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From whaling to whale watching: Identifying fin whale critical foraging habitats off the Chilean coast

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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 of Isla Chañaral and Islas Choros-Damas (approximately 29°S) 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 for periods ranging between 4 and 162 days (mean = 68 ± 52 days), covering an average distance of 3225.7 ± 2871.6 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 at middle latitudes, probably using critical habitats 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 for this species in Chile.

KEYWORDS

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., 2006, 2011). 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' in the International Union for Conservation of Nature (IUCN) Red List.

Information of the distribution and movements of fin whales in the south-east 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 4500 individuals taken, mainly in January, in coastal and oceanic waters between 18 and 22°S and between 29 and 40°S (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 Juan Fernández Islands (33°77'S, 80°78'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 more often in the oceanic habitats of Chilean waters (Clarke, 1962). This notion is now changing, however, because of the regular presence of fin whales in coastal waters at latitudes between 23 and 29°S during spring and summer (Pacheco, Villegas, Riascos, & Van Waerebeek, 2015; Pérez et al., 2006; Sepúlveda, Oliva, Pavez, & Santos-Carvalho, 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). Recent studies on migration patterns of baleen whales suggest that this traditional migration pattern may not be valid for all populations, however (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-Ruiz, 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 (approximately 29°S) during the austral summer months of January and February. 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 the 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 economic 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: termed 'whale watching'. Whale watching has exponentially grown globally over 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 in 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 suggests that there is high potential for this activity to expand in the south-east Pacific Ocean. Thus, the 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: (i) investigate the movements and habitat use of this species in the south-east Pacific Ocean; and (ii) to identify high-use areas, which could potentially be used for expanding whale-watching activities.

2 | METHODS

2.1 | 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 24 November and 5 December 2015, daily trips to search for fin whales were undertaken under calm and favourable weather and 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 for assessing preferred habitats during a time of the year that was convenient for whale watching, as the summer represents the peak of the tourist season.

2.2 | Satellite tag deployment and biopsy collection

Six Argos implantable tags were deployed on fin whales. 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 temperature and depth profiles, in addition to location data (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 the 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 the impact to individual whales (Zerbini et al., 2017).

Satellite tags were deployed using a modified pneumatic line thrower: 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 programmed 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 0.22-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 performed two or three times per individual, and DNA from an individual of known sex was amplified as a positive control.

2.3 | 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 4 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

