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DELL'AMBIENTE**

**Corso di Laurea Magistrale  
Biologia Marina**

**Cinematica del comportamento di foraggiamento delle  
balenottere azzurre cilene (*Balaenoptera musculus chilensis*)**

**Kinematics of foraging behavior of Chilean blue whales  
(*Balaenoptera musculus chilensis*)**

Tesi di Laurea Magistrale di:

Adi Ayoub

Relatore:

Chiar.ma Prof.ssa Emanuela Fanelli

Correlatore:

Dott. Francesco Caruso

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## **Abstract**

The northern Chilean Patagonia region is a key feeding ground and a nursery area in the southern hemisphere, where a new subpopulation of blue whales (*Balaenoptera musculus chilensis*) was recently discovered. Previous studies showed that baleen whales are critically dependent on krill density and distribution, and they have a high energy cost of foraging due to drag associated with the feeding technique. In this study, the kinematics of foraging behavior of 18 Chilean blue whales was investigated using bio-logging tags during four separate research cruises (2014-2017). During the years 2016 and 2017, active acoustics (scientific echosounders) was used to record prey (euphausiids) density and distribution simultaneously with tag data. Chilean blue whales showed a higher feeding rate during nighttime on shallow and disperse krill patches rather than feeding on dense and deeper krill aggregations. The results showed less energetically costly maneuvers when foraging near the surface, with lower values of pitch and speed during feeding events. Therefore, the whales preferred waiting for the migration of krill to shallow waters, and this behavior increases risk of ship collision during nighttime. This study provides valuable information to promote specific conservation plans of blue whales in the study area.

# **INDEX**

## **1. Introduction**

1.1. Feeding ecology of Mysticetes

1.2. Blue whales (*Balaenoptera musculus*)

1.3. Chilean blue whales (*Balaenoptera musculus chilensis*)

Aims of the study

## **2. Materials and Methods**

2.1 Study area

2.2 Data collection

2.2.1 Bio-logging tags

2.2.2 Scientific echosounder

2.3 Data analysis

2.3.1 Dive pattern & lunge detection

2.3.2 Prey abundance & distribution

2.4 Statistical analysis

## **3. Results**

3.1 Characterization of foraging events

3.1.1 Depth analysis

3.1.2 Speed analysis

3.1.3 Pitch analysis

3.1.4 Inter-Lunge Interval (ILI)

3.2 Prey mapping

## **4. Discussion**

## **5. Conclusions**

## **REFERENCES**

## **Chapter 1: Introduction**

*"The margin between life and death is defined by an animal's ability to navigate its environment and find food."* (William T. Gough).

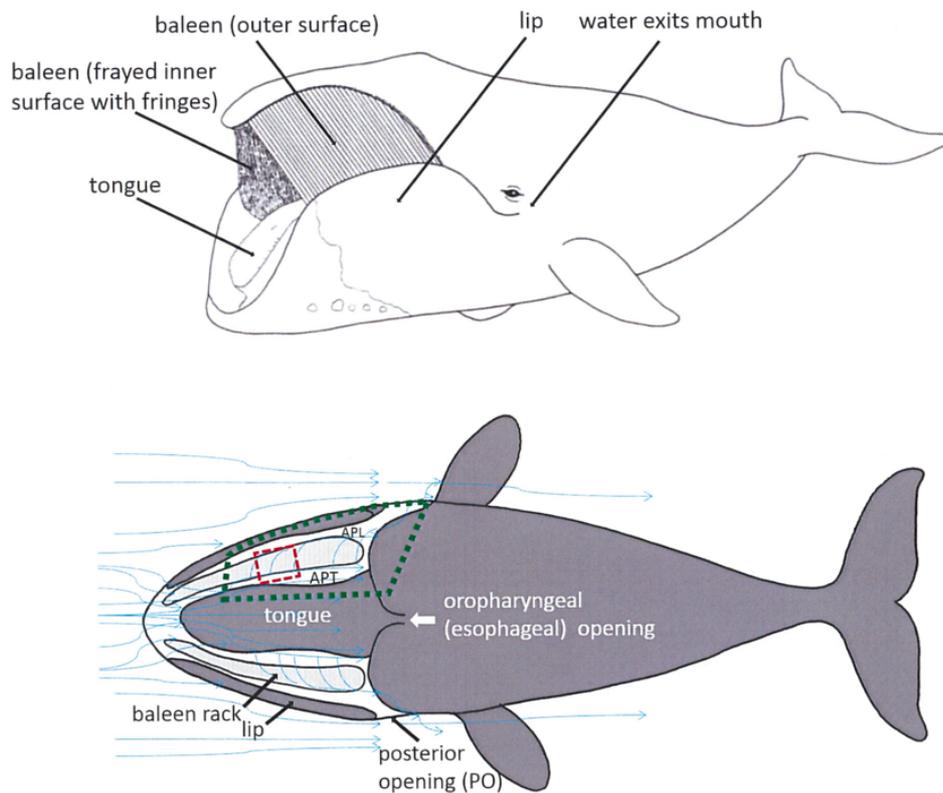
### **1.1 Feeding ecology of Mysticetes**

Among marine animals, mysticete whales stand at the extreme end of the body size spectrum of animal organisms and include the blue whale (*Balaenoptera musculus*), the largest animal ever lived on Earth. All baleen whale species (Mysticetes) are characterized by a complete absence of teeth in adults (although teeth are found in fetal baleen whales; Deméré et al., 2008). Their feeding apparatus includes keratinized (fingernail-like) baleen plates that extend ventrally from both rostral sides of the mouth and are separated by a prominent longitudinal ridge running along the midline (Williamson, 1973; Werth, 2000). The number of plates may vary between 100 and 400 plates on each side of the baleen, depending on the species (Nemoto, 1970; Werth, 2000). Also, plate length can vary among species. It ranges between 50 cm and 5 m and is spaced apart by one or two centimeters, leaving a narrow gap between them (Werth, 2000). However, the spacing may vary along the length of the rack (Young, 2012) (Fig. 1).



**Figure 1.** A humpback whale's exposed baleen plates made of keratin (fingernail-like protein). Image Credit: mendicantmonks.org

These anatomical adaptations and morphological specializations allow baleen whales to filter-feed on aggregations of small-bodied organisms, such as small fish, krill, and copepods. Filter feeding occurs by scooping large quantities of prey-laden water. The seawater then gets expelled from the mouth through the plates and fringes, aiding prey capture by direct interception and channeled flow (Werth and Potvin, 2016) (Fig. 2).



