Sepulveda Maritza (Orcid ID: 0000-0002-1403-176X)

FROM WHALING TO WHALE-WATCHING: IDENTIFYING FIN WHALE CRITICAL FORAGING HABITATS OFF THE CHILEAN COAST

Maritza Sepúlveda[1,2,*], María José Pérez-Álvarez[2,3], Macarena Santos-Carvallo[1,2], Guido Pavez[1,2], Carlos Olavarría[2,4], Rodrigo Moraga[2] & Alexandre N. Zerbini[5,6]

[1]Centro de Investigación y Gestión de los Recursos Naturales (CIGREN), Instituto de Biología, Facultad de Ciencias, Universidad de Valparaíso, Valparaíso, Chile

[2]Centro de Investigación Eutropia, Santiago, Chile

[3]Instituto de Ecología y Biodiversidad (IEB), Facultad de Ciencias, Universidad de Chile, Santiago, Chile

[4]Centro de Estudios Avanzados en Zonas Áridas (CEAZA), La Serena, Chile

[5]Marine Mammal Laboratory, Alaska Fisheries Science Center, Seattle, WA, USA

[6]Cascadia Research Collective, Olympia, WA, USA

[*]Corresponding author: maritza.sepulveda@uv.cl

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/aqc.2899

Abstract

1. Fin whales (*Balaenoptera physalus*) have been documented along the coast of Chile since the early 20th century. However, information on their ecology and movement patterns remains poorly known.
2. In the spring of 2015, six implantable satellite tags were deployed on fin whales around the Marine Reserves Isla Chañaral and Islas Choros-Damas (~29ºS) to evaluate their movements and habitat use off the coast of Chile. A switching state-space model was used to estimate the predicted track of the whales as well as behavioural modes classified as "transiting" and "area-restricted search" (ARS).
3. Whales were tracked between 4 and 162 days (mean = 68 ± 52 days) covering an average distance of 3,225.7 ± 2,871.6 km. Five of the six whales remained at middle latitudes for prolonged periods of time, moving in a north-south pattern near the coast, and spending most of their time in ARS behaviour (72.5% of the locations). Only one individual showed a clear southbound migratory behaviour and remained in transit behaviour for most of the period it was followed.
4. These results suggest that some of the fin whales that are observed in Chile do follow a migration to high latitudes, whereas others remained in lower latitudes, using critical habitats likely as feeding grounds during the summer. This information not only contributes new information on the behaviour and foraging patterns of this species, but is also of particular interest to promote the growing

whale-watching activity and also to better inform conservation and management efforts of this species in Chile.

Key words: coastal, endangered species, feeding, mammals, marine reserve, ocean, recreation, satellite telemetry

1. Introduction

The dynamics, behaviour, and migration routes for many highly mobile species, such as cetaceans, in an environment with no obvious geographic barriers remain poorly understood (Double et al., 2014). Knowledge on the distribution, movements, and habitat use of whales, however, has been rapidly increasing with the development of satellite telemetry studies (e.g. Bailey et al., 2009; Canese et al., 2006; Double et al., 2014), particularly in areas of limited human access (Zerbini et al., 2011, 2006). Moreover, the development of statistical methods to analyse telemetry data (Jonsen, Flemming, & Myers, 2005) has enabled ecologists to improve their knowledge of the movement patterns of whales, for example by making a distinction between "transiting" and "searching" behaviours (Bailey et al., 2009; Jonsen, Myers, & James, 2007), which, for migratory marine megafauna, could be indicative of migrating and feeding/breeding habitats (Bailey et al., 2009; Jonsen et al., 2007).

One of the least known whale species, the fin whale (*Balaenoptera physalus*) occurs in all major oceans (Mizroch, Rice, & Breiwick, 1984; Reeves, Stewart, Clapham, & Powell, 2002), particularly in middle and high latitudes (Branch & Butterworth, 2001; Mackintosh, 1966; Miyashita, Kato, & Kasuya, 1995; Reilly et al., 2013). Fin whales were commercially exploited in the 20th century. In the Southern Hemisphere alone, more than 725,000 whales were killed, which led to a severe decline in the population (Reilly et al., 2013). The species is currently protected by the International Whaling Commission (IWC) and is listed as "Endangered" by the IUCN Red List.

Information of the distribution and movements of fin whales in the Southeast Pacific Ocean comes primarily from whaling operations conducted in the 20th century off the continental coasts of Chile, Peru and Ecuador and in Antarctica (Clapham & Baker, 2001; Clarke, 1962; Harmer, 1928). In Chile, this species was the main target of whaling operations from 1929 to 1983, with up to 4,500 individuals taken, mainly in January, in coastal and oceanic waters between 18 to 22ºS and between 29 and 40ºS (Aguayo, 1974; Clarke, Aguayo, & Basulto, 1978), International Whaling Commission catch database). Post-whaling information on the presence of fin whales in Chile has come from sighting cruises between Antofagasta (23°29' S) and Cape Horn (56°48' S) (Acevedo, O'Grady, & Wallis, 2012; Aguayo-Lobo, Torres, & Acevedo, 1998; Clarke, 1962; Clarke et al., 1978), including the offshore Archipelago Juan Fernández (33º77' S; 80º78' W, Aguayo-Lobo et al., 1998). Most sightings were reported at distances greater than 100 km offshore, leading to the belief that fin whales occur in more oceanic habitats in Chilean waters (Clarke, 1962). However, this notion is now changing due to the regular presence of fin whales in coastal waters at latitudes between 23 and 29ºS during spring and summer (Pacheco, Villegas, Riascos, & Van Waerebeek, 2015; Pérez et al., 2006; Sepúlveda, Oliva, Pavez, & Santos-Carvallo, 2016; Toro, Vilina, Capella, & Gibbons, 2016).

The seasonal distribution of catches and sightings supported the traditional idea that fin whales, as with other balaenopterids, migrate to higher latitudes for feeding and return to low latitudes for breeding and calving (Clarke, 1962; Mackintosh, 1946; Širović, Hildebrand, Wiggins, & Thiele, 2009). However, recent studies on migration patterns of baleen whales suggest that this traditional migration pattern may not be valid for all populations (Geijer, Notarbartolo di Sciara, & Panigada, 2016). This is particularly true for fin whales, for which their year-round presence in some areas, such as the Mediterranean Sea (Notarbartolo Di Sciara, Zanardelli, Jahoda, Panigada, & Airoldi, 2003), the Gulf of Alaska (Moore, Stafford, Mellinger, & Hildebrand, 2006; Stafford, Mellinger, Moore, & Fox, 2007), and the Gulf of California (Tershy, Urbán-Ramírez, Bréese, Rojas-Bracho, & Findley, 1993; Urbán, Rojas-Bracho, Guerrero-Ruíz, Jaramillo-Legorreta, & Findley, 2005) has been described. For the Southern Hemisphere, however, feeding areas outside Antarctic waters have been scarcely reported and movement patterns and potential seasonal migrations are still poorly known (Reilly et al., 2013).

