. 9) and March (data not shown) during 2011, 2012 and 2013 show SST values between 8 and 18°C; nFLH between 0.00 and 0.06 $\text{mW cm}^{-2} \mu\text{m}^{-1} \text{sr}^{-1}$ (sr = unit of remote sensing reflectance); and chl *a* between 0 and 30 mg m^{-3} . During all 3 summers, SST was highest in January and February (~15°C) compared with March (~13°C); nFLH and chl *a* were highest in January compared with February and March; lowest values of satellite

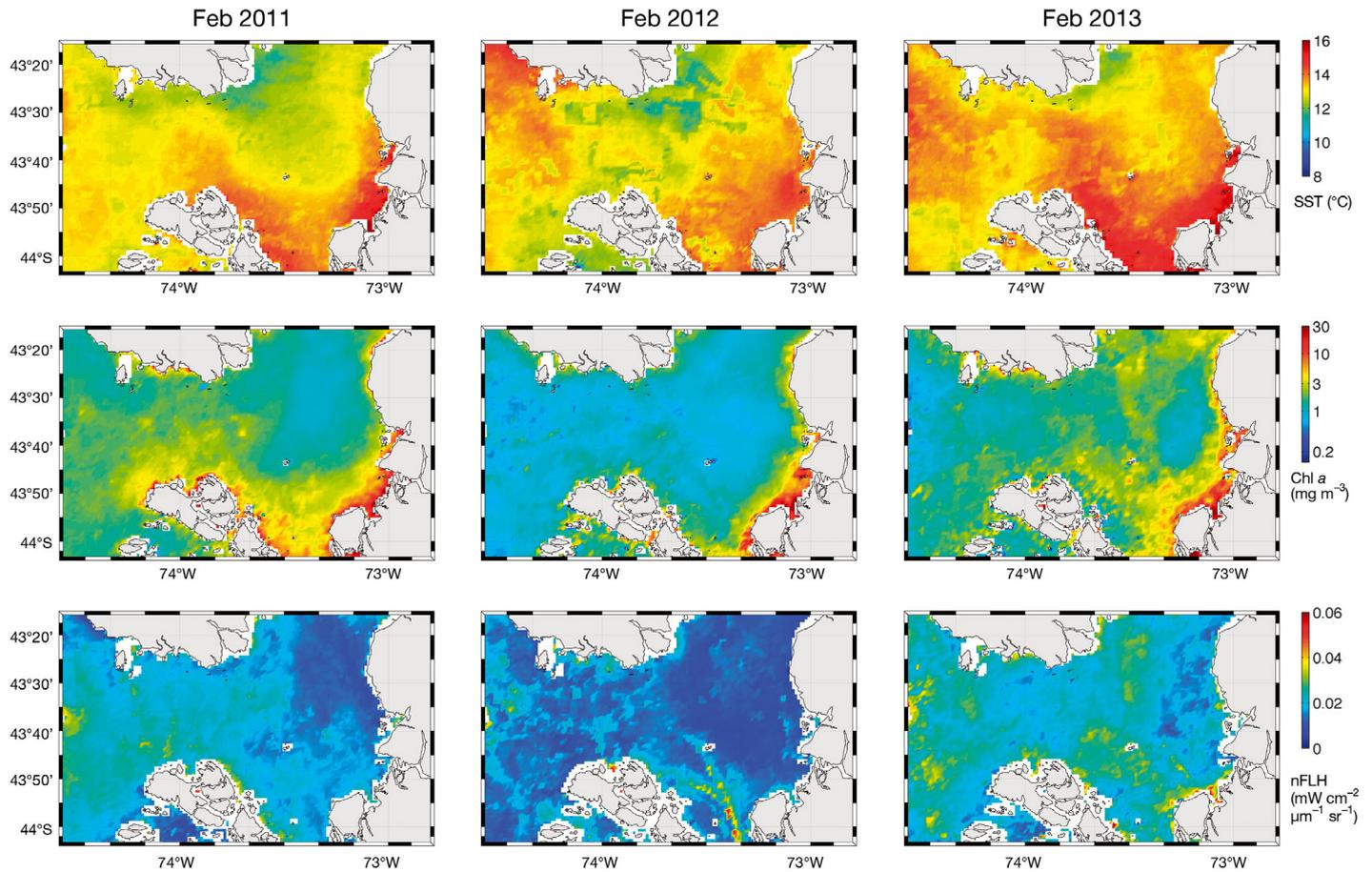


Fig. 9. Monthly average remote-sensed oceanographic data in February 2011, 2012, and 2013 for sea surface temperature (SST), chlorophyll *a* concentration, and fluorescence (nFLH)

nFLH and chl *a* were recorded during 2012 compared with 2011 and 2013 (Fig. 9). Based on our analysis of river discharge time series data (2010 to 2013; data not shown), there was a small but significant ($p < 0.001$) drop in river discharge during 2011, reaching lowest discharge values of the time series at the beginning of 2012 (i.e. summer 2012).