**Figure 2.** Depiction of mouth of baleen whale (bowhead whale) and the water flows through it during filter feeding.

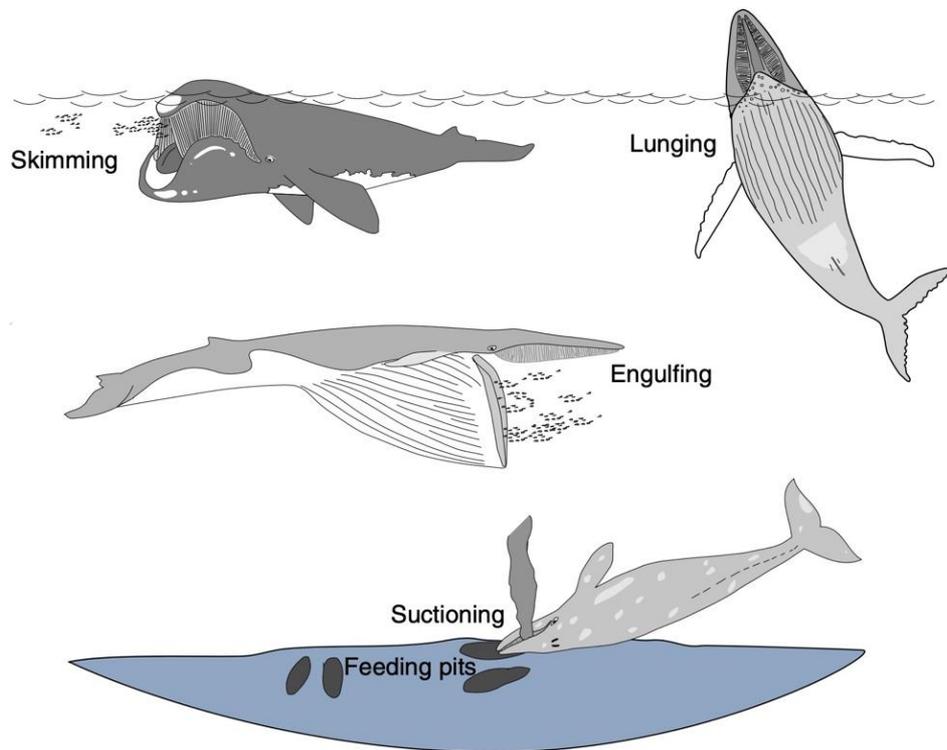
The differences of baleen morphology among mysticete whales reflect the different feeding modes used by the balaenids (e.g., right whale, bowhead whale), rorquals (family Balaenopteridae), and gray whales. For example, length differences can be seen on balaenid baleen plates which are much longer than those of the rorquals or gray whales, reaching lengths of 4–5 m in the bowhead whales. Contrarily, rorqual baleen plates reach a maximum length of 1 m. Moreover, balaenid plates are much narrower, with finer bristles than rorqual or gray whale plates. In balaenids, small bristle diameters correspond

with small prey size; they feed on copepods and other tiny (<10 mm) zooplankton (Nemoto, 1970; Werth, 2000).

The four families of baleen whales (Balaenidae, Balaenopteridae, Eschrichtiidae, Neobalaenidae) are filter feeders, but they exhibit several modes and behaviors (Werth, 2007). The large balaenids (right and bowhead whales) feed on aggregations of zooplankton through continuous ram filtration that can occur at different depths (surface, water column, and bottom), similar to the feeding behavior of basking whale sharks (Sims et al., 1999; Lambertsen et al., 2005; Werth, 2004). While the whale swims with an open mouth, water and prey enter through a gap between the two baleen plates in the front of the mouth and water exits along the sides of the mouth. Prey is swept into the back of the mouth by the dynamically controlled water flow through the mouth and the side-to-side sweeping action of the large muscular tongue. In contrast, members of Balaenopteridae, also called rorquals (e.g., humpback, fin, blue, sei, and minke whales), use intermittent lunge feeding to engulf seawater (Simon et al., 2012; Goldbogen et al., 2017). Their long, parallel grooves run the length of the throat, allowing it to distend and capture enormous quantities of prey. Lunge feeding is characterized by an acceleration when approaching prey and sudden deceleration when opening their mouth to engulf quantities of prey-laden saltwater (Goldbogen et al., 2010). Among the Eschrichtiidae

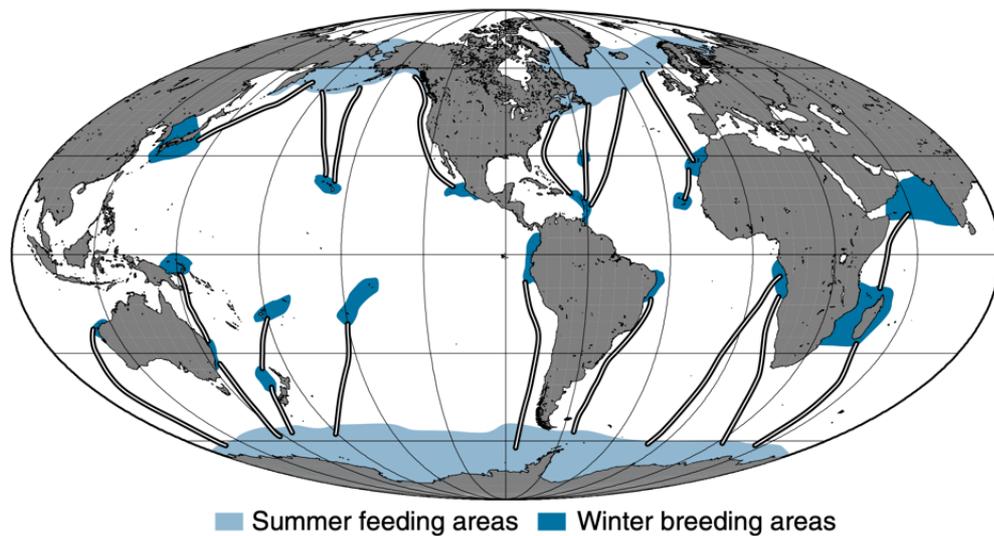
family, the gray whale is the only extant member, and it feeds on benthic organisms by suction-feeding (Johnson and Nelson, 1984; Oliver and Slattery, 1985). It rolls to one side and sucks benthic invertebrate prey and bottom sediments, with some distension of the mouth cavity through the expansion of the throat grooves. Water and mud are expelled through the side of the mouth (Berta and Sumich et al., 2015). Suction feed and filtration are facilitated due to short plates and thick, coarse, and stiff bristles (Young, 2012; Young et al., 2015). A fourth family, e.g., Neobalaenidae, is represented by only one member, the pigmy right whale, and shares morphological characteristics with balaenids which suggest a similar feeding mechanism (“Encyclopedia of Marine Mammals - 3rd Edition,”; Marx and Fordyce, 2016) (Fig. 3).