Recent studies have proposed the existence of summer-spring foraging areas for fin whales in certain coastal habitats off Chile. Pérez et al. (2006) and Toro et al. (2016)

observed feeding behaviour near a cluster of four islands located in the Humboldt Current System in north-central Chile (~29ºS) during January and February austral months. Strong and persistent upwelling centres of high productivity are present in these regions (Camus, 2001), supporting large biomasses of krill, the primary prey for fin whales (Kawamura, 1994). Thus, the presence of fin whales in coastal waters along the north-central coast of Chile may be associated with highly productive habitats that may serve as a local feeding ground for this species (Littaye, Gannier, Laran, & Wilson, 2004). Strong upwelling is also observed in other regions along the Chilean coast (Camus, 2001), but the presence of fin whales in these regions is unknown.

The use of satellite transmitters, together with powerful statistical tools, may improve our understanding of movement and migration habits of fin whales summering along the coast of Chile. Such information is critical to better describe the habitat use patterns and the importance of certain habitats to this species along the Chilean coast and has direct implications for the development of local conservation and management for this threatened species. Information on the habitat use of whales may also contribute to the development of economical activities in regions where these animals can be found in a predictable fashion. One example of these activities is the practice of observing whales and dolphins in their natural environment for recreational, educational or touristic purposes (‘*whale-watching*’). Whale-watching has shown an exponential growth globally during the last few decades (Cisneros-Montemayor, Sumaila, Kaschner, & Pauly, 2010; Hoyt, 2001). O’Connor, Campbell, Cortez, and Knowles (2009) estimated that nearly 13 million people participated on whale-watching activities and that this industry generated more the US$2 billion in direct or indirect revenue.

The regular presence of fin whales, as well as other cetacean species, during austral summer months in north-central Chile, led local fishermen to initiate whale-watching tours for tourists visiting the area (Sepúlveda et al., 2016). This activity represents an excellent opportunity for fishermen to expand and diversify their traditional fishery activities where few alternatives may exist, thus allowing for new income sources in the face of declining fisheries (Garrod & Wilson, 2004; Pauly et al., 2002). Whale-watching is still incipient in Chile, but the regular presence of various species of whales suggest that there is high potential for this activity to expand in the Southeast Pacific Ocean. Thus, identification of other potential areas with a frequent presence of whales in Chile could be of interest to further develop this economic activity in the country.

In this study, satellite transmitters were implanted in fin whales off the coast of Chile at the end of the austral spring of 2015 in order to (1) investigate movements and habitat use of this species in the Southeast Pacific Ocean, and (2) to identify high use areas, which could potentially be used for expanding whale-watching activities.

2. Material and Methods

Study area and timing

Tagging operations were conducted in the vicinity of the Marine Protected Areas "Reserva Marina Isla Chañaral" (29°02'S, 71°36'W) and "Reserva Marina Islas Choros-Damas" (29°14'S, 71°32'W), north-central Chile (Figure 1). Between November 24 and December 5, 2015, daily trip to search for fin whales were undertaken under calm and favourable weather/sea conditions (Beaufort sea state ≤ 3) using two 9 m fishing boats.

Tagging in late spring was preferred because it corresponded to the late spring arrival of the fin whales in the region and because it preceded the opening of the whale-watching season in the area (Sepúlveda et al., 2016). It would therefore allow for tracking animals during and after their feeding season and allow for assessing preferred habitats during the time of the year convenient for whale-watching as the summer represents the peak of the tourist season.

Satellite tag deployment and biopsy collection

Six Argos implantable tags were deployed on fin whales (*Balaenoptera physalus*). Two configurations were used: the SPOT 6 (n = 2) and the SPLASH 10 (n = 4) tags manufactured by Wildlife Computers (Redmond, WA, USA). The former corresponds to location-only transmitters, whereas SPLASH tags provide, in addition to location data, temperature and depth profiles (e.g. via "time series" and "behavioural log" modes). The tags were cylindrical in shape and made of surgical quality stainless steel and measured 29 cm in length and 2.4 cm in diameter. Tags were designed to penetrate skin and the blubber layer and to anchor underneath the fascia, a layer of stiff connective tissue between blubber and muscle. The anchoring system used with these tags was identical to the one described by Gales et al. (2009), except that the head of the tag was fixed (and not articulated) and the anchor and transmitter components of the tag were fully integrated. Fully integrated tags have been shown to be more robust and to minimize impact to individual whales (Zerbini et al., 2017).

Satellite tags were deployed using a modified pneumatic line thrower: the Air Rocket Transmitting System, (the Air Rocket Transmitting System, Heide-Jørgensen et al., 2001) set to pressures ranging from 8 to 12 bars. SPOT 6 and SPLASH 10 satellite tags were programed to transmit every day during periods of high overpass coverage of the Argos satellites. SPLASH tags were also set to collect daily behavioural log information and weekly time series data.

Skin biopsy samples were obtained from five of the six tagged whales for molecular sex identification using a hollow-tipped dart fired from a modified PaxArms .22 caliber rifle (Krützen et al., 2002). The sex of each individual was identified by simultaneously using two sets of oligonucleotide primers, which amplify a fragment of the ZFX/ZFY genes (Aasen & Medrano, 1990) and a fragment from the SRY gene (Gilson, Syvanen, Levine, & Banks, 1998). Sex identification was done 2–3 times per individual and DNA from an individual of known sex was amplified as a positive control.

Switching state-space modelling

The Argos location data were fitted with a Bayesian switching state-space model (SSSM) (Jonsen et al., 2005, 2007) in order to estimate whale movement parameters and behavioural states from telemetry data. The model was fitted to five of the six-tagged whales. An individual with tag duration of just four days (see below) was not included in the analysis.

This SSSM was used because it allows location estimates to be inferred from observed data (satellite locations) by accounting for errors (measurement equation) and from dynamics of the movement process (transition equation) (Bailey et al., 2009). Model fitting was performed using the package “bsam” in the freely available software R (R Development Core Team, 2013). This package fits the SSSM using Markov Chain Monte Carlo (MCMC) simulations with software JAGS (Plummer, 2003). The model was fitted to each individual dataset with a total of 70,000 MCMC samples with the first 40,000 discarded as a burn-in. In order to reduce auto-correlation, the remaining 30,000 samples were reduced to 3,000 by retaining one out of every 10 samples, from which the marginal posterior distribution of parameters of interest was computed.

The correlation random walk model used in SSSM switches between two unobservable behavioural states (b) thought to represent transiting (b=1) and area-restricted search (ARS) (b=2). Because b is a discrete parameter, the means of the MCMC samples were used to compute two behavioural modes for predicted locations: transiting, with $b < 1.25$, and ARS with b > 1.75 (Jonsen et al., 2007). These two modes are defined according to travel speed and turning angles. Mean estimates between 1.25 and 1.75 were considered as uncertain following the conservative approach of Jonsen et al. (2007) and Bailey et al. (2009). Predicted locations and behavioural modes were computed at 6-h intervals.

Occupancy time

In order to identify areas of high use by whales, the zones visited by fin whales and predicted by SSSM were plotted in grids of 50 x 50 km. The average time (in hours) spent by whales in each grid square was computed by multiplying the total number of positions per grid square by 6 (h) and dividing by the number of individuals that visited each grid cell. This method was incorporated into the analysis because it complements the SSSM method, with both providing relevant information to habitat use (Garrigue, Clapham, Geyer, Kennedy, & Zerbini, 2015).