For the physical-chemical variables, the GLM for summer 2012 revealed no association between blue whale presence and explanatory variables (data not shown). For the summer 2013 GLM, negative relationships with chl *a* ($p < 0.000$) and temperature ($p < 0.001$) were found to be highly significant (Table 4a), explaining 63% of deviance ($R^2 = 0.6303208$), which was the best fit of the 3 physical-chemical GLMs. These relationships were also seen in the GLM that pooled the summers 2012 and 2013 together, but with a lesser degree of significance (not shown). Similarly, for the euphausiid GLMs, no significant relationships were found for summer 2012 or for both

summers together (data not shown). The best model fit was for summer 2013 alone, albeit with a relatively low R^2 , explaining 13% of the deviance (Table 4b). In summer 2013, a significant negative relationship was found with juvenile euphausiids; a negative relationship was also found with adult *E. vallentini*, although this was not found to be significant.

DISCUSSION

The majority of blue whale sightings in the south-east Corcovado Gulf involved known foraging behaviors for blue whales (Table 1, Fig. 2), which further confirms the Corcovado Gulf as a seasonal feeding ground for blue whales, as first reported by Hucke-Gaete et al. (2004). We found higher sighting rates of foraging blue whales during summer vs. winter, as previously reported (Hucke-Gaete 2004, Branch et al. 2007, Hucke-Gaete et al. 2010, Förs-

terra & Häussermann 2012, Galletti-Vernazzani et al. 2012, Buchan et al. 2015).

Euphausiids, the preferred prey of blue whales (Nemoto 1970), dominated the mesozooplankton community and their abundances in summer were high but also highly variable (in the order of 1000 to 5000 ind. 1000 m⁻³). *Euphausia vallentini* was by far the most abundant euphausiid species (90.3% of adult abundance), compared to the only other species identified (*Nematocelis megalops*), in line with findings by Palma & Silva (2004) and González et al. (2010). We can, therefore, say with a high degree of certainty that the subantarctic euphausiid *E. vallentini* is the target prey species for blue whales in the Corcovado Gulf feeding ground.

In the southeast Corcovado during summer, consistently high chl *a* concentrations and nFLH levels were confirmed by satellite images (Fig. 9). Huccke-Gaete (2004) found the high satellite chl *a* concentrations (>20 mg m⁻³) in the southeast Corcovado coincided with blue whale preference for this area. In NCP, NO₃⁻ and PO₄³⁻ are supplied by oceanic water inputs and SiO₄⁴⁻ by freshwater inputs from the continent, all 3 of which are key nutrients for phytoplankton—specifically diatom—growth (Silva & Guzmán 2006, Sievers & Silva 2008, González et al. 2010, Torres et al. 2014). We identified the following water masses (Fig. 8) in the southeast Corcovado Gulf: ESW in surface layers (0–30 m), MSAAW at intermediate depths (30–100 m), and SAAW and below 100 m, as previously reported (Silva & Guzmán 2006, Sievers & Silva 2008, Pérez-Santos et al. 2014, Silva & Vargas 2014). MSAAW is not a source water mass but a product of mixing: SAAW becomes SiO₄-enriched by the surface estuarine waters (Torres et al. 2014), forming MSAAW (Guzmán & Silva 2002). The high levels of rainfall and volcanic activity in this region are likely to contribute to high levels of surface water SiO₄ enrichment (Silva & Guzmán 2006, Torres et al. 2014), and in turn may boost biological productivity. This may explain recent observations (summers of 2015 and 2016, pers. obs. S. J. Buchan), of high densities of blue whales (35 whales over 4 d) foraging in the area at the mouth of the Yelcho River, which

Table 4. Generalized linear models (GLMs). (a) Physical-chemical variables in summer 2013; explanatory variables: chl *a*, NO₃⁻, PO₄³⁻, SiO₄⁴⁻, SiO₄⁴⁻:NO₃⁻ ratio, temperature, and salinity; 81 observations. (b) For euphausiids for in summer 2013; explanatory variables: *E. vallentini* adults, juvenile euphausiids; 67 observations. Response variable: blue whale presence/absence. AIC: Akaike's information criterion. Significance determined at *p < 0.01; **p < 0.001; ***p < 0.0001