Foraging consists of searching, capturing, and handling prey. The optimal foraging theory states that individuals should continue foraging until the energetic gain for consumption outweighs the search time, capture, and handling of prey (Pyke, 1984). No further expansion should be undertaken when it would lead to more significant losses than gains (MacArthur and Pianka, 1966).



**Figure 3.** Baleen whales' filter-feeding techniques. Skim feeding, Engulfment, Lunge feeding, and Suction feeding (adapted from Pivorunas, 1979; Werth, 2000).

The baleen whale's life history is characterized by its annual migration based on the seasonal pattern in prey abundance. Baleen whales feed in highly productive areas at high latitudes and breed at lower latitudes (Corkeron and Connor, 1999; Rasmussen et al., 2007). For example, humpback whales seasonally migrate from a tropical calving ground to higher latitude feeding areas where schooling fish and krill become seasonally abundant (Berta and Sumich et al., 2015; Rasmussen et al., 2007).



**Figure 4.** Distribution of principal humpback whale feeding and breeding areas and the migration routes linking them. Partly from Slijper (1979).

In relation to their enormous size, baleen whales have high energetic demands. This can only be met by foraging on high-density prey patches that also permit them to store energy within the blubber in order to survive when they are in oligotrophic waters with limited prey, away from their feeding grounds (Goldbogen et al., 2010; Brodie, 1975). This lipid cache is built up during intensive feeding bouts in the summer months and has been demonstrably correlated with increases in food availability and reproductive success (Lockyer, 1986). Considering that energy use and gain occur at such large temporal and spatial scales, baleen whales are predicted to have efficient

feeding mechanisms that maximize net energy gain (Goldbogen et al., 2010; Goldbogen et al., 2007).

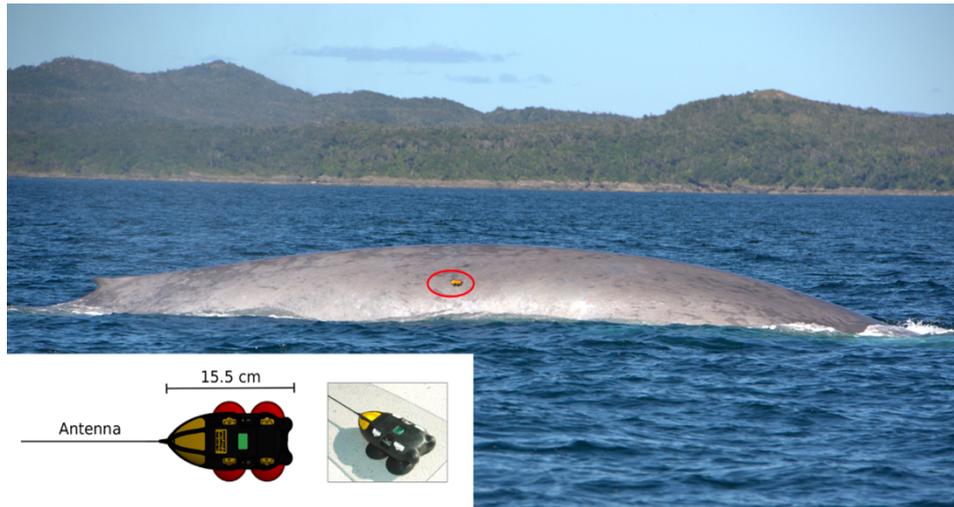
In general, the distribution and movement patterns of most rorquals consist of a seasonal migration from high latitudes where foraging takes place to low latitudes where they mate and give birth. However, data from blue whales in the Pacific indicate that feeding also takes place at low latitude, in "upwelling-modified" waters, and data from both the Pacific and the Indian Oceans indicate that some blue whales may remain at low latitudes year-round. Concerning daily cycle, different species of baleen whales were found to concentrate their foraging effort on dense aggregations of krill at depth of 150–300 m during the day and may cease feeding when krill becomes more dispersed near the surface at night (Croll et al., 1998; Croll et al., 2005; Caruso et al., 2021).

Foraging behavior of baleen whales has been studied by visual monitoring and through anatomical dissections (Werth, 2000). Large whales are impossible to study in captivity and what we know about their behavior was mostly studied from opportunistic observations at the sea surface. Recently, the advancement of bio-logging technology enables the analysis of fine-scale movements during feeding dives. Researchers are able to directly observe whale behavior using multiparametric sensors attached to the animal. Our

understanding of whale feeding behavior and performances has been vastly improved using this type of data, in addition to a better understanding of fundamental ecological and evolutionary processes (Potvin et al., 2012). Furthermore, various sensors of bio-logging instruments are increasingly contributing to monitor ocean physical properties (Fedak, 2013) and how animals' behavior is being studied in relation to them (e.g., Jaud et al., 2012; Bestley et al., 2013). There are many types of animal-borne tags, ranging from high-resolution behavior and acoustic loggers (Goldbogen et al., 2006; Johnson and Tyack, 2003), to satellite-linked tags that provide tracking information over wide spatial and temporal scales (Bailey et al., 2009). Most of the applications of bio-logging have involved sea birds, cetaceans, and pinniped (Ropert-Coudert et al., 2012).

In the context of energy expenditure, accelerometer-equipped tags have allowed researchers to finely observe whale behavior at the individual foraging dive level (Goldbogen, 2012). Moreover, large-scale projects at the scale of ocean basins have provided a wealth of information on habitat use and animal migration, integrating different techniques and sensors across taxa Fields (Block et al., 2011; Costa et al., 2012). For example, combining archival tags with multiple sensors, such as hydrophones and magnetometers, is becoming a

powerful technique to quantify both animal behavior and acoustic environment at an extremely high resolution (Johnson et al., 2009).



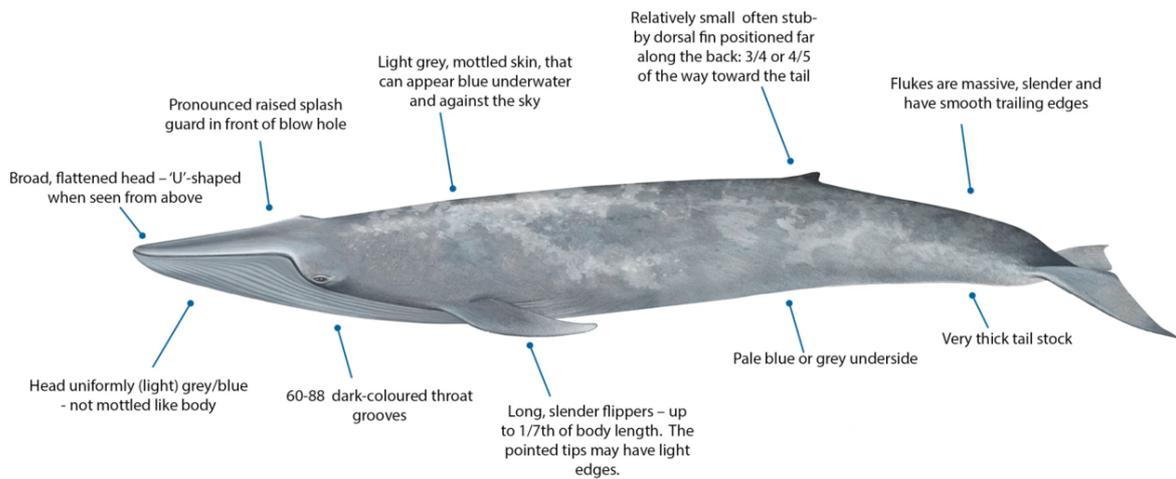
**Figure 5.** Picture showing a Chilean blue whale with DTAG attached. On the bottom two perspectives of the DTAG (Caruso et al., 2021).