Environmental data

Chlorophyll-a concentration in mg/m^3 (Chl-a) was used as a proxy for primary productivity and was obtained as monthly images from the Moderate Resolution Imaging Spectroradiometer (MODIS) on board the Aqua satellite (data available at http://oceancolor.gsfc.nasa.gov/). Monthly CHL raster images for the period September 2015 to January 2016 were downloaded and processed using the Marine Geospatial

Ecology Tools (MGET) version 0.8a49 in ArcGIS (Roberts, Best, Dunn, Treml, & Halpin, 2010). These images consisted of a binned product at a 9-km resolution. Monthly images were averaged in ArcMap 10.1, ESRI (2011). Predictions from the SSSM were overlaid to the averaged Chl-a raster to evaluate the relationship between fin whale occurrence and primary productivity. Because fin whales are expected to occur at the peak of zooplankton abundance and because there is a three month time lag between peaks of phytoplankton and zooplankton concentration (Visser, Hartman, Pierce, Valavanis, & Huisman, 2011), Chl-a images included a period prior to the onset of tagging operations.

3. Results

Movement of individual whales

The six tagged fin whales were tracked periods ranging from 4 to 162 days (mean = 67.5 ± 52.3 days), rendering an average of raw 723.5 ± 885.3 locations for each individual (range: 21 – 2,484). Throughout the tracking period, satellite tagged whales covered an average distance of 3,225.7 ± 2,871.6 km (range: 128.6 – 8,541.9 km) (Table 1). Of the five whales with sex identification, four were females and one was a male (Table 1).

The tagged fin whales moved in different directions after tagging, showing a high individual variability (Figure 1a). Three whales (PTT numbers: 121195, 120946, 123226) stayed near to the coast, moving in a north-south direction and revealing a preference for inshore habitats (Figure 1b). In general these animals remained relatively close to the tagging location for the period they were tracked, although two of them travelled nearly 400 km to the south towards the central coast off Chile and then returned to the north. Another whale (PTT 121206) showed a different pattern; it moved nearly 450km towards the west in oceanic waters travelled to the south and, at latitude of about 36ºS, this individual moved inshore and then travelled back to the north. It remained in the waters near Coquimbo (30ºS) (Figure 1b) for another four months until transmissions stopped on 11 May 2016. Finally, PTT 112726, the only male, was mainly associated with oceanic waters beyond the Chilean continental shelf. It moved offshore after tagging, approached the coast on two occasions, but then consistently moved through offshore waters in a direct pattern and without noticeable stops. The tag stopped transmitting on 21 January 2016, 47 days after tagging, when this individual was at the approximate latitude of 52ºS (Figure 1a).

Results of the Switching State-Space Model and occupancy time

The SSSM showed fin whales predominantly engaged in ARS behavioural mode (72.5% of the locations) during the period they were monitored. Transiting behaviour was classified in 19.4% of the locations; the remaining 8.1% of locations were classified as uncertain (Figure 2). The tracking data revealed that some inshore habitats appear to be important for fin whales, because the SSSM and also the occupancy time indicate substantial use of these areas (Figures 2 and 3). The SSSM showed that most of the locations estimated as ARS were situated in specific areas, typically over the continental shelf, from near Copiapó (27°S) to the south of Coquimbo, Valparaíso, and Concepción (36°30'S) (Figure 2). Erratic movements and extended periods of time spent in those areas indicate that whales are not just passing through but using these habitats for relatively extensive periods of time. Areas of highest occupancy were consistent with the SMM results, showing higher utilization of the continental shelf between Coquimbo and Valparaíso (Figure 3).

High-use habitats by the statistical analysis carried out in this study are consistent with areas of high productivity (Figure 4). Locations identified as ARS behaviour were observed in or near areas where chlorophyll-a concentration was the highest along the Chilean coast immediately prior and during the period fin whales were monitored.

4. Discussion

To our knowledge, this is the first study examining the movements, behaviour and habitat use of fin whales in the Southeast Pacific Ocean. Despite the small sample of whales tracked, information on movement and habitat use derived from satellite tag data provides novel insights with regard to the critical habitats used by this species along the Chilean coast. The findings not only contribute new and relevant information about the behaviour and potentially to their foraging patterns of fin whales, but also could be of particular interest for the development of the whale-watching activity and also as a baseline for on going conservation and management efforts for this species in Chile. However, a greater sample size is required to assess movement patterns of fin whales off Chile with greater confidence.

Fin whale movements

It has been commonly reported that balaenopterid whales, including the fin whales, show a traditional migratory pattern, occupying low-latitude breeding and calving grounds in the winter and migrating to summer feeding areas (Mackintosh, 1946; Mizroch et al., 1984). Four of a total of 11 fin whales were marked with Discovery marks off the central coast off Chile (30º24' – 33º40'S) in the spring of 1958 were recovered in the Antarctic sector of the IWC Management Area II (from 0ºto 60ºW, e.g. Donovan, 1991) during summer months, two or three years after marking. These findings led Clarke (1962) to suggest that fin whales encountered in Chilean waters during the austral spring and summer might be individuals migrating to Antarctic waters to feed; and that animals sighted in the autumn might be individuals returning from Antarctic waters towards low-latitude breeding habitats (Acevedo et al., 2012).

However, the movement patterns observed in this study for fin whales tagged off Chile differ from Clarke's (1962) hypothesis and with traditional migratory patterns of balaenopterids. Four out of five whales followed during this study for periods greater than 47 days remained in the coastal waters off Chile during the summer and even early autumn and did not engage in typical migratory behaviour towards higher latitudes. The movement patterns of these four individuals did not conform to a spring/summer southern migration, as most of the animals remained in the north-central coastal region within 27º and 37ºS. Despite the small sample size, these results suggest that not all the fin whales perform concerted seasonal migrations. Lack of defined migratory patterns has also been found for fin whales in other localities. For instance, fin whales have been observed during the winter in high latitudes, such as the North Pacific Ocean (Mizroch, Rice, Zwiefelhofer, Waite, & Perryman, 2009), or even all year in high latitudes in both Northern (i.e. North Atlantic Ocean off Norway and near the Faroe Islands; Jonsgard, 1966) and Southern (near South Georgia; Mackintosh, 1946) Hemispheres (Edwards, Hall, Moore, Sheredy, & Redfern, 2015). On the other hand, the presence of fin whales in the summer months at lower latitudes has also been reported, in both the Northern (Notarbartolo Di Sciara et al., 2003; Oleson, Širović, Bayless, & Hildebrand, 2014) and Southern Hemispheres (Pérez et al., 2006; Sepúlveda et al., 2016).

Our results support the current view that at least some fin whale populations may not follow the typical seasonal migratory pattern of other baleen whales (e.g. humpback whales) with clearly defined low-latitude breeding grounds and high-latitude feeding habitats and that seasonal movements and habitat use are probably more complex (Edwards et al., 2015; Geijer et al., 2016; Mizroch et al., 2009). The presence of fin whales during summer in Chile, as well as information that many of the catches off Chile occurred in the same season than those in the Antarctica (International Whaling Commission catch records), suggest that there may be at least two different feeding sites for this fin whale population. Unfortunately, to our knowledge, no information exists about potential segregation between fin whales from Chile and Antarctica. Interestingly, the individual that departed earlier and travelled to higher latitudes was the only male tagged in this study. However, the low number of tagged whales precludes any speculation about potential sexual differentiation in fin whale movement patterns. Future studies should try to investigate if a potential foraging segregation exists among individuals and, in that case, if it relates to sex and/or age related issues.

