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# Diel differences in blue whale (*Balaenoptera musculus*) dive behavior increase nighttime risk of ship strikes in northern Chilean Patagonia

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## Abstract

The northern Chilean Patagonia region is a key feeding ground and a nursing habitat in the southern hemisphere for blue whales (*Balaenoptera musculus*). From 2014 to 2019, during 6 separate research cruises, the dive behavior of 28 individual blue whales was investigated using bio-logging tags (DTAGs), generating ≈190 h of data. Whales dove to significantly greater depths during the day compared to nighttime (day: 32.6 ± 18.7 m; night: 6.2 ± 2.7 m; $P < 0.01$). During the night, most time was spent close to the surface (86% ± 9.4%; $P < 0.01$) and at depths of less than 12 m. From 2016 to 2019, active acoustics (scientific echosounders) were used to record prey (euphausiids) density and distribution simultaneously with whale diving data. Tagged whales appeared to perform dives relative to the vertical migration of prey during the day. The association between diurnal prey migration and shallow nighttime dive behavior suggests that blue whales are at increased risk of ship collisions during periods of darkness since the estimated maximum ship draft of vessels operating in the region is also ≈12 m. In recent decades, northern Chilean Patagonia has seen a large increase in marine traffic due to a boom in salmon aquaculture and the passenger ship industry. Vessel strike risks for large whales are likely underestimated in this region. Results reported in this study may be valuable for policy and mitigation decisions regarding conservation of the endangered blue whale.

**Key words:** bio-logging tags, blue whale, diving profile, ocean conservation, prey distribution

## INTRODUCTION

Blue whales are the largest animal living on earth and have survived despite being hunted nearly to extinction by whalers in the 1900s (Clarke *et al.* 1978; Branch *et al.* 2007). In the Southeast Pacific, blue whales were primarily taken off the Chilean coast, but some were also

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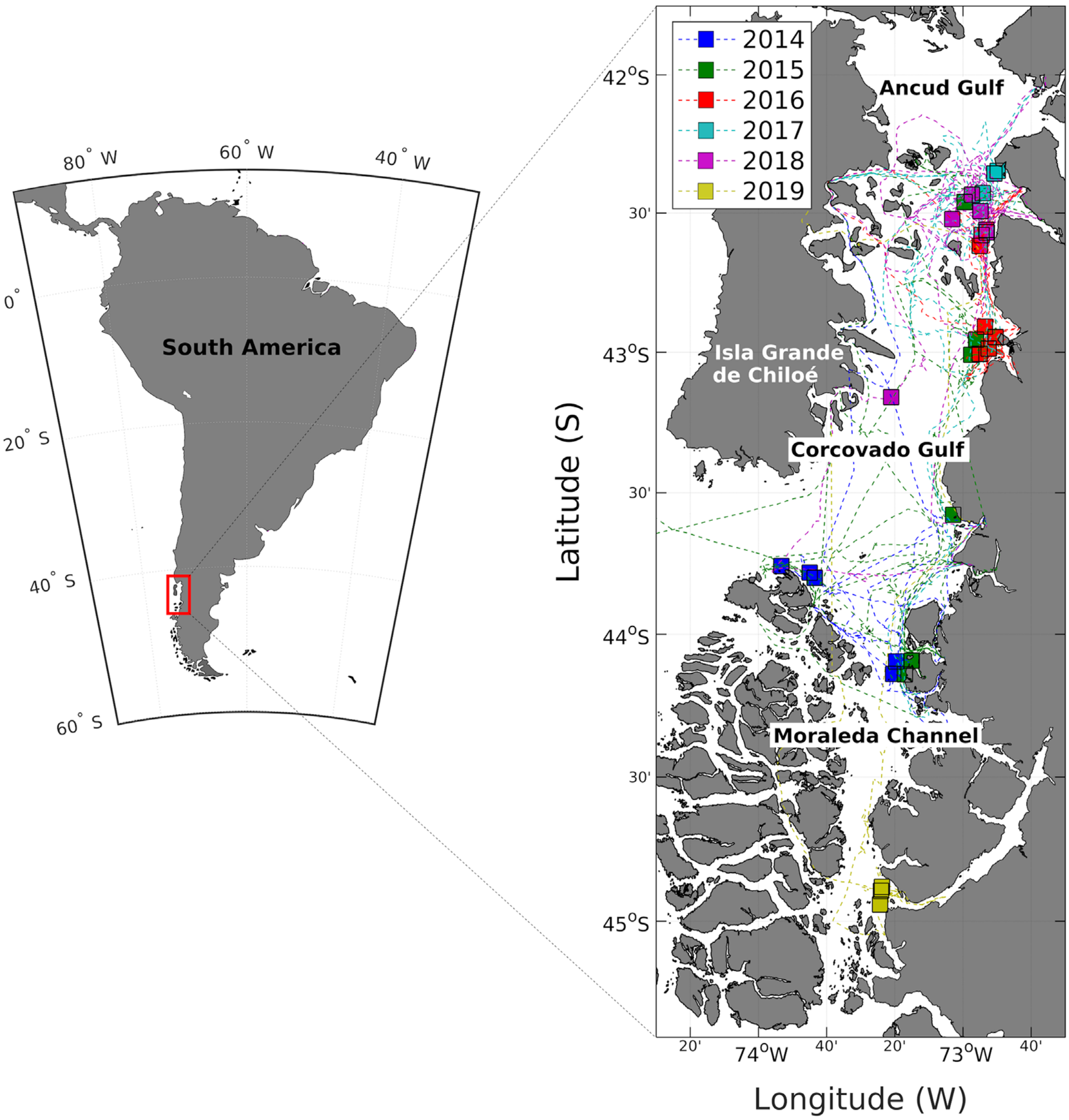

**Figure 1** Map of the study region off the coast of Chile (on the right, reference to the location in South America), showing color correlated tag deployments (filled squares) and cruise tracks (dashed lines) for each survey year.

caught around Peru and Ecuador (Clarke *et al*. 1978; Ramírez 1983; Van Waerebeek *et al*. 1997). In Chile, the first commercial catches occurred in 1908 (Pastene & Quiroz 2010), and between 1926 and 1971 thousands of catches were reported in the southern region of the country (Aguayo-Lobo *et al*. 1998; Williams *et al*. 2011). Globally, the species has been protected by the International Whaling Commission (IWC) since 1966, but illegal whaling continued into the early 1970s (Laws 1977; Yablokov 1994; Clapham *et al*. 1999; Thomas *et al*. 2015). The current status of the species is “Endangered” (IUCN red list, Cooke 2018), and its recovery is now a key international conservation goal (Roman *et al*. 2014).

Since protection measures were enacted, blue whale populations slowly recovered and an important discovery was made in January 1998, when a population was found in the Gulf of Corcovado in the Chiloense Ecoregion of southern Chile (Thiele *et al*. 1998). This area, situated in northern Chilean Patagonia (Fig. 1), is one of the most important fjord regions in the world and considered a key feeding and nursing habitat for blue whales in the southern hemisphere (Hucke-Gaete *et al*.