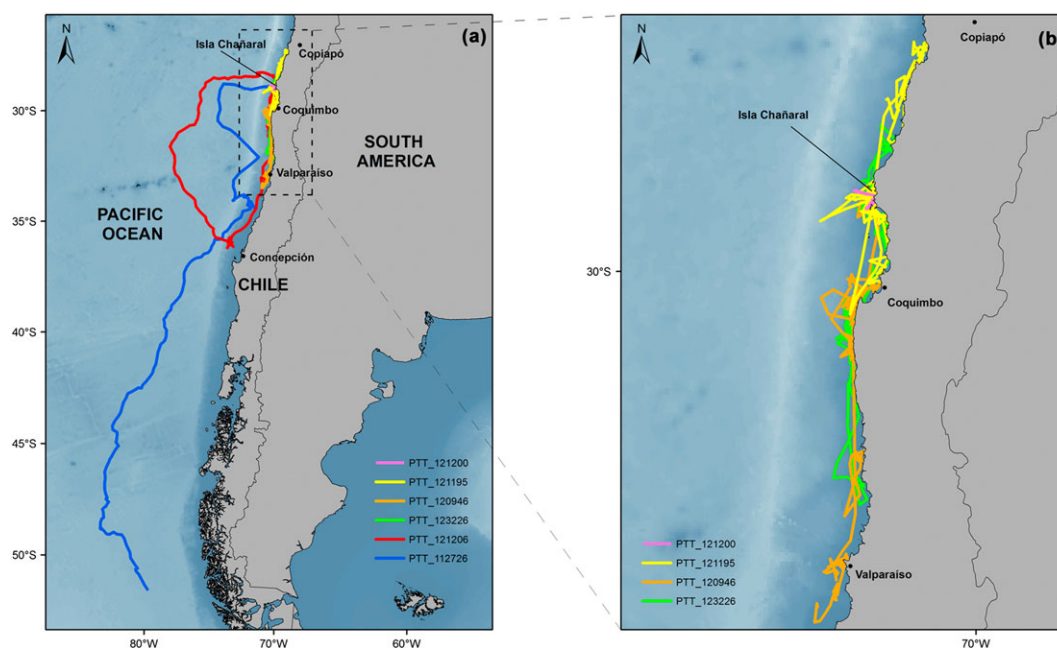


FIGURE 1 (a) Tracks of individual fin whales instrumented with satellite tags near the marine reserves Isla Chañaral and Choros-Damas. Colours indicate the trajectory followed by each individual. (b) Zoomed-in view of the north-central area showing the tracked movements for four of the six individuals that remained in this area

errors (measurement equation) and from the 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 *JAGS* (Plummer, 2003). The model was fitted to each individual data set, with a total of 70 000 MCMC samples, and with the first 40 000 discarded as burn-in. In order to reduce autocorrelation, the remaining 30 000 samples were reduced to 3000 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.

2.4 | 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 50×50 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, providing relevant information on habitat use (Garrigue, Clapham, Geyer, Kennedy, & Zerbini, 2015).

2.5 | 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-*a* raster images for the period September 2015 to January 2016 were downloaded and processed using the Marine Geospatial Ecology Tools (MGET 0.8a49) in the ArcGIS geographic information

system (Roberts, Best, Dunn, Trembl, & Halpin, 2010). These images consisted of a binned product at a 9-km resolution. Monthly images were averaged in ARCMAP 10.1 (ESRI, Redlands, CA, USA). 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 3-month time lag between the peak of phytoplankton and the peak in zooplankton concentration (Visser, Hartman, Pierce, Valavanis, & Huisman, 2011), Chl-*a* images included a period prior to the onset of the tagging operations.

3 | RESULTS

3.1 | Movement of individual whales

The six tagged fin whales were tracked for periods ranging from 4 to 162 days (mean = 67.5 ± 52.3 days), rendering an average of 723.5 ± 885.3 raw locations for each individual (range 21–2484). Throughout the tracking period, satellite-tagged whales covered an average distance of 3225.7 ± 2871.6 km (range 128.6–8541.9 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 high individual variability (Figure 1a). Three whales (Platform Transmitter Terminal (PTT) numbers: 121195, 120946, and 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 that 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 450 km towards the west in oceanic waters, travelled to the south, and, at a latitude of about 36°S , moved inshore and then travelled back to the north. It remained in the waters near Coquimbo (30°S) (Figure 1a) for another 4 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 52°S (Figure 1a).

TABLE 1 Summary of satellite-tag performance and movement descriptors from the Argos location data

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
SPLASH 10	120946	Female	12/04/2015	61	2088.3
SPLASH 10	112726	Male	12/05/2015	47	3907.8
				67.5 ± 52.3	3225.7 ± 2871.6

Platform Transmitter Terminal (PTT), code for each fin whale.

3.2 | Results of the switching state-space model and occupancy time

The SSSM showed that fin whales predominantly engaged in the ARS behavioural mode (72.5% of the locations) during the period that 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).