Our sample size is small and the period whales were tracked is relatively short to reach firm conclusions about the migratory patterns (and connectivity) and the potential for age or sex-specific migratory timing and habitat use of fin whales off the western coast of South America. However, the results do suggest that some fin whales will remain along the coast of Chile during the summer and into the winter, exhibiting temporal residence for several months similar to other areas where the species occur, such as in the Mediterranean Sea (Notarbartolo Di Sciara et al., 2003), the Gulf of Alaska (Moore et al., 2006; Stafford et al., 2007), and the Gulf of California (Tershy et al., 1993; Urbán et al., 2005).

To further test hypotheses about movements, migratory behaviour and migratory destination of this species in the Southwest Pacific, additional satellite tagging studies with a substantially greater sample size is required. Satellite telemetry is an effective method to describe movements of highly migratory marine megafauna because it provides detailed information on location and extension of critical habitats (e.g. breeding and feeding) and the pathways used between these habitats (Bailey et al., 2009). However, telemetry studies should always be integrated with other methodologies such as individual photo-identification (Burns et al., 2014) and/or genetic identification (Rizzo & Schulte, 2009) as these methods can provide additional information on migration and migratory connectivity.

Habitats used as foraging spots

This study found that most of the tagged fin whales spent a substantial proportion (72.5%) of their time engaged in ARS behaviour in nearshore waters off Chile. While this behavioural mode could potentially represent different behavioural types (e.g. foraging, resting, breeding and other social interactions; Silva, Prieto, Jonsen, Baumgartner, & Santos, 2013), we believe that the observed ARS behaviour off Chile is likely associated with feeding. Some of the areas used by the tagged whales in this study have been previously documented as foraging places of fin whales through *in-situ* observation of feeding activity upon krill (*Euphausia mucronata*) and observation of faeces in the vicinity of fin whales (Pérez et al., 2006; Toro et al., 2016).

Higher proportions of ARS type behaviour and relatively high occupancy were recorded in three main areas: south of Copiapó to Coquimbo, near Valparaíso and near Concepción (Figures 2 and 3). Of these, only in the northernmost one, and specifically near Isla Chañaral (29ºS), had the regular presence of fin whales in the summer been previously documented (Pérez et al., 2006; Sepúlveda et al., 2016; Toro et al., 2016). The waters off Chile are well recognized for their relatively high biological productivity due to the presence of the Humboldt Current and important wind-driven coastal upwelling (Camus 1991). These three areas present biophysical conditions characterized by strong wind-driven upwelling in spring and summer seasons (Arcos & Salamanca, 1984; Johnson, Fonseca, & Sievers, 1980; Strub, Mesias, Montecino, Rutllant, & Salinas, 1998). Krill, the principal known prey of fin whales in Chile (Pérez et al., 2006), form an abundant component of the zooplankton fauna around these areas of coastal phytoplankton blooms (Riquelme-Bugueño et al., 2012), playing a keystone role in the food web of the Humboldt Current System (Antezana, 2010). The environmental characteristics of the central coast of Chile strongly suggest that fin whales use these zones as feeding grounds, in a manner similar to those observed for the Marine Reserves Isla Chañaral and Choros-Damas (Pérez et al., 2006; Toro et al., 2016).

Implications for further development of whale-watching and conservation

Our results emphasize that fin whales frequently occur and remain in different geographic areas along the coast of Chile, especially in the north-central areas. The occurrence of this species in different areas near the coast provides the opportunity for the development of whale-watching activities in peripheral coastal areas, where conditions for the successful development of this activity are particularly favourable (Garrod & Wilson, 2004). This has been the case of the fishing cove of Chañaral de Aceituno, close to the Marine Protected Area Reserva Marina Isla Chañaral, in which local fishermen provide whale-watching tours to tourists that visit the area with the certainty of encountering whales (Sepúlveda et al., 2016). The high levels of occupancy found in this area in the present study corroborates the relevance of this zone as a feeding ground for fin whales, thus supporting the continued development of a whale-watching activity there.

In addition, the results presented demonstrate that fin whales may occur at relatively high density and remain for extended periods of time in other areas along the Chilean coast. Similarities of these other areas with Chañaral de Aceituno (e.g. presence of small fishing coves between 28º and 32ºS) indicate the potential for the development of whale-watching activities elsewhere along the central Chilean coast. The information provided here may be used as a baseline for both local and national governments to evaluate the feasibility and to potentially plan, develop and regulate whale-watching activities in these areas.

Telemetry studies are effective to understand how whales use their habitat and therefore can provide data and elements for the development of marine protected areas. Currently, a Marine Protected Area of Multiple Uses is being moved forward to protect part of the habitat near Coquimbo (based partially on the presence of fin whales, Secretary of Environment Coquimbo), an area where thermoelectric power stations and mining sea ports have been projected. These projects could expose the animals to increased threats, such as ship strikes, which has been documented as an important source of mortality for fin whales (e.g. Panigada et al., 2006; Redfern et al., 2013). Other indirect but relevant threats related to these projects include anthropogenic underwater noise coming from different sources such as shipping and seismic explorations. In this respect it is crucial that measures are introduced to minimize noise levels overall and especially in biologically important areas, as well as implementing a monitoring programme to assess cumulative and synergistic effects on cetaceans from such developments (Weilgart, 2007). Thus, while the information on fin whale habitat use provided here is a first step to improve marine coastal planning, additional research and future tagging studies would be useful to develop a comprehensive database that could be considered in planning and regulating anthropogenic activities and mitigating their effects on a species with important conservation needs, such as the fin whale in Chile.

5. Acknowledgments

This research was funded by INNOVA-CORFO, project 14BPCR-33451, and approved by the Regional Council (CORE) of Atacama's Region. We acknowledge the participation of Daniel Díaz and Ricardo Curiqueo from the National Tourist Board, and Jorge Guerra from the Undersecretariat of Fisheries and Aquaculture. We are also very grateful to Patricio Ortiz and Luis González by their support in the field. This research was conducted under Permit No 2982/2015 of the Undersecretariat of Fisheries and Aquaculture, Ministry of Economy, Chile. MJP-A was financially supported by CONICYT Postdoctoral

FONDECYT Program 3140513. GP acknowledge CONICYT-PCHA/Doctorado Nacional/2016-21161109 PhD scholarship.

6. Literature cited

Aasen, E., & Medrano, J. F. (1990). Amplification of the Zfy and Zfx Genes for Sex Identification in Humans, Cattle, Sheep and Goats. *Nature Biotechnology, 8*, 1279-1281.

Acevedo, J., O'Grady, M., & Wallis, B. (2012). A note on a sighting of a large school of fin whales in the Eastern Subtropical South Pacific. *International Whaling Commission, 64*, SH2.

Aguayo, L. A. (1974). Baleen whales off continental Chile. In W. E. Schevill (Ed.), *The Whale Problem: A Status Report* (pp. 209–217). Cambridge, MA: Harvard University Press.

Aguayo-Lobo, A., Torres, D., & Acevedo, J. (1998). Los mamíferos marinos de Chile: 1. Cetacea. *Serie Científica INACH, 48*, 142.

Antezana, T. (2010). *Euphausia mucronata*: A keystone herbivore and prey of the Humboldt Current System. *Deep Sea Research Part II: Topical Studies in Oceanography, 57*, 652-662.

Arcos, D. F., & Salamanca, M. A. (1984). Distribucion de clorofila y condiciones oceanograficas frente a Chile central (latitudes 32 S–38 S, Febrero 1982). *Biologia Pesquera, 13*, 5-14.