2003), and a critical habitat for other cetacean species (Español-Jiménez & van der Schaar 2018). In general, three subspecies of blue whales are currently recognized in the southern hemisphere: the pygmy blue whale (*Balaenoptera musculus brevicauda*) in the Indian Ocean and western Pacific Ocean; the Antarctic blue whale (*B. m. intermedia*) in the Antarctic Zone, and the yet unnamed Chilean blue whale (*B.m.* spp.), which was added in the List of Proposed Subspecies by the Taxonomy Committee of the Society for Marine Mammalogy (https://marinemammalscience.org/species-information/list-marine-mammal-species-subspecies/list-of-proposed-un-named-marine-mammal-species-and-subspecies/). These three subspecies all appear to be present in northern Chilean Patagonia and they are morphologically (Branch *et al.* 2007; Pastene *et al.* 2020; Leslie *et al.* 2020), genetically (LeDuc *et al.* 2007, 2017), and acoustically (McDonald *et al.* 2006; Buchan *et al.* 2018) distinct. Recently, Leslie *et al.* (2020) confirmed using aerial photogrammetry that blue whales from the Gulf of Corcovado are a unique subspecific taxon, the Chilean blue whale. In this study, henceforth the reference to blue whale will not take into account the three subspecies distinction.

In the Chiloense Ecoregion, distribution and dive behavior of blue whales is often driven by the distribution of their krill (*Euphausiacea*) prey (Buchan *et al.* 2014), which is linked with high levels of primary productivity originated by upwelling phenomena, topographic breaks, and/or frontal regions (Croll *et al.* 2005; Gill *et al.* 2011). Goldbogen *et al.* (2011) considered a prey biomass requirement for an average-sized blue whale (25 m) of 1120 ± 359 kg krill per individual per day, in order to meet energetic demands. Blue whales are known to feed during the austral summer and autumn in northern Chilean Patagonia region (from late December to early August), off Isla Grande de Chiloé (Cummings & Thompson 1971a,b; Gilmore 1971; Findlay *et al.* 1998; Hucke-Gaete *et al.* 2003; Cabrera *et al.* 2005; Abramson & Gibbons 2010; Forsterra & Haussermann 2012; Galletti Vernazzani *et al.* 2012; Buchan *et al.* 2014).

The dominant mesozooplankton species in the area is *Euphausia vallentini* (Antezana 1976), being twice as abundant in spring compared to winter and with a seasonal peak during late summer (González *et al.* 2010; Buchan *et al.* 2014). Foraging success of blue whales depends not only on the abundance of euphausiid aggregations, but also on their density (Goldbogen *et al.* 2011). The significance of prey abundance and density contribute to evidence that whales concentrate their efforts in relatively small areas ($<1$ km$^2$) while foraging (Acevedo-Gutiérrez *et al.* 2002). Therefore, they are mainly concentrated in small areas during feeding behavior and this creates a potentially dangerous habitat for the species, especially in relation to the large increase of marine traffic that has occurred during recent decades in northern Chilean Patagonia (Wilmsmeier 2013).

The peak in marine traffic in the area occurs during the austral summer, which is also the season with the highest density of feeding blue whales. The large increase in ship traffic was mainly due to the booming salmon aquaculture industry (Quiñones *et al.* 2019). Chile is currently the second-largest producer and exporter of farmed salmon in the world (Asche *et al.* 2013; Poblete *et al.* 2019). The vessels serving this industry are predominantly small work boats and cargo vessels; transporting fish feed and equipment throughout the region. Additionally, passenger vessels, medium size bulk carriers, and container ships are important components of the marine traffic in this area (Wilmsmeier 2013). Commercial shipping to and from the two main ports of the northern Chilean Patagonia region, Chacabuco and Puerto Montt, has grown by 9.9% in the last 15 years (Wilmsmeier 2013). The max allowable draft for ships navigating to both these ports is 12.2 m (data received by local Port Authorities, www.empormontt.cl). Together with the port of Quellon, situated in core blue whale habitat, these are some of the busiest ports in Chile (DIRECTEMAR 2018; https://www.directemar.cl/directemar/site/artic/20180626/asocfile/20180626110701/baem2018.pdf). Consequentially, ship-related threats for baleen whales in the area are collisions (Hucke-Gaete *et al.* 2013; Calambokidis *et al.* 2019), accidents (e.g. oil spills, marine debris, bycatch) and noise pollution (Colpaert *et al.* 2016). This is the region with the highest density of cetacean stranding along Chile (Alvarado-Rybak *et al.* 2020).

Nowadays, the average size of modern merchant ships has increased around the world, with a concomitant increase in draft that extends the “strike zone” for marine mammals (van der Hoop *et al.* 2012). Moreover, strike risk has also increased due to both faster speeds of modern vessels (van der Hoop *et al.* 2012), and specifically in northern Chilean Patagonia due to a booming austral summer cruising/tourism market (Wilmsmeier 2013). Passenger ships sail from Puerto Montt to southern destinations including Puerto Natales, Punta Arenas, Cape Horn and Antarctica, travelling at a speed of 18–20 kn (A. Bocconcelli, pers. comm.). While the economic development resulting from these industries is positive to the Chiloense Ecoregion, the increase in human activities is a serious challenge to its natural heritage and marine biodiversity (Pantoja *et al.* 2011; Aguilera *et al.* 2019).

Multidisciplinary research efforts have recently been used to monitor the status of blue whales in northern Chilean Patagonia, increasing knowledge of their ecology (Branch *et al*. 2007; Williams *et al*. 2011), genetics (LeDuc *et al*. 2007), morphology (Durban *et al*. 2016), acoustic behavior (Buchan *et al*. 2010, 2014; Bocconcelli *et al*. 2016; Saddler *et al*. 2017), and potential anthropogenic noise impacts (Colpaert *et al*. 2016).

Here we utilize a dataset acquired using non-invasive digital acoustic recording tags (DTAGs; Johnson & Tyack 2003) during six annual (2014–2019) research cruises. We tagged 28 different animals to study diving behavior of individual blue whales and, from 2016, we concurrently conducted prey sampling (euphausiids). Diel changes in dive behavior of blue whales and their prey distribution were examined in order to study the risk of ship collisions. It is hoped that this data will aid the decisions of policy makers regarding marine traffic and protection measures for this endangered species in northern Chilean Patagonia.

## MATERIALS AND METHODS

### Study area

The study area comprises the Moraleda Channel, the Corcovado Gulf and the Ancud Gulf in Chilean Patagonia (Fig. 1). According to the classification of Marine Ecosystems of the World (Spalding *et al*. 2007), this area belongs to the Chiloense Ecoregion. It is characterized by a highly fragmented coastline composed of islands, peninsulas, channels, fjords, and wave-protected bays that are generated by the abundance of islands (Aguilera *et al*. 2019). Bathymetry in this area can vary greatly especially near shore and adjacent to the various fjords. While much of the Gulf has depths of several hundred meters, there are numerous sills and shallow regions ($<$100 m depth) capable of generating frontal zones, internal waves and a variety of oceanographic phenomena (Artal *et al*. 2019). The general oceanographic conditions in the area are influenced by the West Wind Drift (Viddi *et al*. 2010; Aguilera *et al*. 2019). In particular, the Subantarctic Surface Water is moved along the contour of the south American coast where it enters the southern Chilean channels and fjords. Here, it mixes with fresh water from rain, rivers, coastal runoff and glacial melting, creating a large estuarine system (Palma & Silva 2004; Silva *et al*. 2009). Consequently, a strong vertical and horizontal salinity gradient is generated together with high primary production (Palma & Silva 2004; Viddi *et al*. 2010; Aguilera *et al*. 2019), having a strong seasonal peak in spring/summer (González *et al*. 2010). This region is also characterized by ecological complexes that include high diversity of marine megafauna (e.g. penguins, otters, dolphins, whales) among different ecosystems (Hucke-Gaete *et al*. 2003, 2013; Viddi *et al*. 2010; Catalan *et al*. 2011; Häussermann *et al*. 2012; Buchan *et al*. 2016).