## 1.2 Blue whale (*Balaenoptera musculus*)

The blue whale (*Balaenoptera musculus*, Linnaeus, 1758) is a baleen whale belonging to the family Balaenopteridae. This includes the group of toothless whales characterized by their ability to feed on patches of relatively small prey like krill or fish schools using their baleen filter. The body size of a blue whale may range in length up to 28 m and in body mass over 100 tons

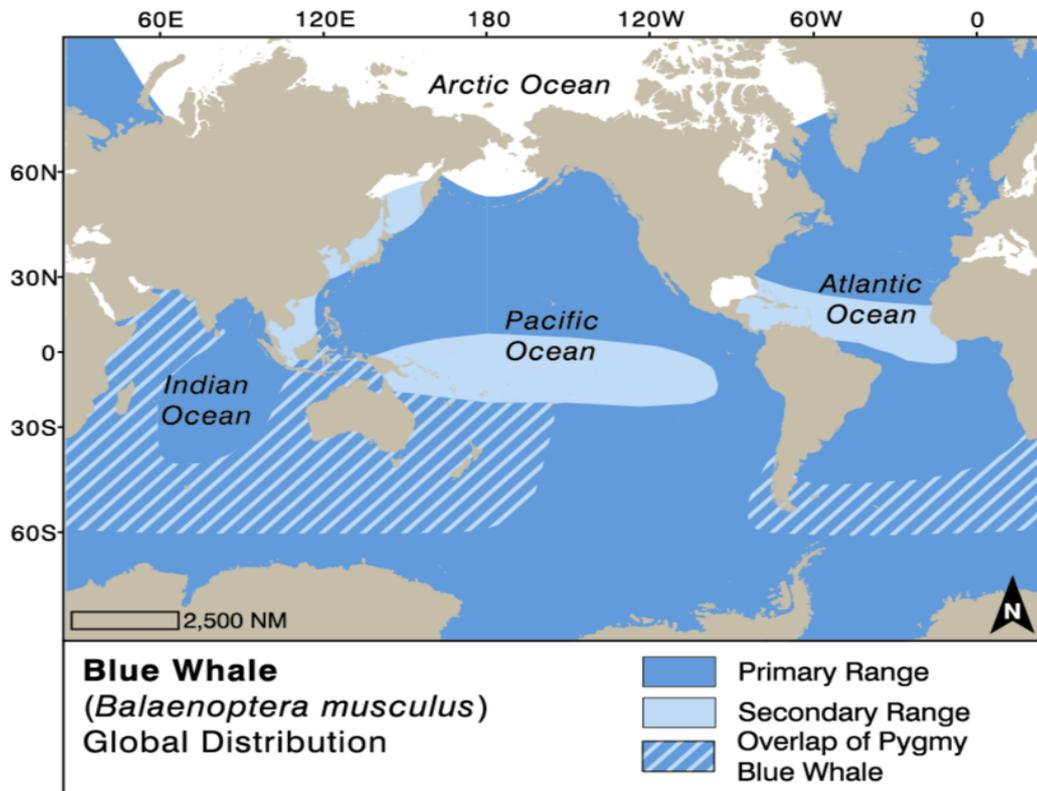
(Mackintosh, 1942). Since female baleen whales are larger than males, female measurements are used for the maximum size descriptions.

Following a description of blue whales according to Richards Sears and William F. Perrin (Encyclopedia of Marine Mammals - 3rd Edition, n.d.):  
*“Blue whales project a tall (up to 10–12m) spout, denser and broader than that of the fin whale, B. physalus, which in calm conditions can help distinguish between the two species...The prominent fleshy ridge just forward of the blowhole, known as the splash guard, is strikingly large in this species. When seen from above, blue whales have a tapered elongated shape...with a broad, relatively flat, U-shaped head adorned by a prominent ridge and massive mandibles. The baleen is black, half as broad as its maximum 1 m length, and 270–395 plates can be found on each side of the upper jaw. There are 60–88 throat grooves or ventral pleats running longitudinally parallel from the tip of the lower jaw to the navel, which enables the throat or ventral pouch to distend when feeding. The dorsal fin is proportionally smaller than in other balaenopterids...The flippers are long and bluntly pointed, slate gray, with a thin white border dorsally and white ventrally; they reach up to 15% of the body length”* (Fig. 6).



**Figure 6.** Illustration of a blue whale (*Balaenoptera musculus*).

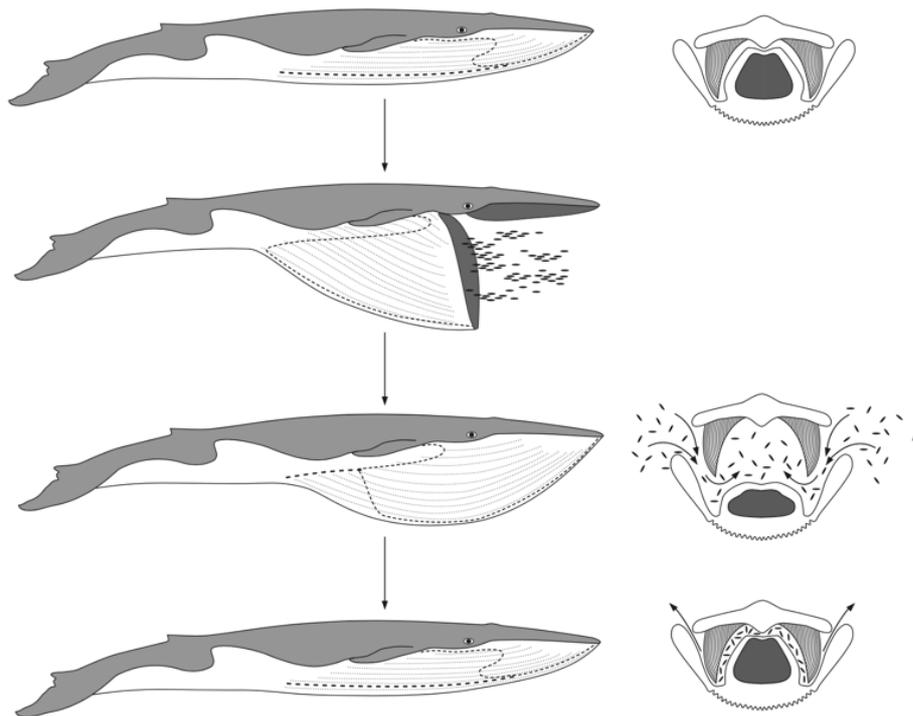
Blue whales exhibit the unique lunge filter feeding mechanism of rorqual whales (Balaenopteridae). Unlike some rorqual species, such as humpback whales (*Megaptera novaeangliae*) and minke whales (*Balaenoptera acutorostrata*) that feed on multiple prey types, blue whales feed almost exclusively on krill. This specialization on a patchy, ephemeral food resource, together with their extreme body size, defines much of their life history and ecology. The large body size confers a meager energetic transport cost, which facilitates undertaking long-distance migrations. Blue whales migrate across ocean basins, from breeding grounds at low latitudes to foraging grounds at high latitudes. The global population has been severely reduced by whaling during the 20th century, but several populations still inhabit all the oceans (Fig. 7).