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

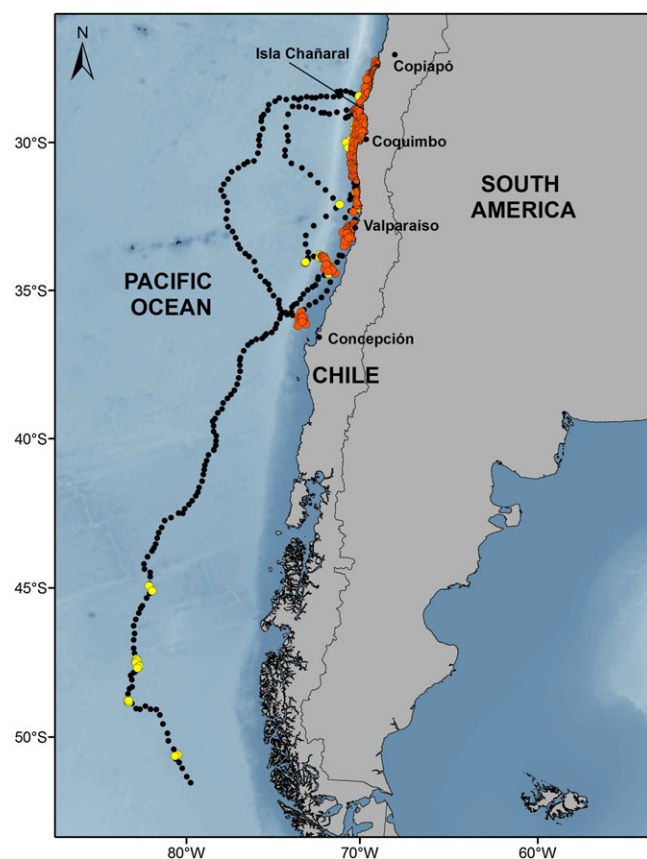


FIGURE 2 Behavioural states estimated by the switching state-space model (SSSM) applied to the Argos data for fin whales. States are colour-coded as follows: red dots, area-restricted search (ARS); black dots, transiting; and yellow dots, uncertain

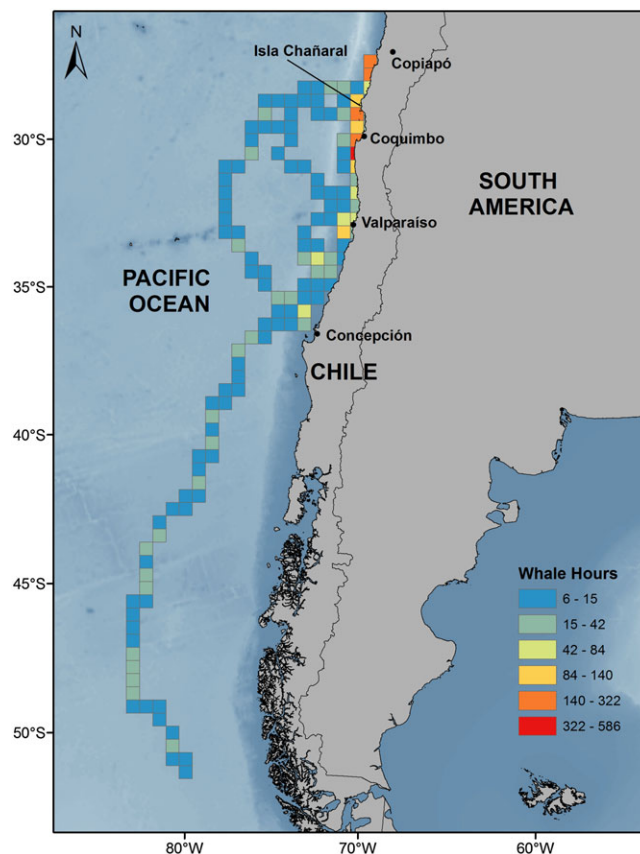


FIGURE 3 Occupancy time (whale hours) computed for five fin whales tagged off Chile (see text for details). Grids are 50 × 50 km in size

4 | DISCUSSION

To our knowledge, this is the first study examining the movements, behaviour, and habitat use of fin whales in the south-east 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 about the foraging patterns of fin whales, but also could be of particular interest for the development of whale-watching activity, and also as a baseline for continuing conservation and management efforts for this species in Chile. A greater sample size is required to assess the movement patterns of fin whales off Chile with greater confidence, however.

4.1 | 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 then migrating to summer feeding areas (Mackintosh, 1946; Mizroch et al., 1984). Four of a total of 11 fin whales tagged with Discovery marks off the central coast of Chile (30°24'–33°40'S) in the spring of 1958 were recovered in the Antarctic sector of the IWC Management Area II (from 0° to 60°W; e.g. Donovan, 1991) during the summer months, 2 or 3 years after marking. These findings led Clarke (1962) to