### Data collection

Field effort was conducted in the moths of February and March during by 6 annual research cruises (2014–2019). These months were chosen based on historical sightings, acoustic detections, and suitability of conditions for whale tagging. Visual survey effort to detect marine mammals began at sunrise from the upper decks of modified live-aboard local fishing vessels (M.V.'s *Centinela*, *Khronos*, and *Solidaridad*), that acted as the main research platforms, equipped with a small inflatable tag-boat powered by a 4-stroke outboard engine.

The DTAG acoustic recording tag (Johnson & Tyack 2003) was used to acquire information on locomotion, behavior, and acoustic behavior of individual blue whales (Bocconcelli *et al*. 2016; Saddler *et al*. 2017). DTAGs are equipped with very high frequency (VHF) transmitters to track the whales during deployments and to retrieve the tag post-release. This bio-logging tag contains two hydrophones programmed to sample at either 120 or 500 kHz, as well as pressure sensors (depth) and 3-axis accelerometers and magnetometers, which sampled at either 200 or 500 Hz. Tags were attached to animals with four suction cups (Fig. 2), using a hand-held 8 m carbon fiber pole and programmed to release after durations of up to 24 h. In this study, we analyzed depth data acquired from 28 tags deployed on a corresponding number of blue whales, resulting in a dataset of $\approx$190 h (Table 1).

Prey mapping was conducted using a two frequency (38 and 200 kHz, each single-beam) scientific echosounder (Simrad ES60), deployed at a depth of approximately 1 m from a pole-mount on board the main vessel during expeditions in 2016–2019. Pulse lengths were 256–512 microseconds with a ping rate of 0.5–1 Hz providing backscatter data with vertical and horizontal resolutions of approximately 10 cm and 1–10 m. The system was operated during both general survey cruise tracks as well as during whale tagging and focal follow events. During prey mapping the ship operated at a reduced speed, generally 4–5 kn, but occasionally in calm seas at speeds of up to 8 kn. The system was calibrated using a standard 38.1 mm Tungsten carbide sphere at least once during each field season (Foote 1982).

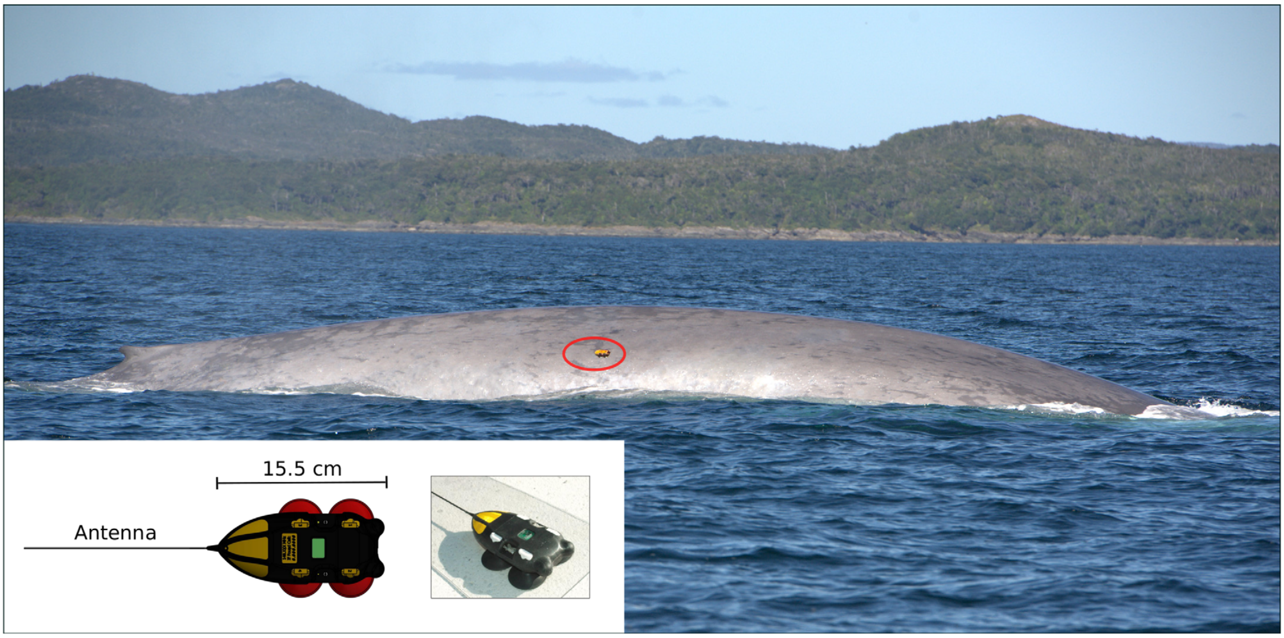

**Figure 2** DTAG attached to a blue whale off the coast of Chile (24-Mar-2014). Lower left: DTAG illustration in two different perspectives.

Acoustic backscatter data were collected in areas where tagged blue whales were present, but we did not attempt to collect exactly co-located data on the tagged whale, so as not to cause behavioral reactions associated with the vessel presence or noise. The majority of data was collected with the vessel between 200 m and 1 km from the tagged animal, with distances estimated based on visual observations of surfacing animals. A ring net (≈60 cm diameter, 250 um mesh) was used to collect organisms to ground truth acoustic backscatter observations by vertical casts in the upper 50–100 m of the water column. A subset of krill was digitally photographed immediately following capture and prior to preservation. Krill lengths (standard length 2) were measured using a ruler (more details in the “Prey distribution” section).

## Data analysis

### *Dive patterns*

A custom algorithm was developed in MATLAB (The MathWorks, Inc., United States) to analyze the pressure sensor data acquired during each tag deployment. The original data (sampled at 25 Hz) were decimated to 1 Hz sampling rate for further analysis (one value each second). The algorithm simulates the dive profile (the tag pressure exposure over time) of the tagged animal and determines the period belonging to day or night phases, in relation to local sunrise and sunset times in the study area (example in Fig. 3). Diurnal cycle data were obtained from the website of the US Naval Observatory (https://www.usno.navy.mil/USNO). In order to study the variability in ship strike risk relative to the diel cycle, the algorithm selects the mean depth during day and night phases and the percentage of time the animal was at depths where possible collisions could occur. The maximum ship draft in the Chiloense Ecoregion was defined at ≈12 m from review of the max allowable draft for the two largest and deepest ports (Puerto Montt and Chacabuco) and vessel types that transit through the study area (data received by local Port Authorities). A weight was assigned to each whale, defined as the time the tag was on-animal (minutes of recording) during day or nighttime (Table 1), to determine its value on the total result. Therefore, the weighted arithmetic mean (Bland *et al*. 1998; Terr 2019) was used to measure the average value for all the whales, taking into consideration each deployment duration. A weighted two sample $t$ test (weighted comparison of means) was applied to explore significant difference following Bland *et al*. (1998). Lastly, whale depth was also analyzed in 5-min time bins (local maxima and median value) to reduce the influence of ascent/descent phases of diving behavior and surface intervals for comparison with prey distribution data.