**Figure 7.** Blue whale global distribution. Adapted by Nina Lisowski from Jefferson, T.A., Webber, M.A. and Pitman, R.L. (2015).

During lunge filter feeding on krill aggregations, once a patch of krill is detected, blue whales accelerate to speeds of up to 4 m/s and engulf a volume of prey-laden water that is bigger than the whale's body. The whale slows down due to the high resistance undergone by its open mouth during high-speed movement while imparting its momentum to the ingested body of water. After the blue whale's jaws close around the engulfed water, the animal forces the water out of the mouth through a relatively small window of baleen that is framed by the upper and lower jaws (Fig. 8). The fringes on the interior side of the baleen rack filter and retain the krill from the water flowing out of the

mouth, a process that takes nearly approximately 40–60 seconds (Goldbogen et al., 2017; Kahane-Rapport et al., 2020). After the engulfed water has been expelled from the buccal cavity, a blue whale may perform another lunge towards the same krill patch. During foraging, dives last about 10 minutes, and a blue whale often lunges, on average, three times per dive and then returns to the sea surface to breathe and replenish body oxygen stores (Croll et al., 2001).



**Figure 8.** Lunge filter feeding in blue whales, demonstrating expansion of the throat pleats in invagination of the tongue. From Berta and Sumich (1998).

An unanswered question is how blue whales find ephemeral and patchy resources, such as krill, in a seemingly featureless ocean. However, at different temporal and spatial scales, tag-derived evidences show that various senses play a role in finding patchy prey. Tracks from satellite tags at long-term and ocean basin scale investigations suggest that blue whales use long-term memory to track long-term averages in the ocean productivity (Abrahms et al., 2019). At finer scales, from meters to seconds, surface foraging behavior through drone observations of blue whales suggests that vision is used to distinguish krill patches (Torres et al., 2020). Inertial sensors from suction-cup archival tags have revealed some of the complex three-dimensional trajectories used by blue whales when lunge feeding, including 360-degree rolls and up-and-down pitching movements through krill patches (Goldbogen et al., 2012). Often lunge feeding occurs from below a krill patch, which could be a strategy where blue whales can create shade, limiting the amount of light that would otherwise betray their approach and trigger an early escape response from krill. Foraging in bulk on aggregations of zooplankton and fish is considered among the most energy-efficient strategies among marine organisms (Goldbogen et al., 2011).

Blue whales and their relatives developed their gigantic body size (>15 m and >50 tons) alongside the baleen filter feeding mechanism relatively

recently, around 5 million years ago (Goldbogen and Madsen, 2018; Slater et al., 2017). As a result of increased wind-driven upwelling, zooplankton patches such as krill increased in number and density during the Pliocene-Pleistocene climate transition. Wind-driven upwelling results in phytoplankton and zooplankton progressing from spring to summer, forming the basis for whale trophic progression. Such high-quality prey patches combined with specialized filter-feeding modes, such as lunge feeding, provided baleen whales with an evolutionary pathway to larger bodies by enabling them to forage efficiently (Slater et al., 2017).

### **1.3 Chilean blue whales (*Balaenoptera musculus chilensis*)**

Blue whales have survived despite being hunted nearly to extinction by whalers in the 1900s (Clarke, 1978; Branch et al., 2007). In the Southeast Pacific, blue whales were taken off around Peru and Ecuador but primarily caught on the Chilean coast (Clarke, 1978; Van Waerebeek et al., 1997). The year 1908 was the beginning of commercial catches in Chile (Pastene and Quiroz, 2010), reaching a peak between 1926 and 1971 when thousands of catches were reported in the southern region of the country (Williams et al., 2011). Illegal whaling has continued into the early 1970s (Clapham et al., 1999) despite the

species has been protected globally by the International Whaling Commission (IWC) since 1966 (Clapham et al., 1999). Nowadays, the recovery of the species is a critical international conservation goal (Roman et al., 2014) and is considered "Endangered" (IUCN red list; Cooke, 2018). Since protection measures were enacted worldwide, blue whale populations are slowly recovering.

Within the Southern Hemisphere, two different subspecies of blue whales have been recognized (Branch et al., 2007b, 2007a). In January 1998, an important discovery was made when a population was found in the Gulf of Corcovado in the Chiloense Ecoregion of southern Chile (Thiele et al., 1998). In 2016, the population of Chilean blue whales was recognized as a separate unnamed subspecies (Committee on Taxonomy, 2016). In 2020, considering body measurements (Norris and Sciences, 1966), acoustic call types (Buchan et al., 2018), and genetic evidence (LeDuc et al., 2007, 2017), Chilean blue whales resulted substantially different from Antarctic blue whales and pygmy blue whales. The population of Chilean blue whales is now recognized as subspecies, *Balaenoptera musculus chilensis* (Khalaf et al., 2020).

The three subspecies of blue whales that are currently recognized in the southern hemisphere are the pygmy blue whale (*Balaenoptera musculus breviceauda*) in the Indian Ocean and western Pacific Ocean, the Antarctic blue

whale (*B. m. intermedia*) in the Antarctic Zone, and the recently named Chilean blue whale (*B.m. chilensis*, Khalaf, 2020). These three subspecies, all appear to be present in the northern Chilean Patagonia (Branch et al., 2007b). Adult female blue whales caught off Chile were reported to have an intermediate length between the total lengths of the two subspecies (Branch et al., 2007b). In terms of genetic differences, a recent study (LeDuc et al., 2007) identified mitochondrial and nuclear differences, using molecular markers, between blue whales from the Indian Ocean, the Antarctic, and the southeastern Pacific. Torres-Florez et al. (2014) reported the three blue whale populations to be genetically different, and the vocalizations recorded in southern Chile differed from those of the Antarctic blue and pygmy whales (Buchan et al., 2014).