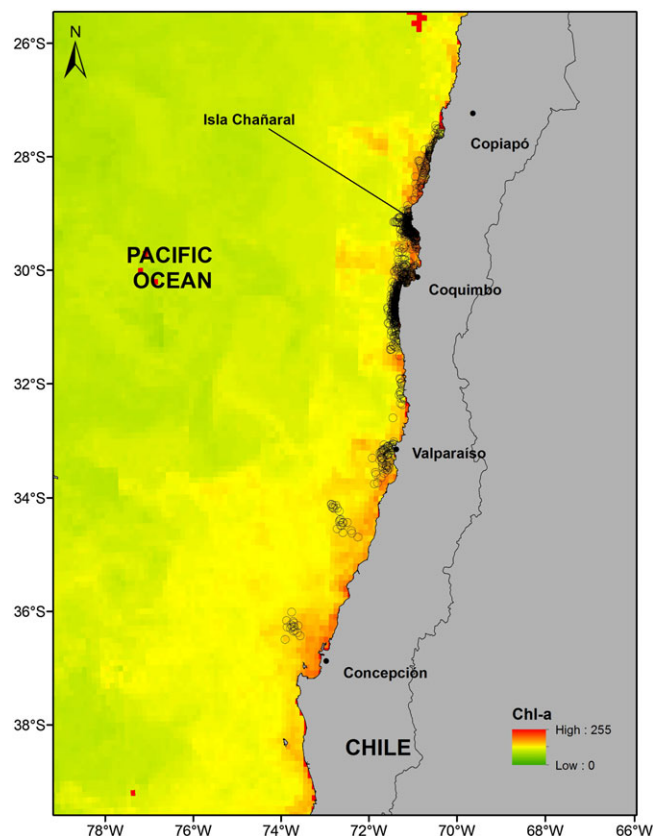


FIGURE 4 Relationship between locations classified as hosting whales demonstrating area-restricted search (ARS) behaviour (black circles), as predicted by the switching state-space model (SSSM), and seasonal (September 2015–January 2016) chlorophyll-*a* concentration (mg m^{-3}). Note the consistency between ARS locations and areas of high productivity

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).

The movement patterns observed in this study for fin whales tagged off of Chile differ from Clarke's (1962) hypothesis, and with the traditional migratory patterns of baleenopterids. However, 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 27°–37°S. Despite the small sample size, these results suggest that not all of the fin whales perform concerted seasonal migrations. A 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 round in high latitudes in both the Northern Hemisphere (i.e. North Atlantic Ocean off Norway and near the Faroe Islands; Jonsgard, 1966) and the Southern Hemisphere (near South Georgia;

Edwards, Hall, Moore, Sheredy, & Redfern, 2015; Mackintosh, 1946). On the other hand, the presence of fin whales in the summer months at lower latitudes has also been reported, in both the Northern Hemisphere (Notarbartolo Di Sciara et al., 2003; Oleson, Širović, Bayless, & Hildebrand, 2014) and the Southern Hemisphere (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 of Chile occurred in the same season as those in 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 whether potential foraging segregation exists among individuals and, in that case, if it relates to sex and/or age-related factors.

Our sample size was small and the period for which the whales were tracked was 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. The results do suggest, however, 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 any hypotheses about movements, migratory behaviour, and migratory destination of this species in the south-west Pacific, additional satellite-tagging studies with substantially greater sample sizes are required. Satellite telemetry is an effective method to describe the movements of highly migratory marine megafauna because it provides detailed information on the 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.

4.2 | 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. Although 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 to be 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 through the 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 levels were recorded in three main areas: from south of Copiapó to Coquimbo, near Valparaíso, and near Concepción (Figures 2 and 3). Of these, only in the northernmost area, and specifically near Isla Chañaral (29°S), 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 of Chile are well recognized for their relatively high biological productivity because of the presence of the Humboldt Current and important wind-driven coastal upwelling (Camus, 2001). These three areas present biophysical conditions characterized by strong wind-driven upwelling in the 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 protected areas Isla Chañaral and Islas Choros-Damas (Pérez et al., 2006; Toro et al., 2016).

4.3 | Implications for the further development of whale watching and conservation

Our results emphasize that fin whales frequently occur and remain in different geographical 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 whale-watching activity in this place.

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 28° and 32°S) 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 for understanding 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 forwards to protect part of the habitat near Coquimbo an area where thermoelectric power stations and mining sea ports have been proposed. 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 exploration. 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 the cumulative and synergistic effects on cetaceans from such developments (Weilgart, 2007). Thus, although 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.

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