**Table 1** Summary deployment information including date, start time of data acquisition (local time GMT-3), on-animal time (duration tag was attached), deployment duration (day and night), and mean depth (day and night) for the 28 blue whales tagged in northern Chilean Patagonia from 2014 to 2019

| | | Start (local) | On-animal | Duration [min] | | Depth [m] (mean ± SD) | |
|---|---|---|---|---|---|---|---|
| Whale ID | Date | h:min | h:min | Day | Night | Day | Night |
| bm14_076a | 17-Mar-14 | 13:15 | 00:07 | 7 | ND | 10.3 ± 9.7 | ND |
| bm14_076b | 17-Mar-14 | 18:36 | 05:04 | 94 | 210 | 15 ± 14.8 | 4.4 ± 5.7 |
| bm14_082a | 23-Mar-14 | 13:00 | 03:51 | 231 | ND | 14.3 ± 20.6 | ND |
| bm14_082b | 23-Mar-14 | 13:59 | 01:22 | 82 | ND | 14.9 ± 14.2 | ND |
| bm14_083a | 24-Mar-14 | 13:22 | 10:10 | 396 | 214 | 14.4 ± 17 | 9.5 ± 11.6 |
| bm15_048a | 17-Feb-15 | 18:39 | 24:44 | 866 | 618 | 16.8 ± 14.7 | 9.2 ± 15.1 |
| bm15_050a | 19-Feb-15 | 13:21 | 06:53 | 413 | ND | 15.9 ± 19.9 | ND |
| bm15_053a | 22-Feb-15 | 11:55 | 09:00 | 535 | 5 | 11.3 ± 7.7 | 21 ± 17.9 |
| bm15_054a | 23-Feb-15 | 15:58 | 10:18 | 290 | 328 | 15.9 ± 15.9 | 4.8 ± 4.4 |
| bm15_057a | 26-Feb-15 | 11:19 | 03:31 | 212 | ND | 9.1 ± 7.3 | ND |
| bm15_064a | 05-Mar-15 | 20:39 | 10:17 | ND | 617 | ND | 5.8 ± 11 |
| bm16_049a* | 18-Feb-16 | 17:48 | 12:45 | 189 | 576 | 37.2 ± 30.6 | 6.3 ± 6.4 |
| bm16_050a | 19-Feb-16 | 14:37 | 06:52 | 378 | 34 | 51.4 ± 37.2 | 10 ± 11.7 |
| bm16_054a* | 23-Feb-16 | 13:58 | 08:48 | 411 | 117 | 36.3 ± 28 | 6.5 ± 8.3 |
| bm16_057a | 26-Feb-16 | 16:00 | 00:16 | 17 | ND | 59.1 ± 38.8 | ND |
| bm16_059a | 28-Feb-16 | 17:01 | 00:42 | 42 | ND | 21.3 ± 30.5 | ND |
| bm16_062b | 03-Mar-16 | 10:51 | 09:05 | 545 | ND | 55.9 ± 36.8 | ND |
| bm17_060a | 01-Mar-17 | 15:49 | 00:22 | 22 | ND | 10.9 ± 10.3 | ND |
| bm17_063a* | 04-Mar-17 | 09:26 | 01:35 | 95 | ND | 41.7 ± 29.6 | ND |
| bm17_063b* | 04-Mar-17 | 12:28 | 01:17 | 77 | ND | 84.8 ± 56.5 | ND |
| bm18_054a* | 23-Feb-18 | 09:46 | 19:53 | 661 | 532 | 42 ± 35.6 | 1.4 ± 1.7 |
| bm18_055a* | 24-Feb-18 | 14:36 | 05:45 | 345 | ND | 41.5 ± 36.7 | ND |
| bm18_056a* | 25-Feb-18 | 18:20 | 01:30 | 90 | ND | 14.6 ± 12.4 | ND |
| bm18_058a* | 28-Feb-18 | 09:20 | 05:40 | 340 | ND | 66.2 ± 43.3 | ND |
| bm18_061a* | 02-Mar-18 | 17:18 | 12:39 | 197 | 562 | 30.1 ± 27.1 | 7.9 ± 11.8 |
| bm19_051a* | 20-Feb-19 | 10:11 | 07:02 | 422 | ND | 57.5 ± 39.2 | ND |
| bm19_052a | 21-Feb-19 | 14:12 | 01:10 | 70 | ND | 47.6 ± 39.5 | ND |
| bm19_053a* | 22-Feb-19 | 12:05 | 07:04 | 424 | ND | 32.8 ± 37.4 | ND |

Asterisks next to the whale ID indicate which whales had concurrent and co-located active acoustic data collected and where dive depth and krill layer depth were analyzed. ND, no data.

### *Prey distribution*

Post-processing of acoustic backscatter data was conducted in Echoview (Myriax, Inc) and MATLAB and consisted of: filtering raw data for noise, subtracting background noise, removing regions from analysis including near the surface where bubbles may occur, and near the seafloor. The data were classified as being from krill when the Sv (volume backscattering coefficient) measured at 200 kHz was 2–18 dB higher than that measured at 38 kHz following the methods used by Reiss *et al.* (2008) and Warren and Demer (2010). The dB difference window used was based on lengths of krill (12–20 mm range although there were occasionally smaller