	Estimate	SE	z	Pr (> z)
a) Physical-chemical GLM				
(Intercept)	36.64050	15.03615	2.437	0.014817*
Chl <i>a</i>	-5.30971	1.58459	-3.351	0.000806***
Salinity	-0.47029	0.32795	-1.434	0.151559
Temperature	-1.46958	0.55174	-2.664	0.007733**
NO ₃ ⁻	-0.01705	0.12121	-0.141	0.888155
NO ₂ ⁻	-3.39086	1.88319	-1.801	0.071766
PO ₄ ³⁻	2.25324	1.37368	1.640	0.100942
SiO ₄ ⁴⁻	0.02387	0.10358	0.230	0.817753
NO ₃ ⁻ :SiO ₄ ⁴⁻	0.565584	1.62785	0.348	0.728139
Null deviance	106.107 on 76 df			
Residual deviance	39.226 on 68 df (4 observations deleted due to missingness)			
AIC	57.226			
R ²	0.6303208			
b) Euphausiid GLM				
(Intercept)	0.8440	0.4512	1.870	0.06142
Adult <i>E. vallentini</i>	-1.2423	0.7447	-1.668	0.09527
Juvenile euphausiids	-1.8425	0.5806	-3.173	0.00151**
Null deviance	91.068 on 66 df			
Residual deviance	78.843 on 64 df			
AIC	84.843			
R ²	0.1342413			

drains the area surrounding the Chaiten volcano, which erupted in 2008. Lower surface salinities (Fig. 7) and a tendency toward the ESW end-member (Fig. 8) at the EC site compared with SC reflected the influence of the Palena River. In summer, a low salinity surface layer overlaying a higher salinity layer was present; this structure was largely absent in winter. Along with the supply of nutrients by water masses, this vertical structure is likely to be essential for the development of phytoplankton blooms in this area (González et al. 2010, Jacob et al. 2014).

Lastly, bathymetry in the Patagonian Archipelago Inner Sea could play a role in concentrating planktonic organisms, as seen elsewhere (e.g. Genin 2004, Sourisseau et al. 2006). In effect, at the shallower and more bathymetrically complex SC site, chl *a* and euphausiid abundance, and sightings of foraging blue whales were significantly higher (p < 0.001, p < 0.05, and p < 0.05, respectively). At the SC site, (1) a submarine canyon (>200 m deep) runs east–west from the Pacific Ocean into the gulf, and could expedite macronutrient-rich oceanic waters into the Inner Sea; canyons have been identified as important for-

aging habitats for cetaceans (Moors-Murphy 2014), including blue whales (Croll et al. 2005). (2) Island land masses could promote phytoplankton blooms due to the 'island mass effect', i.e. nutrient injection via localized upwelling (Hasegawa et al. 2009). (3) At shallow depths, euphausiids can become trapped (Genin 2004), which might benefit foraging by reducing the energetic costs of deep diving (Doniol-Valcroze et al. 2011, 2012, Goldbogen et al. 2011). Thus, blue whales might select areas, such as the SC, where shallow depths and land masses confine euphausiid aggregations, in a sort of topographic 'krill trap' that may increase their feeding efficiency.

Inter-annual variation

Significant inter-annual changes in blue whale sighting rates and some oceanographic variables were detected between the summers 2012 and 2013 (Table 3). Our results indicate that summer 2012 was a low-sighting low-productivity summer; while summer 2013, which presented much higher sighting rates, can be considered a productive summer, providing better feeding conditions for blue whales. Although summer 2011 was not included in our statistical analyses because no *in situ* oceanographic data were available, satellite data suggest higher productivity in 2011 compared with 2012, and in the same range as 2013. Also, the high numbers of sightings in 2011 coincided with visual observations of extensive and dense surface aggregations of euphausiids, possibly in the order of 50 000 ind. 1000 m⁻³ (based on photographic evidence, data not shown). This reveals high variability in feeding hotspots year to year, which we hypothesize is in some way linked to changes in water masses and nutrient inputs.

Two oceanographic/hydrographic scenarios could be responsible for the environmental conditions (water masses, nutrients and biological productivity) observed in 2012 (see Table 3): a first hypothesis is the increased inflow of oceanic water masses into the Inner Sea, which could have modified the balance of MSAAW vs. SAAW, particularly in surface and intermediate layers. SAAW is a cool and characteristically low-SiO₄⁴⁻ high-NO₃⁻ (Llanillo et al. 2013). High spring/summer primary productivity in Northern Patagonia is known to be caused by high diatom abundance (Iriarte et al. 2007), a group which is known to require silicate for growth (Dugdale & Wilkerson 1998). Low Si availability (Si:N = 1:5) has been found to limit diatom growth in fjords in this area, favouring dinoflagellates (Torres et al.