Bailey, H., Mate, B. R., Palacios, D. M., Irvine, L., Bograd, S. J., & Costa, D. P. (2009). Behavioural estimation of blue whale movements in the Northeast Pacific from state-space model analysis of satellite tracks. *Endangered Species Research*, *10*, 93-106.

Branch, T. A., & Butterworth, D. S. (2001). Estimates of abundance south of 60ºS for cetacean species sighted frequently on the 1978/79 to 1997/98 IWC/IDCR-SOWER sighting surveys. *Journal of Cetacean Research and Management*, *3*, 251-270.

Burns, D., Brooks, L., Harrison, P., Franklin, T., Franklin, W., Paton, D., & Clapham, P. (2014). Migratory movements of individual humpback whales photographed off the eastern coast of Australia. *Marine Mammal Science*, *30*, 562-578.

Camus, P. A. (2001). Biogeografía marina de Chile continental. *Revista Chilena de Historia Natural*, *74*, 587-617.

Canese, S., Cardinali, A., Fortuna, C. M., Giusti, M., Lauriano, G., Salvati, E., & Greco, S. (2006). The first identified winter feeding ground of fin whales (*Balaenoptera physalus*) in the Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, *86*, 903-907.

Cisneros-Montemayor, A. M., Sumaila, U. R., Kaschner, K., & Pauly, D. (2010). The global potential for whale watching. *Marine Policy*, *34*, 1273-1278.

Clapham, P. J., & Baker, C. S. (2001). How many whales were killed in the Southern Hemisphere in the 20th century? *Report of the International Whaling Commission*, *53*, 3 pp.

Clarke, R. (1962). Whale observation and whale marking off the coast of Chile in 1958 and from Ecuador towards and beyond the Galapagos Islands in 1959. *Norsk Hvalfangsttid, 51*, 265-287.

Clarke, R., Aguayo, A., & Basulto, S. (1978). Whale observation and whale marking off the coast of Chile in 1964. *The Scientific Reports of the Whales Research Institute, 30*, 117-178.

Donovan, G. P. (1991). A review of IWC stock boundaries. *Report of the International Whaling Commission, 13*(special issue), 39-68.

Double, M. C., Andrews-Goff, V., Jenner, K. C. S., Jenner, M. N., Laverick, S. M., Branch, T. A., & Gales, N. J. (2014). Migratory movements of pygmy blue whales (*Balaenoptera musculus brevicauda*) between Australia and Indonesia as revealed by satellite telemetry. *PLoS ONE, 9*, e93578.

Edwards, E. F., Hall, C., Moore, T. J., Sheredy, C., & Redfern, J. V. (2015). Global distribution of fin whales *Balaenoptera physalus* in the post‐whaling era (1980–2012). *Mammal Review, 45*, 197-214.

Gales, N., Double, M. C., Robinson, S., Jenner, C., Jenner, M., King, E., . . . Raymond, B. (2009). Satellite tracking of southbound East Australian humpback whales (*Megaptera novaeangliae*): challenging the feast or famine model for migrating whales. *International Whaling Comission, SC61/SH17*, 12.

Garrigue, C., Clapham, P. J., Geyer, Y., Kennedy, A. S., & Zerbini, A. N. (2015). Satellite tracking reveals novel migratory patterns and the importance of seamounts for endangered South Pacific humpback whales. *Royal Society open science, 2*, 150489.

Garrod, B., & Wilson, J. C. (2004). Nature on the edge? Marine ecotourism in peripheral coastal areas. *Journal of Sustainable Tourism, 12*, 95-120.

Geijer, C. K., Notarbartolo di Sciara, G., & Panigada, S. (2016). Mysticete migration revisited: are Mediterranean fin whales an anomaly? *Mammal Review, 46*, 284-296.

Gilson, A., Syvanen, M., Levine, K., & Banks, J. (1998). Deer gender determination by polymerase chain reaction: Validation study and application to tissues, bloodstains, and hair forensic samples from California. *California Fish and Game, 84*, 159-169.

Harmer, S. F. (1928). The history of whaling. *Proceedings of the Linnaean Society of London, 140*, 1-95.

Heide-Jørgensen, M. P., Nordøy, E. S., Øien, N., Folkow, L. P., Kleivane, L., Blix, A. S., . . . Laidre, K. L. (2001). Satellite tracking of minke whales (*Balaenoptera acutorostrata*) off the coast of northern Norway. *Journal of Cetacean Research and Management, 3*, 175-178.

Hoyt, E. (2001). *Worldwide tourism numbers, expenditures, and expanding socioeconomic benefits*. Yarmouth Port, MA, USA: International Fund for Animal Welfare.

Johnson, D. R., Fonseca, T., & Sievers, H. (1980). Upwelling in the Humboldt coastal current near Valparaíso, Chile. *Journal of Marine Research, 38*, 1-16.

Jonsen, I. D., Flemming, J. M., & Myers, R. A. (2005). Robust state–space modeling of animal movement data. *Ecology, 86*, 2874-2880.

Jonsen, I. D., Myers, R. A., & James, M. C. (2007). Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Marine Ecology Progress Series, 337*, 255-264.

Jonsgard, A. (1966). The distribution of Balaenopteridae in the north Atlantic Ocean. In K. S. Norris (Ed.), *Whales, dolphins and porpoises* (pp. 114-124). Berkely: University of California Press.

Kawamura, A. (1994). A review of baleen whale feeding in the Southern Ocean. *Report of the International Whaling Commission, 44*, 261-271.

Krützen, M., Barré, L., Möller, L., Heithaus, M., Simms, C., & Sherwin, W. (2002). A biopsy system for small cetaceans: darting success and wound healing in *Tursiops* spp. *Marine Mammal Science, 18*, 863-878.

Littaye, A., Gannier, A., Laran, S., & Wilson, J. P. (2004). The relationship between summer aggregation of fin whales and satellite-derived environmental conditions in the northwestern Mediterranean Sea. *Remote Sensing of Environment, 90*, 44-52.

Mackintosh, N. A. (1946). The natural history of whalebone whales. *Biological Reviews, 21*, 60-74.

Mackintosh, N. A. (1966). The distribution of southern blue and fin whales. In K. S. Norris (Ed.), *Whales, dolphins, and porpoises* (pp. 125-144). Berkley: University of California Press.

Miyashita, T., Kato, H., & Kasuya, T. (1995). *Worldwide Map of Cetacean Distribution Based on Japanse Sighting Data.* (Vol. 1). Shimizu, Shizuoka, Japan: National Research Institute of Far Sea Fisheries.

Mizroch, S. A., Rice, D. W., & Breiwick, J. M. (1984). The fin whale, Balaenoptera physalus. *Marine Fisheries Review, 46*, 20-24.

Mizroch, S. A., Rice, D. W., Zwiefelhofer, D., Waite, J., & Perryman, W. L. (2009). Distribution and movements of fin whales in the North Pacific Ocean. *Mammal Review, 39*, 193-227.

Moore, S. E., Stafford, K. M., Mellinger, D. K., & Hildebrand, J. A. (2006). Listening for large whales in the offshore waters of Alaska. *Bioscience, 56*, 49-55.

Notarbartolo Di Sciara, G., Zanardelli, M., Jahoda, M., Panigada, S., & Airoldi, S. (2003). The fin whale *Balaenoptera physalus* (L. 1758) in the Mediterranean Sea. *Mammal Review, 33*, 105-150.