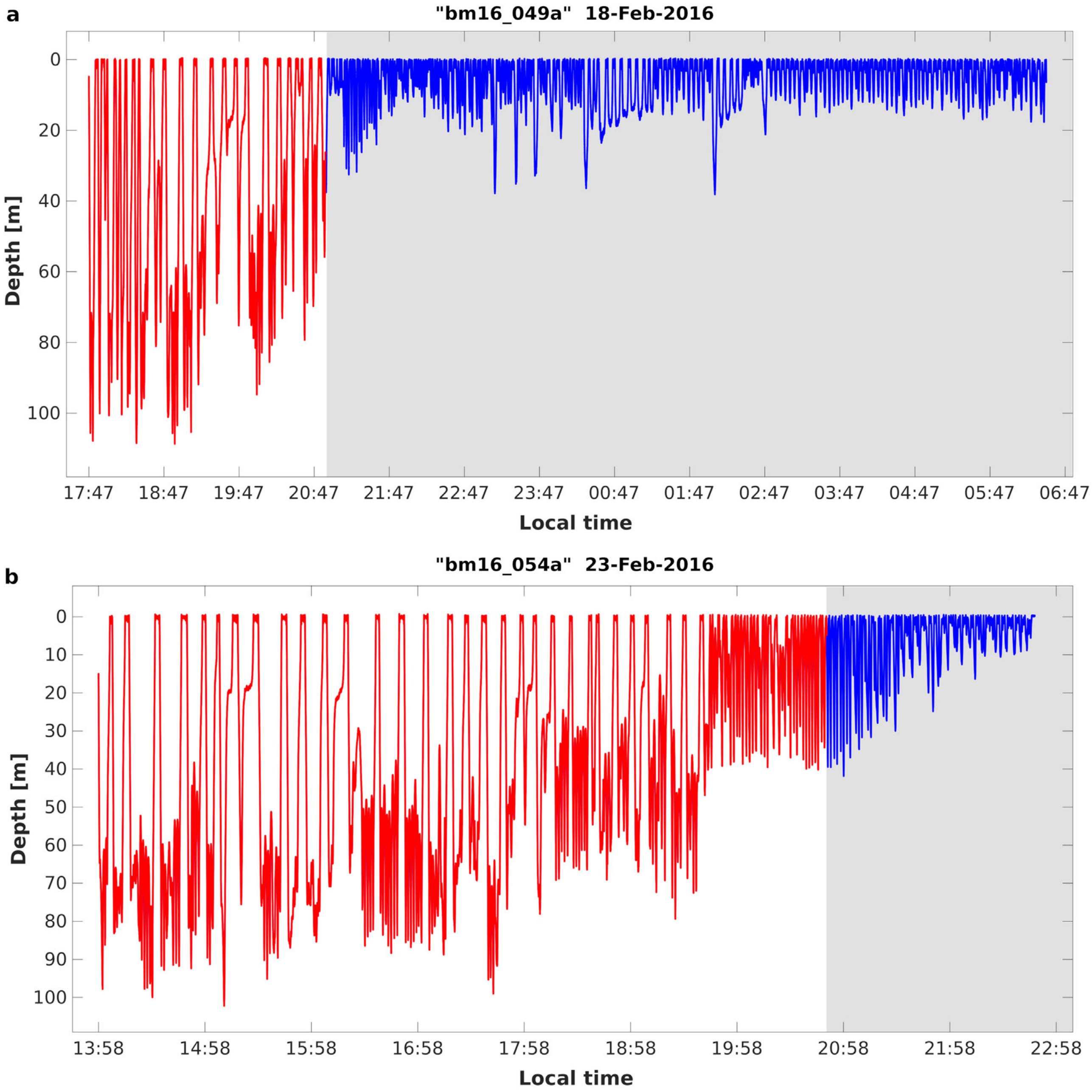

**Figure 3** Dive profiles of 2 whales tagged on February 2016 (bm16_049a and bm16_054a), showing deeper daytime dives in red and shallower nighttime dives in blue. Greyed areas indicate sunset time and periods of night (information about local diurnal cycles was obtained from the US Naval Observatory, https://www.usno.navy.mil/USNO).

(8–10 mm) larval krill) that were captured from net tows during the cruises. Scattering aggregations from non-krill aggregations were occasionally encountered, most often these were small aggregations or multiple individuals of near-bottom fish (based on their scattering characteristics). These non-krill scatterers were filtered out by the dB difference algorithm. Processed krill backscatter data were binned (1 m vertical, 100 m horizontal) and exported as Nautical Area Scattering Coefficient (NASC), being a function of the amount of echo energy detected in each bin and is widely used as a proxy for biomass (Simmonds & MacLennan 2008). The center-of-mass depth

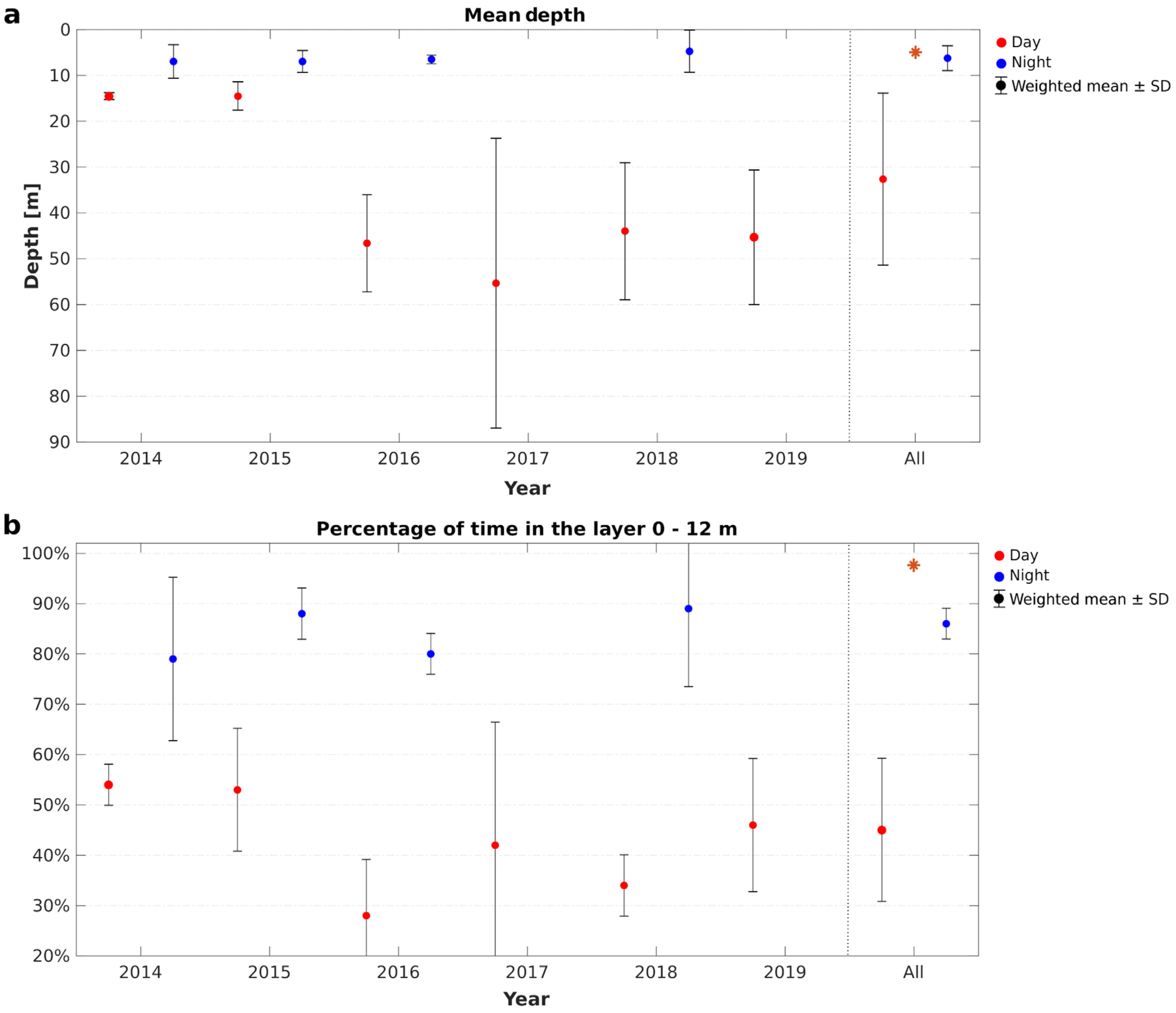

**Figure 4** Error bar plot showing diving patterns of tagged whales during day (red) and night (blue) for each year (2014–2019) and for all deployments (on the right). Weighted mean ± SD are shown for mean depth (a) and percentage of time each whale spent in the layer between the surface and 12 m depth (b). *Indicates significant difference for all tagged whales between day and night ($P < 0.01$).

of acoustically-measured prey biomass and whale depth were averaged in 5-min time bins, and then the correlation of these vertical distributions was calculated (Parks *et al*. 2012). In this study, acoustic measures of prey distribution and abundance were analyzed for 11 tagged blue whales over the 4 years where acoustic prey data were collected (Table 1). These deployments were selected because: sufficient tag-on duration occurred, the acoustic data overlapped well both spatially and temporally with deployments of tags, included data from both day and nighttime, or occurred in regions of varying bathymetry (depths ranging from 40 m to more than 300 m).