2011). Here, we found high Si:N values (>1:1) during summer 2013, but not during winter or summer 2012 (<1:1) (Table 3, Fig. 6). The importance of sufficient Si:N for primary productivity in Chilean Patagonia has been highlighted by several authors (González et al. 2010, Iriarte et al. 2010, Torres et al. 2011, 2014).

Additionally, the oceanic intrusion could have led to 'low-food' conditions that favor salp growth or the transport of oceanic salps into the study area, leading to top-down control (grazing) on phytoplankton, and outcompeting euphausiids, as observed in the Southern Ocean (Voronina 1998, Atkinson et al. 2004, Smetacek & Nicol 2005). In NCP during the year 2010, there was a mass intrusion of salps (*Ihleia magalhanica*) that coincided with a 1°C drop in SST, a weaker vertical thermohaline gradient and a drop in chl *a* concentrations (no data on SiO₄⁴⁻ were provided) (Giesecke et al. 2014); this is similar to the conditions observed in the present study during summer 2012. Interestingly, Giesecke et al. (2014) provided the following possible explanation for the oceanic inflow: a change in the intensity of the Southern Annular Mode (SAM). In effect, our examination of the SAM time series between January 2010 and December 2013 (data available at www.nerc-bas.ac.uk/icd/gjma/sam.html) reveals a series of negative anomalies between July 2011 and February 2012 of similar magnitude to the anomaly identified by Giesecke et al. (2014).

Alternatively, or additionally, lower silicate concentrations could be explained by the apparent reduction in continental water inputs into the southeast Corcovado Gulf during 2011, until austral summer 2012. We hypothesize that this slight but significant drop in freshwater inputs during 2011, plus the negative SAM anomalies observed in July 2011 and February 2012, were responsible for low silicate concentrations and low productivity during summer 2012 in this area, and consequently low sightings of foraging blue whales.

In any case, our findings support the hypothesis that sufficient SiO₄⁴⁻ supply is key for supporting primary productivity in NCP (Iriarte et al. 2010, González et al. 2010, Torres et al. 2011, 2014), and, as a consequence, supports the diatom–euphausiid–blue whale food chain. Our results suggest that a reduction in SiO₄⁴⁻ supply, whether driven by ocean–atmosphere forcing (inflow of SiO₄⁴⁻-poor oceanic waters possibly due to SAM anomalies), or anthropogenic changes to continental runoff (e.g. hydroelectric dams, climate change), could negatively impact foraging conditions for blue whales.