O'Connor, S., Campbell, R., Cortez, H., & Knowles, T. (2009). Whale watching worldwide: tourism numbers, expenditures and expanding economic benefits, a special report from International Fund for Animal Welfare. Yarmouth MA, USA.

Oleson, E. M., Širović, A., Bayless, A. R., & Hildebrand, J. A. (2014). Synchronous seasonal change in fin whale song in the North Pacific. *PLoS ONE, 9*, e115678.

Pacheco, A. S., Villegas, V. K., Riascos, J. M., & Van Waerebeek, K. (2015). Presence of fin whales (*Balaenoptera physalus*) in Mejillones Bay, a major seaport area in northern Chile. *Revista de Biología Marina y Oceanografía, 50*, 383-389.

Panigada, S., Pesante, G., Zanardelli, M., Capoulade, F., Gannier, A., & Weinrich, M. T. (2006). Mediterranean fin whales at risk from fatal ship strikes. *Marine Pollution Bulletin, 52*, 1287-1298.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T. J., Sumaila, U. R., Walters, C. J., . . . Zeller, D. (2002). Towards sustainability in world fisheries. *Nature, 418*, 689-695.

Pérez, M., Thomas, F., Uribe, F., Sepúlveda, M., Flores, M., & Moraga, R. (2006). Fin Whales (*Balaenoptera physalus*) Feeding on Euphausia mucronata in Nearshore Waters off North-Central Chile. *Aquatic Mammals, 32*, 109-113.

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In K. Hornik, F. Leisch, & A. Zeileis (Eds.), *Proceedings of the 3rd international workshop on distributed statistical computing*. Viena: Technische Universität Wien.

R Development Core Team. (2013). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria.

Redfern, J. V., McKenna, M. F., Moore, T. J., Calambokidis, J., Deangelis, M. L., Becker, E. A., . . . Chivers, S. J. (2013). Assessing the risk of ships striking large whales in marine spatial planning. *Conservation Biology*, *27*, 292-302.

Reeves, R., Stewart, B., Clapham, P., & Powell, J. (2002). *Guide to marine mammals of the world*. New York: Knopf, Inc.

Reilly, S. B., Bannister, J. L., Best, P. B., Brown, M., Brownell Jr., R. L., Butterworth, D. S., . . . Zerbini, A. N. (2013). *Balaenoptera physalus*. *The IUCN Red List of Threatened Species, 2013*, e.T2478A44210520.

Riquelme-Bugueño, R., Núñez, S., Jorquera, E., Valenzuela, L., Escribano, R., & Hormazábal, S. (2012). The influence of upwelling variation on the spatially-structured euphausiid community off central-southern Chile in 2007–2008. *Progress in Oceanography, 92*, 146-165.

Rizzo, L. Y., & Schulte, D. (2009). A review of humpback whales' migration patterns worldwide and their consequences to gene flow. *Journal of the Marine Biological Association of the United Kingdom, 89*, 995-1002.

Roberts, J. J., Best, B. D., Dunn, D. C., Treml, E. A., & Halpin, P. N. (2010). Marine Geospatial Ecology Tools: An integrated framework for ecological geoprocessing with ArcGIS, Python, R, MATLAB, and C++. *Environmental Modelling & Software, 25*, 1197-1207.

Sepúlveda, M., Oliva, D., Pavez, G., & Santos-Carvallo, M. (2016). *Caleta Chañaral de Aceituno: Destino turístico de alta calidad para el avistamiento de cetáceos, otros mamíferos y aves marinas*. Valparaíso, Chile: Obra independiente.

Silva, M. A., Prieto, R., Jonsen, I., Baumgartner, M. F., & Santos, R. S. (2013). North Atlantic blue and fin whales suspend their spring migration to forage in middle latitudes: building up energy reserves for the journey? *PLoS ONE, 8*, e76507.

Širović, A., Hildebrand, J. A., Wiggins, S. M., & Thiele, D. (2009). Blue and fin whale acoustic presence around Antarctica during 2003 and 2004. *Marine Mammal Science, 25*, 125-136.

Stafford, K. M., Mellinger, D. K., Moore, S. E., & Fox, C. G. (2007). Seasonal variability and detection range modeling of baleen whale calls in the Gulf of Alaska, 1999–2002. *The Journal of the Acoustical Society of America*, *122*, 3378-3390.

Strub, P. T., Mesias, J. M., Montecino, V., Rutllant, J., & Salinas, S. (1998). Coastal ocean circulation off western South America. In A. R. Robinson & K. H. Brink (Eds.), *The Sea, 11* (pp. 273-313). New York: John Wiley and Sons.

Tershy, B. R., Urbán-Ramírez, J., Bréese, D., Rojas-Bracho, L., & Findley, L. T. (1993). Are fin whales resident to the Gulf of California. Rev. Invest. Cient., Univ. Auton. de Baja California Sur, 1, 69-71. *Revista de Investigación Cientifica, 1*, 69-71.

Toro, F., Vilina, Y. A., Capella, J. J., & Gibbons, J. (2016). Novel Coastal Feeding Area for Eastern South Pacific Fin Whales (*Balaenoptera physalus*) in Mid-Latitude Humboldt Current Waters off Chile. *Aquatic Mammals*, *42*, 47-55.

Urbán, R. J., Rojas-Bracho, L., Guerrero-Ruíz, M., Jaramillo-Legorreta, A., & Findley, L. T. (2005). Cetacean diversity and conservation in the Gulf of California. . In J. E. Cartron, G. Ceballos, & R. S. Felger (Eds.), *Biodiversity, ecosystems, and conservation in northern Mexico* (pp. 276-297). New York: Oxford University Press.

Visser, F., Hartman, K. L., Pierce, G. J., Valavanis, V. D., & Huisman, J. (2011). Timing of migratory baleen whales at the Azores in relation to the North Atlantic spring bloom. *Marine Ecology Progress Series, 440*, 267-279.

Weilgart, L. S. (2007). The impacts of anthropogenic ocean noise on cetaceans and implications for management. *Canadian Journal of Zoology, 85*, 1091-1116.

Zerbini, A. N., Andriolo, A., Heide-Jørgensen, M. P., Moreira, S. C., Pizzorno, J. L., Maia, Y. G., . . . DeMaster, D. P. (2011). Migration and summer destinations of humpback whales (*Megaptera novaeangliae*) in the western South Atlantic Ocean. *Journal of Cetacean Research and Management, 3*, 113-118.

Zerbini, A. N., Andriolo, A., Heide-Jørgensen, M. P., Pizzorno, J. L., Maia, Y. G., VanBlaricom, G. R., . . . Bethlem, C. (2006). Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the Southwest Atlantic Ocean. *Marine Ecology Progress Series, 313*, 295-304.

Zerbini, A. N., Robbins, J., Andrews, R., Andrews-Goff, V., Baumgartner, M., Clapham, P. K., . . . Wilon, S. (2017). *Development of robust large whale satellite tags improve tag performance and reduces animal welfare problems.* Paper presented at the 22nd Biennial Conference on the Biology of Marine Mammals, Halifax, Canada.

Tables

Table 1. Summary of satellite tags performance and movement descriptors from the Argos location data. data. Ptt indicates the code for each fin whale.