Blue whales' distribution and dive behavior are often driven by the distribution of their prey (krill, Euphausiacea) (Goldbogen et al., 2011). In the Chiloense Ecoregion, this can be highly influenced due to high levels of primary productivity originated by upwelling phenomena, topographic breaks, and frontal regions (Croll et al., 2005; Gill et al., 2011). According to Goldbogen et al. (2011), the foraging success of blue whales depends on the abundance of euphausiid aggregations and their density. In order to meet its energetic demands, an average-sized blue whale (25 m) requires prey biomass of  $1120 \pm 359$  kg krill per day.

In the northern Chilean Patagonia region, blue whales are known to feed during the austral summer and autumn (from late December to early August), off Isla Grande de Chiloé (Buchan and Quiñones, 2016; Caruso et al., 2021; Försterra and Häussermann, n.d.) with a seasonal peak of the main species in the area *Euphausia vallentini* during late summer and being twice as abundant in spring compared to winter (Buchan and Quiñones, 2016). The prey abundance and density contribute to the evidence that whales concentrate their efforts in relatively small areas (<1 km<sup>2</sup>) while foraging (Acevedo-Gutiérrez et al., n.d.). Therefore, they are mainly concentrated in small spaces during feeding behavior, creating a potentially dangerous habitat for the species, especially in relation to the significant increase of marine traffic that has occurred during recent decades in northern Chilean Patagonia (Wilmsmeier, 2013; Caruso et al., 2021).

## **Aims of the study**

The northern Chilean Patagonia region is a key feeding ground and a nursery area for blue whales (*Balaenoptera musculus*). In this region, growing salmon aquaculture and passenger ship industry, have boosted marine traffic, placing whales at significant risk of vessel strikes (Caruso et al., 2021). In this study, we analyzed the data of 18 tagged whales (using DTAGs) during four separate and yearly research cruises (2014-2017), for a total of 126 h of bio-logging data analyzed. From 2016 to 2017, active acoustics (scientific echosounders) were also used to record prey density and distribution simultaneously with whale diving data.

The main aim of this thesis was to characterize and understand the kinematics of Chilean blue whales foraging behavior, and how it is related to the density and distribution of their prey (euphausiids). By understanding the behavior of foraging of baleen whales, we could estimate the anthropogenic threats that the animals face in northern Chilean Patagonia. Furthermore, this study provides an example for broader comparative investigations of the evolutionary forces that shape the behavioral ecology of marine animals across different taxonomic groups, body sizes, locomotion techniques and environments.

## **CHAPTER 2: Materials and Methods**

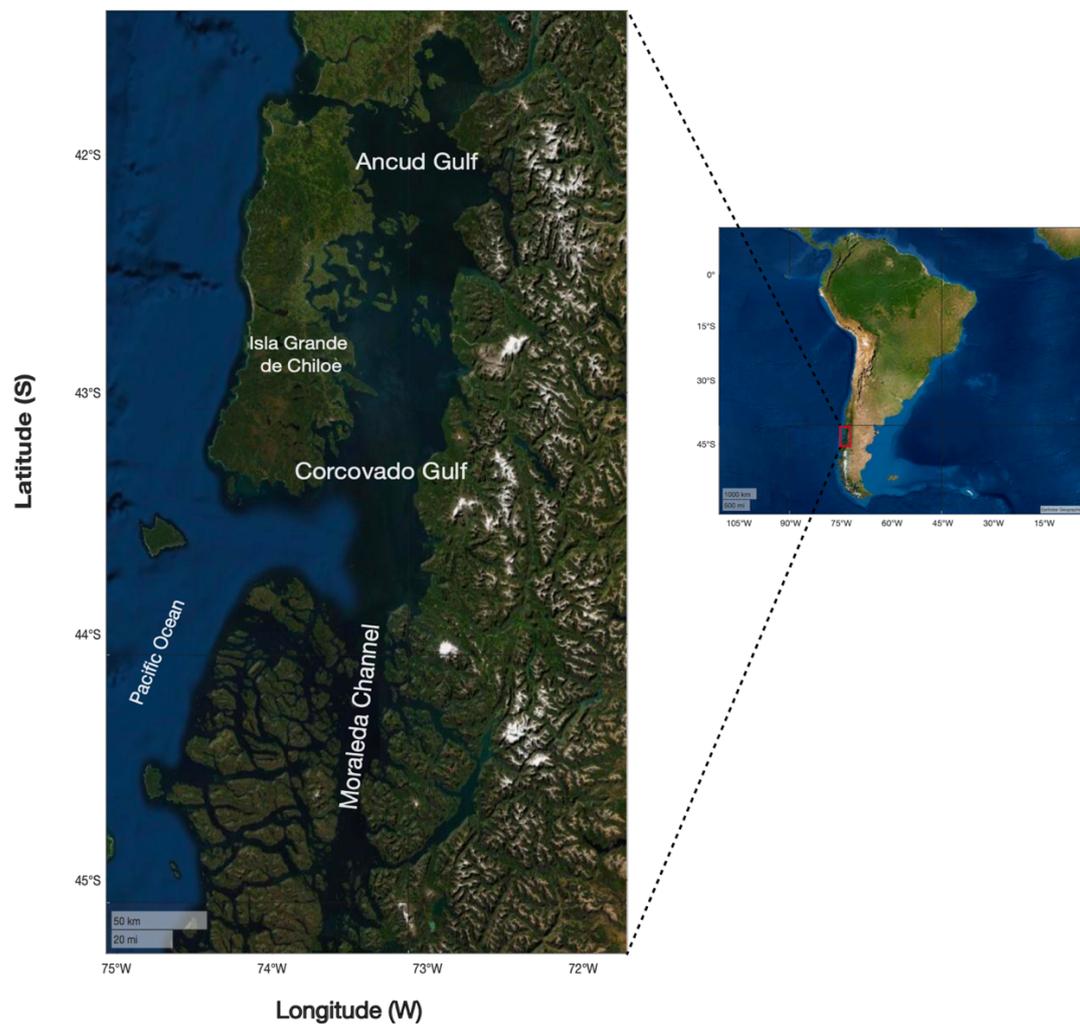
### **2.1 Study area**

The study area is situated on the southeastern border of the Pacific Ocean in Chilean Patagonia and extends from the Ancud Gulf to the Moraleda Channel (Fig. 9). This is one of the most extensive fjord regions in the world. It is considered part of the Los Lagos administrative region (Molinet et al., 2014), and according to the classification of Marine Ecosystems of the World (MEOW), it belongs to the Chiloense Ecoregion (CER; Spalding et al., 2007).