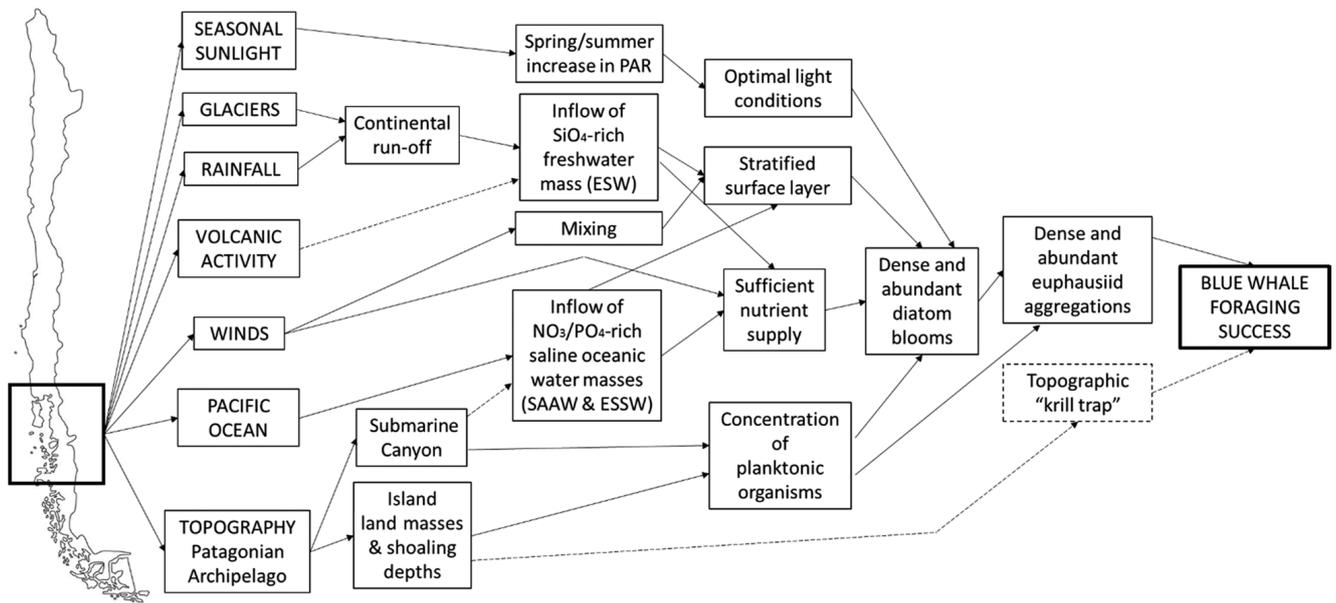


Fig. 10. Conceptual scheme of possible direct and indirect environmental factors and processes that contribute to blue whale foraging success in northern Chilean Patagonia ($41^{\circ}30'–47^{\circ}00'S$), based on the results of this study and references herein from the scientific literature. Dashed lines and boxes indicate insufficient supporting evidence (see 'Discussion'). PAR: photosynthetically active radiation; ESW: saline estuarine water; SAAW: subantarctic water; ESSW: equatorial subsurface water

Synoptic scale variation

The GLM analyses (Table 4) revealed that a decrease in chl *a* and temperature was significantly associated with a greater chance of sighting foraging blue whales during summer 2013. The relationship with chl *a* was highly significant and reflected in our field observations and daily average satellite data (not shown): feeding events were observed for ca. 10 d to 2 wk following intra-seasonal pulses in primary productivity, effectively during periods of relatively low *in situ* chl *a* and satellite chl *a* and nFLH. This time lag could be plausibly explained by the temporal succession (days to weeks) in the growth of phytoplankton blooms—euphausiid aggregation—and the arrival of blue whales at a feeding site. This remains a qualitative observation and to the best of our knowledge these fine-scale temporal dynamics have not been described in the literature. This synoptic effect might also explain the negative relationship with temperature: phytoplankton blooms in this open gulf area might develop during periods of high irradiation, stratification and increased surface stability, reflected by higher surface temperatures, but this remains pure speculation. The driving factors of synoptic peaks in primary production remain unexplained in this open gulf area. In more enclosed fjords in the region, synoptic peaks in primary production have been linked to some degree to freshwater and oceanic water inputs,

tidal circulation, and wind mixing, among other factors (Iriarte et al. 2007, Torres et al. 2011, Jacob et al. 2014, Pérez-Santos et al. 2014). During the low-productivity summer of 2012, blue whale sightings and biological productivity remained at very low levels throughout the season, and thus sightings were not correlated with any environmental variable in the summer 2012 GLM.

For the euphausiid GLM, it is interesting that euphausiids were found to be negatively correlated with whale sightings. The model fit was relatively poor so these results should be interpreted with caution. It is important to note the inherent limitations of our sampling methods for estimating euphausiid abundance: given the semi-diel vertical migrations carried out by zooplankton in this region (Valle-Levinson et al. 2014), and by most euphausiid species worldwide (Mauchline 1980), including *E. vallentini* (Hamamé & Antezana 2010), daytime net sampling which does not reach down to maximum depths (in this case only 100 m) will very likely underestimate euphausiid abundance. Moreover, euphausiids are well known to avoid nets (Brinton & Townsend 1981, Everson 2000). Correctly estimating euphausiid abundance with net sampling is also complicated by the high degree of patchiness of euphausiid aggregations; whales can detect patchy swarms that net sampling may miss (Brodie et al. 1978). In effect, our abundance estimates are lower than those reported

by Palma & Silva (2004) and Sánchez et al. (2011). On the other hand, it is possible that the negative correlation in the summer 2013 GLM indicates that where foraging blue whales were sighted, euphausiid abundance was reduced due to the predation pressure by blue whales on euphausiid aggregations.

Concluding remarks

We present the very first exploration of the *in situ* oceanographic data at blue whale feeding sites in Patagonia, providing the first insights into the oceanographic factors that influence feeding conditions for the endangered blue whales that use this subantarctic mega-estuarine feeding ground. Given this particularly complex oceanographic and climatic setting, understanding how, where and why blue whale feeding hotspots arise is a huge challenge. Based on the findings of this study and the current literature, we put forward a conceptual scheme in Fig. 10 of the possible direct and indirect environmental factors and processes that might contribute to blue whale foraging success in NCP. This is by no means exhaustive but can serve as a framework for future hypothesis testing.

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