Tag type	Ptt numbers	Sex	Deployment date	Tracking duration (days)	Track distance (Km)
SPLASH 10	121200	Female	11/24/2015	4	128.6
SPLASH 10	121195	-	11/25/2015	77	2168.1
SPOT 6	123226	Female	11/29/2015	54	2519.5
SPOT 6	121206	Female	12/01/2015	162	8541.9
SPLASH10	120946	Female	12/04/2015	61	2088.3
SPLASH10	112726	Male	12/05/2015	47	3907.8
				67.5 ± 52.3	3225.7 ± 2871.6

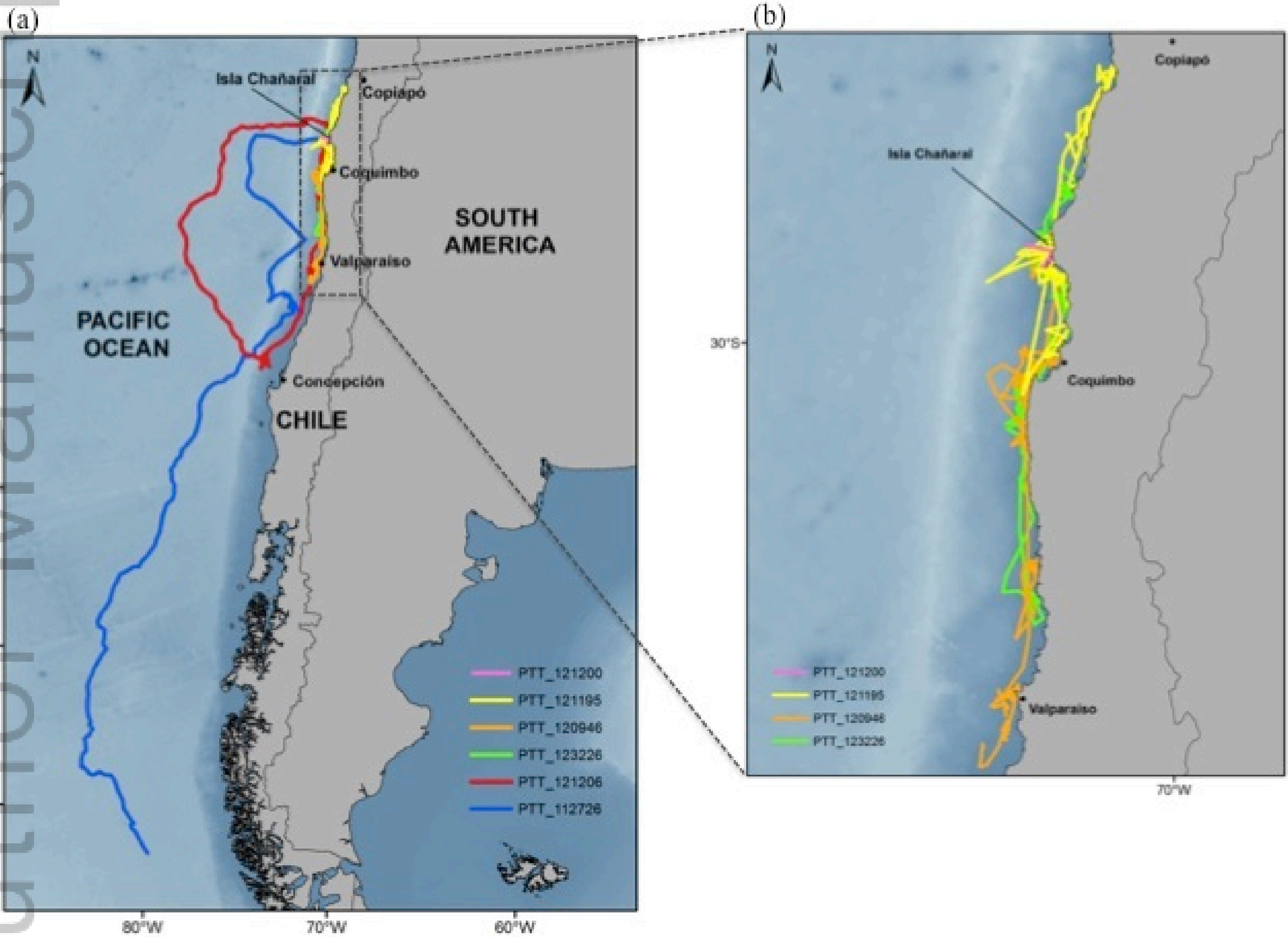
Figure captions

Figure 1. (a) Tracks of individual fin whales instrumented with satellite tags near the Marine Reserves Isla Chañaral and Choros-Damas. Colors indicate the trajectory followed by each individual. (b) Zoomed view of the north-central area showing the movements followed by four of the six individuals does remain in that area.

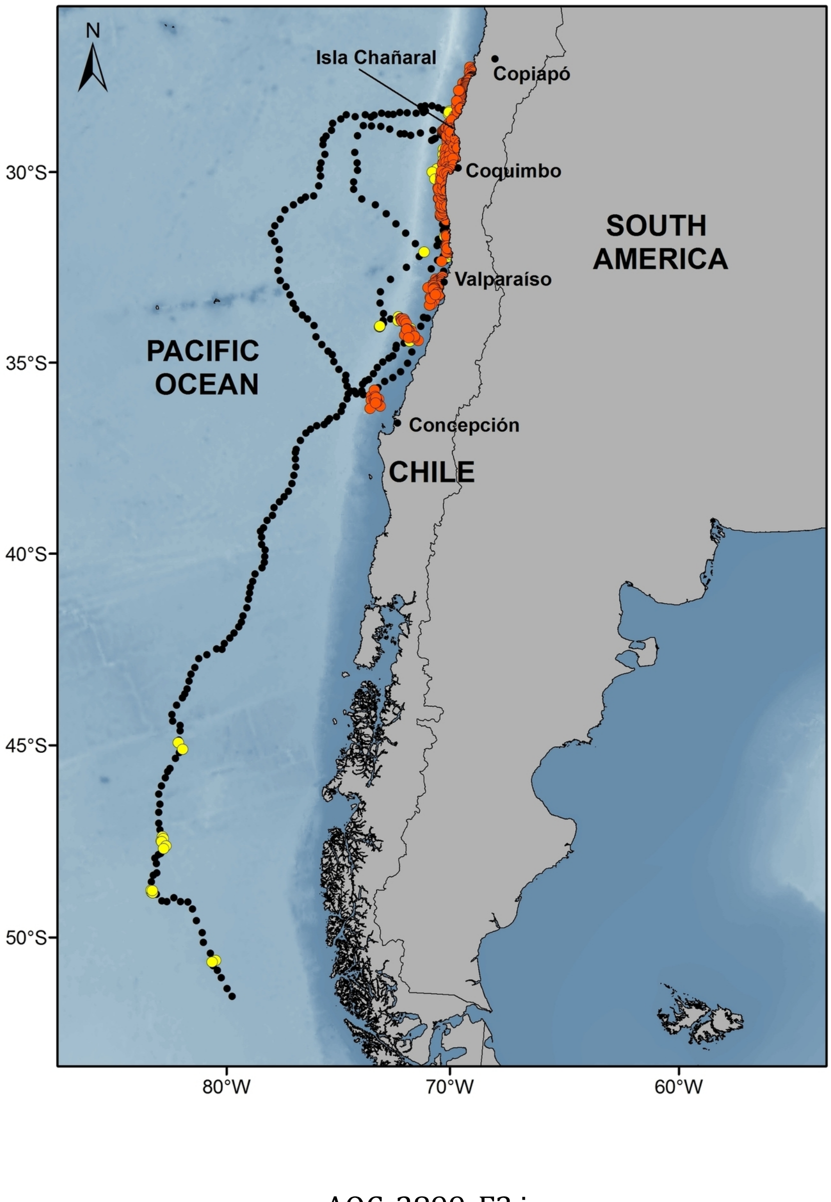
Figure 2. Behavioural states estimated by the switching state-space model (SSSM) applied to fin whale Argos data. States are color-coded as follows: area-restricted search (ARS) - red dots; transiting - black dots, and uncertain - yellow dots.