# RESULTS

The dive patterns of 28 blue whales, collected during the six cruises (2014–2019) were analyzed, resulting in ≈190 h of data from DTAG deployments (Table 1). Blue whales were found to dive to significantly greater depths (Table 1 and Fig. 4a) during the day (weighted mean ± SD = 32.6 ± 18.7 m; $n$ = 27 tags, number of deployments) than during the night (6.2 ± 2.7 m; $n$ = 11 tags; weighted two sample $t$-test, $P < 0.01$). Concerning the probability of ship strike relative to diurnal diving patterns (Table 2 and Fig. 4b), results indicate the

**Table 2** Summary of data about the percentage of time each whale spent in the layer between the surface and 12 m depth during day and night, and corresponding duration in minutes

| | | % of time (0–12 m) | | Duration (min) | |
|---|---|---|---|---|---|
| Whale ID | Date | Day | Night | Day | Night |
| bm14_076a | 17-Mar-14 | 56% | ND | 4 | ND |
| bm14_076b | 17-Mar-14 | 49% | 89% | 46 | 187 |
| bm14_082a | 23-Mar-14 | 58% | ND | 135 | ND |
| bm14_082b | 23-Mar-14 | 49% | ND | 40 | ND |
| bm14_083a | 24-Mar-14 | 52% | 67% | 208 | 142 |
| bm15_048a | 17-Feb-15 | 41% | 85% | 360 | 527 |
| bm15_050a | 19-Feb-15 | 65% | ND | 267 | ND |
| bm15_053a | 22-Feb-15 | 48% | 45% | 259 | 2 |
| bm15_054a | 23-Feb-15 | 51% | 94% | 147 | 308 |
| bm15_057a | 26-Feb-15 | 72% | ND | 153 | ND |
| bm15_064a | 05-Mar-15 | ND | 87% | ND | 535 |
| bm16_049a | 18-Feb-16 | 30% | 81% | 56 | 465 |
| bm16_050a | 19-Feb-16 | 24% | 66% | 91 | 23 |
| bm16_054a | 23-Feb-16 | 28% | 81% | 113 | 95 |
| bm16_057a | 26-Feb-16 | 24% | ND | 4 | ND |
| bm16_059a | 28-Feb-16 | 65% | ND | 27 | ND |
| bm16_062b | 03-Mar-16 | 24% | ND | 133 | ND |
| bm17_060a | 01-Mar-17 | 62% | ND | 14 | ND |
| bm17_063a | 04-Mar-17 | 21% | ND | 20 | ND |
| bm17_063b | 04-Mar-17 | 26% | ND | 20 | ND |
| bm18_054a | 23-Feb-18 | 34% | 100% | 224 | 531 |
| bm18_055a | 24-Feb-18 | 33% | ND | 115 | ND |
| bm18_056a | 25-Feb-18 | 46% | ND | 41 | ND |
| bm18_058a | 28-Feb-18 | 24% | ND | 82 | ND |
| bm18_061a | 02-Mar-18 | 38% | 75% | 75 | 423 |
| bm19_051a | 20-Feb-19 | 26% | ND | 28 | ND |
| bm19_052a | 21-Feb-19 | 32% | ND | 7 | ND |
| bm19_053a | 22-Feb-19 | 52% | ND | 115 | ND |

ND, no data.

percentage of time whales were close to the surface was higher during nighttime (weighted mean ± SD = 86% ± 9.4%; $n = 11$ tags, number of deployments) compared to the day (45.5% ± 14.1%; $n = 27$ tags; weighted two sample *t*-test, $P < 0.01$).

Mapping results reveal a strong overlap between dive depth/duration and the presence of acoustically measured krill biomass (Fig. 5). Layers of krill were abundant in all years that were surveyed, although the depth of the krill aggregations varied with time of day, location, bathymetry, and bottom slope. A one-to-one correlation between the acoustic backscatter and whale dive depth as a function of time is not expected, as the prey data were not co-located (i.e. directly above) with the whales. However, measures of krill aggregations and whale dive depth should be related to each other. Despite the spatial separation of the acoustic measurements and the tagged animals, there was often a very strong correlation

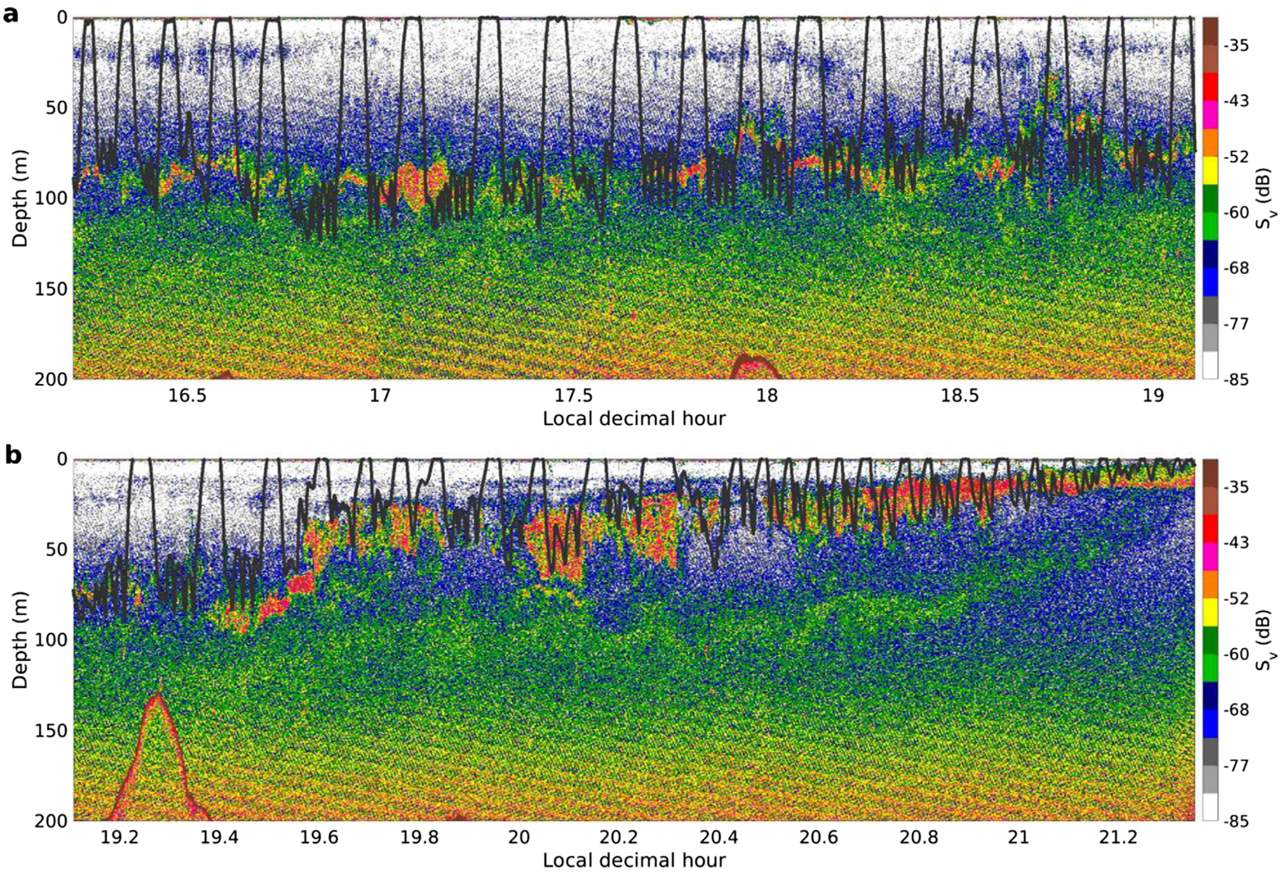

**Figure 5** Echograms of unprocessed 200 kHz backscatter show the location of krill scattering layers, with the dive profile of a tagged blue whale (bm18_055a) overlaid (red line) during day (a) and dusk (local sunset occurred at ≈20.5) (b). Volume backscatter ($S_v$) is proportional to krill abundance or biomass.