Patagonia extends from the Reloncaví Fjord to Cape Horn, covering almost 240,000 km<sup>2</sup>. This area is characterized by a highly fragmented coastline composed of many islands, peninsulas, channels and fjords (Silva and Palma, 2008). The general oceanographic conditions affecting this area are under the direct influence of the West Wind Drift (WWD) or the Antarctic Circumpolar Current (Viddi et al., 2010). However, frontal zones, internal waves, and a variety of oceanographic phenomena are present in a region characterized by high bathymetry variability. Most of the Gulf has depths of several hundred meters, but there are also numerous sills and shallow regions (<100 m depth) (Artal et al., 2019). The Subantarctic Surface Water (SAWS), transported by the Cape Horn Current (CHC) and the Humboldt Current (HC), goes north,

towards the Equator, and south, along the contour of the South American coast. It also enters the southern Chilean channels and fjords, where it mixes with fresh water from rain, rivers, coastal runoff, and glacial melting, generating one of the largest estuarine systems on the planet (Palma and Silva, 2004; Silva et al., 2009). A strong horizontal and vertical salinity gradient - resulting from the interaction of WWD, SASW, tidal currents, and fjord freshwater - facilitates high productivity (Palma and Silva, 2004; Viddi et al., 2010).

Primary production in the CER is high and strongly seasonal, peaking in spring/summer (González et al., 2010). These factors make the CER a hotspot of terrestrial and marine biodiversity (Catalan et al., 2011). The Chiloé Interior Sea is home to a wide range of marine species such as cold-water corals (Försterra and Häussermann, 2012), penguins, marine and freshwater otters, many migratory birds, Chilean and Peale's dolphins, and humpback and blue whales (Hucke-Gaete et al., 2003, 2013; Häussermann et al., 2012; Viddi et al., 2010).



**Figure 9.** Map of the study region off the coast of Chile.

## **2.2 Data collection**

### **2.2.1 Bio-logging tags**

Bio-logging tags are miniaturized instruments attached to animals for logging and/or relaying information about their movements, behavior, physiology, and habitat (Rutz and Hays, 2009). Especially in the aquatic environment, these high-tech tools enhance our ability to observe free-ranging and undisturbed animals by providing opportunities to advance basic and applied biological and ecological research.

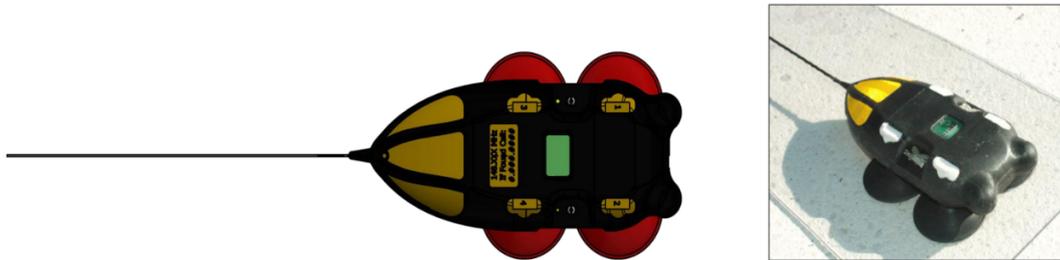
In the 1940s, animal bio-logging in the underwater environment started with the simple time-depth recorder (TDR) attached to seals (Scholander, 1940). Over the following decades, technological advances have facilitated the miniaturization of devices and the incorporation of more sophisticated sensors in animal-borne instruments, increasing their applications and utilities. Among these are: hydrophones used for measuring the acoustic behavior of tagged animals and the environmental soundscape (Johnson et al., 2003), multi-axial motion sensors, particularly accelerometers and magnetometers, to understand fine-scale locomotion activity such as feeding and swimming (Cade et al., 2016), biomedical sampling devices for measuring gas management during

diving (Meir et al., 2009), and cameras to check specific behaviors (Kahane-Rapport et al., 2020).

The data analyzed in this thesis have been collected using the Digital Acoustic Recording Tag (DTAG – v3, Fig. 10) developed by Woods Hole Oceanographic Institution (WHOI, United States). This tag was born to investigate large whales' acoustic and movement behavior (Johnson & Tyack, 2003). In particular, in this study we used DTAGs to acquire information on individual blue whales in Northern Chilean Patagonia (Bocconcelli et al., 2016; Saddler et al., 2017; Caruso et al., 2021). The DTAG is a non-invasive sensor (attached to the animal by suction cups). It contains two hydrophones (programmed to sample at either 120 or 500 kHz), as well as pressure sensors (depth) and 3-axis accelerometers and magnetometers (sampled at either 200 or 500 Hz).

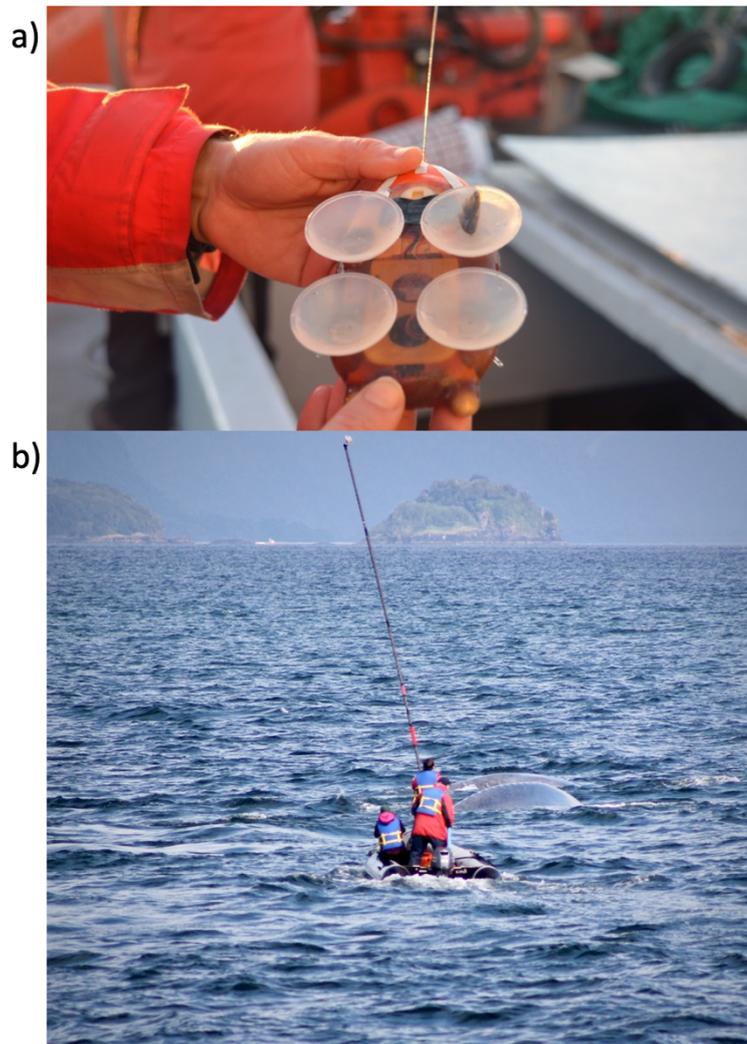
During deployments, the tag is positioned at the end of a hand-held 8 m carbon fiber pole used to reach the animal, which was non-invasively attached with four small suction cups (Fig. 11a). The DTAG can stay on the animal for up to 24h, then detach by venting the suction cups with air via a customized release mechanism. Whales are tracked by integrating a very high frequency (VHF) transmitter, which enables the tag to retrieve post-release. The tagging procedure was applied using a small inflatable boat powered by a 4-stroke