Figure 3. Occupancy time (whale hours) computed for five fin whales tagged off Chile (see text for details). Grids are 50 x 50 km in size.

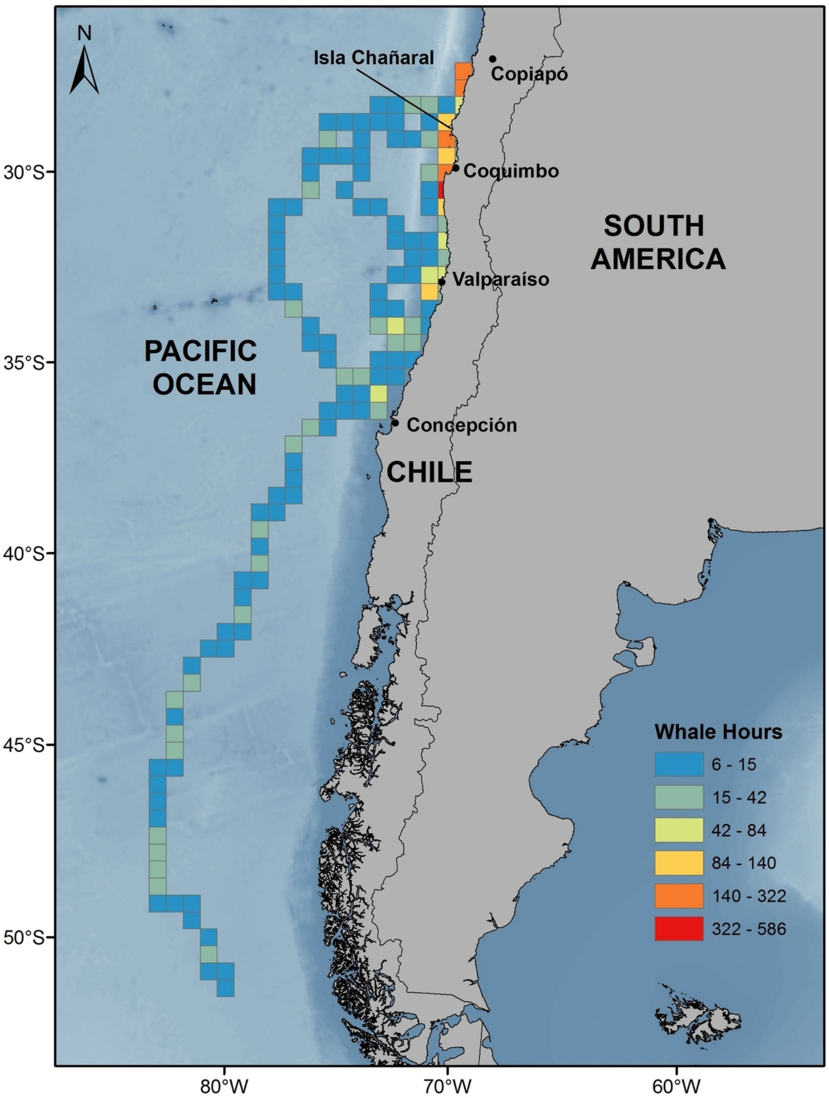
Figure 4. Relationship between SSSM-predicted locations classified as ARS behaviour (black circles) and seasonal (September 2015-January 2016) Chlorophyll-a (mg/mm^3) concentration. Note consistency between ARS locations and areas of high productivity.



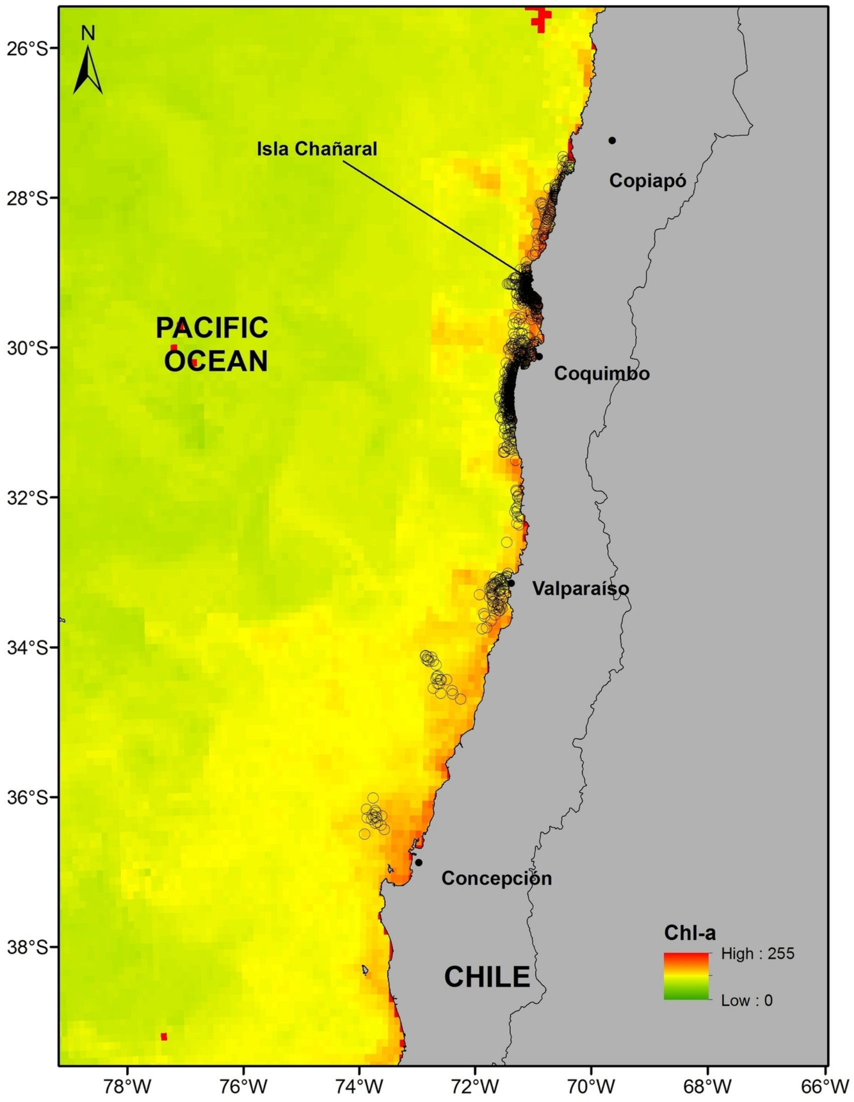
AQC_2899_F1.jpg



AQC_2899_F3.jpg



AQC_2899_F4.jpg



AQC_2899_F5.jpg