between the location of the krill layer (as measured by NASC) and the dive depths of tagged whales (Table 3 and Fig. 6).

A diurnal pattern of transition from the deep daytime habitat preference of krill and therefore deep foraging dives by blue whales, to shallow habitat use by krill and thus shallow diving by whales was directly observed (Fig. 6). This is unsurprising, as vertical migration of zooplankton occurs throughout the world, however the majority of our survey effort in this study took place during daylight hours in order to locate, tag and focal follow blue whales. As a result, there were few tagging events where we were able to collect information on prey abundance and whale dive behavior concurrently during the transition from day to night (as shown in Fig. 5). In this example, the tagged whale dove progressively to more shallow depths during transition periods from dusk to night, altering the dive profile in a manner similar to examples from Doniol-Valcroze *et al*. (2011). As zooplankton prey migrate to shallower depths they often spread out over a larger vertical depth range (Urmy & Horne 2016; Boswell *et al*. 2020) reducing their numerical density, which in turn, may cause feeding blue whales to dive more often (albeit less far) to acquire the same energy as during their deeper daytime dives.

## DISCUSSION

Blue whales are recovering from the intensive commercial hunting that occurred during the first half of the 20th century (see review in Clapham & Baker 2009). They are facing habitat degradation and different anthropogenic threats, such as entanglement (e.g. in fishing gear), underwater noise, and collisions with vessels (Fleming & Jackson 2011). Vessel strike is a significant cause of death for baleen whales, involving at least 11 species

**Table 3** Relation between whale dive depth and krill layer depth (weighted depth of NASC) for the deployments where prey distribution data were co-located with tagged whales

| Whale ID | Date | On-animal (h:min) | Dive depth [m] (mean ± SD) | NASC depth [m][†] (mean ± SD) |
|---|---|---|---|---|
| bm16_049a | 18-Feb-16 | 12:45 | 31.3 ± 54.6 | 55.5 ± 29.9 |
| bm16_054a | 23-Feb-16 | 08:48 | 50.4 ± 26.7 | 62 ± 21.5 |
| bm17_063a | 04-Mar-17 | 01:35 | 67.4 ± 28.4 | 84 ± 7.2 |
| bm17_063b | 04-Mar-17 | 01:17 | 124.1 ± 42 | 90.4 ± 6.4 |
| bm18_054a | 23-Feb-18 | 19:53 | 57.4 ± 37.8 | 81.9 ± 17.2 |
| bm18_055a | 24-Feb-18 | 05:45 | 73.1 ± 32.7 | 69.1 ± 26.4 |
| bm18_056a | 25-Feb-18 | 01:30 | 30.3 ± 9.3 | 57.6 ± 29.2 |
| bm18_058a | 28-Feb-18 | 05:40 | 102.7 ± 25 | 86.3 ± 30.3 |
| bm18_061a | 02-Mar-18 | 12:39 | 29 ± 25.5 | 86.7 ± 32.6 |
| bm19_051a | 20-Feb-19 | 07:02 | 102.5 ± 23 | 87.4 ± 19.5 |
| bm19_053a | 22-Feb-19 | 07:04 | 81.8 ± 38.8 | 84.2 ± 17.9 |

Dive depth were obtained from mean value of local maximum (5-min time bins) to reduce the ascent/descent phases and excluding dives less than 5 m (surface intervals). [†]NASC depths bounded by the surface and 205 m depth: 2016, 2018, 2019; 100 m depth: 2017.

worldwide (Laist *et al.* 2001; Redfern *et al.* 2013), with a dramatic, exponential increase in the number of incidents per decade since the 1950s (Van Waerebeek & Leaper 2008). Nevertheless, when a whale carcass is examined, it is not always possible to determine the cause of death, due to advanced decomposition, or a lack of external evidence of vessel strike (Moore *et al.* 2004, 2020). Thus, the full extent of the ship strike collision issue may be underestimated, as the number of observed vessel-strike mortalities is generally influenced by a plethora of variables (van der Hoop *et al.* 2013; Rockwood *et al.* 2017; Calambokidis *et al.* 2019).

While the nature of individual threats is well recognized, the ecosystem and population level effects of vessel-strike mortality are often poorly understood for most whale species (Panigada *et al.* 2006; Berman-Kowalewski *et al.* 2010; van der Hoop *et al.* 2013). Large whales have a key role in the ocean biological dynamics, influencing marine ecosystems as consumers, prey, detritus, and nutrient vectors (Roman *et al.* 2014). Being long-lived animals with a low reproduction rate, an increase in mortality may also have a strong impact on their population ecology (Laist *et al.* 2001). They are among the first marine species to be protected by national and international laws, including the Convention on Migratory Species; given their broad distribution and movements through various ecosystems and national boundaries, their protection also benefits other members of the ocean environment (Roman *et al.* 2013; van der Hoop *et al.* 2015; Smith *et al.* 2020).

A number of different baleen whale species (e.g. blue, humpback, and minke whales) are present in southern Chile and little is known about their status and ecology (Viddi *et al.* 2010). From 2004 to 2012, marine surveys reported hundreds of photo-identified blue whales in southern Chile, estimating that a population of ≈570–760 animals was feeding seasonally in the region (Galletti Vernazzani *et al.* 2012, 2017). More recently, the northern Chilean Patagonia region is becoming more impacted by increases in vessel traffic from: aquaculture and fisheries, particularly the salmon industry; and maritime traffic from large cruise ships and ferries travelling from Puerto Montt to Punta Arenas and other destinations in the Moraleda and Corcovado areas (Wilmsmeier 2013). These factors contribute to a scenario where, the blue whale is a highly vulnerable cetacean species to the threat of vessel strikes (Berman-Kowalewski *et al.* 2010; Calambokidis *et al.* 2019).

Diving data from the 28 tagged blue whales presented here, suggests that vessel strike risk in northern Chilean Patagonia is significantly higher at night (Fig. 4), when the animals perform shallower and simpler dives close to the surface to reach the vertically-migrating krill (Fig. 5). Calambokidis *et al.* (2019) documented a vulnerability twice as high at night compared to the day for this species, so the results of this study confirmed the indication

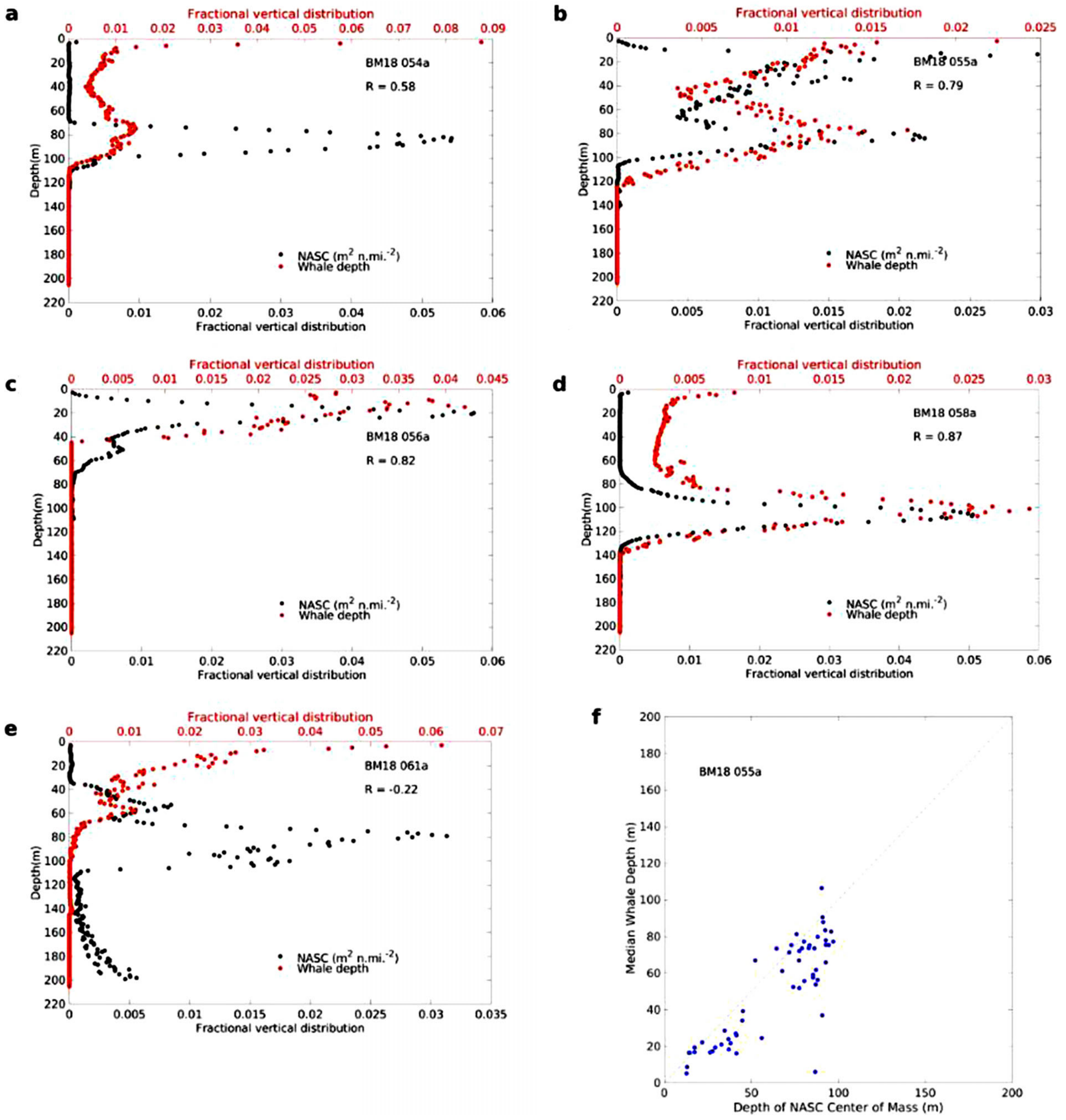

**Figure 6** Correlation between depth of tagged blue whales (red) and distribution of krill biomass (black) as measured by NASC. Data are shown for the 5 blue whales tagged in 2018 (a–e). While krill location in the water column varied depending on geographic location for each tag event, the whale vertical position tracked the prey distributions closely. (f) Example of a scatter plot between whale depth (bm18_055a) and backscatter data binned into 5-min bins. Median whale depth (not including depth values < 1 m, i.e. when the whale was at the surface) and the depth of the center of mass of the backscatter are shown.

reported along the US West Coast. Crucially, this is the phase of the day when it is most difficult for ship operators to visually monitor for the presence of animals. Doniol-Valcroze *et al*. (2011) reported for blue whales in the St Lawrence River estuary (Quebec, Canada), a daytime pattern with multiple vertical excursions at deeper depth and a more intense feeding activity at night with shallower and shorter dives. It might even be possible that the spread of zooplankton over a larger range during night migration may cause feeding blue whales to perform more dives to acquire the same food rewards of daytime activity. However, further analyses using three-dimensional accelerometer and magnetometer of DTAGs are necessary to define feeding behavior of each tagged whale in the study area, and to investigate mechanics, dynamics and energetic cost of their locomotion.

As natural locomotion behaviors of rorqual whales (*Balaenopteridae*) and their krill (*Euphausiacea*) prey will not change, these aspects must be taken in account when restrictions and/or legal framework for vessel traffic are implemented to reduce ship collisions (Silber *et al.* 2012; Vanderlaan & Taggart 2009). In other regions of the world, efforts have included both mandatory and recommended changes in vessel-routing practices and restrictions of vessel speed (Silber *et al.* 2012). Vessel-routing modifications are mainly applied to reduce the vessel strike risk by decreasing the overlap of high density marine traffic and whale aggregation areas (Vanderlaan & Taggart 2009). Slowing vessel speed in whale dense areas is also considered a concrete mitigation measure to reduce strike risk (Silber *et al.* 2012; van der Hoop *et al.* 2015; Smith *et al.* 2020), since lethality of collisions increases with ship speed (Laist *et al.* 2001; Vanderlaan & Taggart 2007; Silber *et al.* 2010; Wiley *et al.* 2011). Equally, van der Hoop *et al.* (2013) report that greater success in reducing vessel-strike mortalities for large whales may be achieved by restructuring shipping lanes, rather than by restricting speeds.

A variety of the world's marine megafauna (e.g. sea turtles, whale sharks, pinnipeds, cetaceans) are killed or injured by vessel strikes (Hazel 2007; Silber *et al.* 2012; Moore *et al.* 2013; Lester *et al.* 2020; Schoeman *et al.* 2020), and new policies to protect endangered species are necessary now more than ever due to habitat degradation resulting from human activities. Results of this study may be beneficial to effect meaningful policy decisions regarding vessel strike risk and protection measures for blue whales in the Chiloense Ecoregion. Further research should also consider the acquisition of data on maritime traffic. In the study area, Satellite Automatic Identification System (SAIS) could perhaps be a possible alternative of the standard AIS technology to monitor the ships in a large region and acquire detailed data about specific vessel speeds in relation to their possible transit through whale aggregation areas (Greig *et al.* 2020). Future research is even more important to establish the degree of isolation of the unnamed Chilean blue whale subspecies, and the health and exchange of the individuals within different populations (Torres-Florez *et al.* 2014). Such data will be fundamental not only for future scientific findings, but for Chilean policy makers to implement management decisions regarding effective conservation plans for this subspecies.

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## CONFLICT OF INTEREST

The authors declare that there is no conflict of interest regarding the publication of this article.

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