outboard engine, so it's possible to arrive very close to the animal with minimal disturbance (Fig. 11b).



**Figure 10.** An illustration of a Digital Acoustic Recording Tag (DTAG – v3) developed by WHOI (United States). On its anterior side: a very high frequency (VHF) transmitter.

The main survey vessel was a modified live-aboard 18.6 m fishing vessel (the MV Centinela) during six-annual research cruises (from 2014 to 2019). Field effort was focused on February-March, based on historical sightings, acoustic detections, and suitable weather data for whale tagging. At sunrise, visual surveys were held on the ship's upper decks to detect marine mammals. In addition to the data from DTAGs, complementary data have been acquired on prey field distribution and abundance, using active hydroacoustic systems (echosounder-Simrad ES60) and plankton net tow to ground truth acoustic backscatter. This information on prey provides an essential ecological context for the whale's feeding behavior. It will also help to estimate how much prey is consumed during each feeding dive (Goldbogen et al., 2013).



**Figure 11.** a) An upside-down picture of a DTAG showing the four suction cups through which it gets attached to the whale. b) Picture shows a group of scientists approaching a Chilean blue whale with a small inflatable boat. One scientist is holding a carbon fiber pole with a DTAG.

### 2.2.2 Scientific echosounder

Prey mapping was conducted during tagging expeditions from 2016 to 2019, allowing to map the distribution and abundance of krill in the vicinity of tagged whales (Hazen et al., 2009). Therefore, using this data is possible to link the feeding lunges of a whale to a direct measure of prey abundance

(Goldbogen et al., 2013). In this thesis, we used the data acquired during the research cruises of 2016 and 2017. Echosounder data were acquired from the main vessel using SIMRAD ES60; a two-frequency (38 and 200 kHz) single-beam quantitative echo-sounders, deployed at a depth of approximately 1 m from a pole-mount on board. The sensor was calibrated using a 38.1 mm tungsten carbide sphere following the procedure described by Foote et al. (1990).

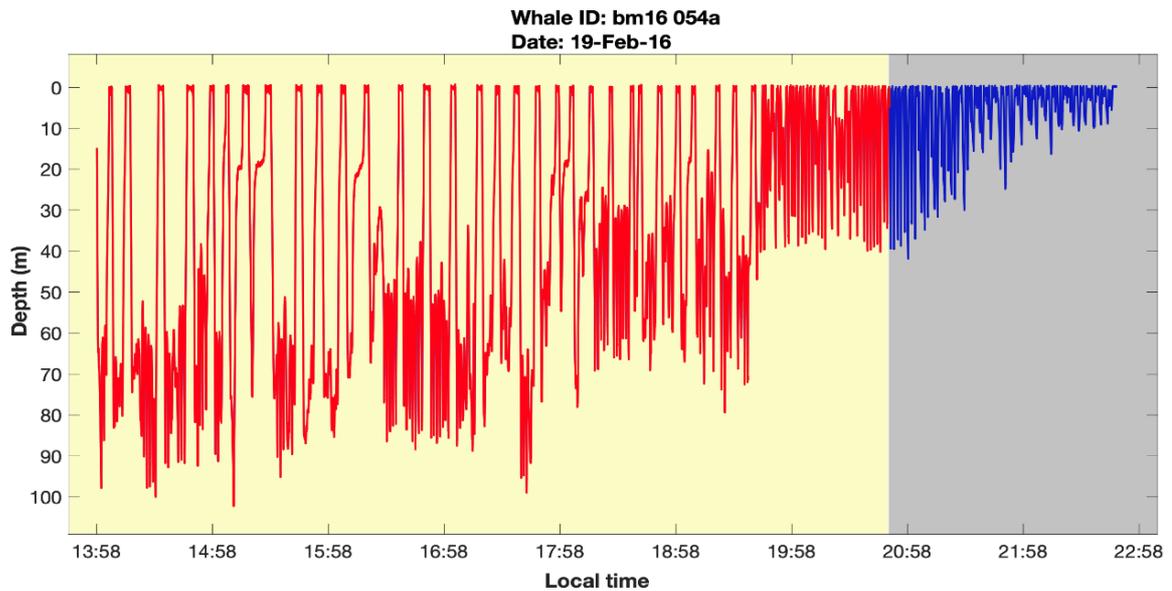
During prey mapping, the ship operated at a reduced speed, generally 4–5 kn, but occasionally in calm seas at speeds of up to 8 kn. Backscatter data with vertical and horizontal resolutions of approximately 10 cm and 1–10 m was derived from pulse lengths at 256–512 microseconds with a ping rate of 0.5–1 Hz. These data were collected in areas where tagged blue whales were present. As soon after the whale dived, the echosounder would pass by its known location. Prey surveys generally expanded radially from the whale's location to a distance of 0.2–1 km (distances estimated based on visual observations of surfacing animals). Nonetheless, the scientists avoided collecting data precisely co-located with the whale so as not to cause behavioral responses due to vessel presence and noise. Also, vertically stratified krill length measures–frequency have been used from net tows ( $\approx$ 60 cm diameter, 250  $\mu$ m mesh) to ground truth acoustic backscattering data. A subset of krill

was digitally photographed immediately following the capture and before preservation (Caruso et al., 2021).

## **2.3 Data analysis**

### **2.3.1 Dive pattern & lunge detection**

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 a 10 Hz sampling rate for further analysis. The algorithm simulates the tagged animal's dive profile (the tag pressure exposure over time). It determines the period belonging to the day or night phases in relation to local sunrise and sunset times in the study area (Fig. 12). Diurnal cycle data were obtained from the website of the US Naval Observatory (<https://www.usno.navy.mil/USNO>). 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 (Caruso et al., 2021).



**Figure 12.** Dive profile of one whale tagged on February 2016 (bm16\_054a), showing deeper daytime dives in red and shallower nighttime dives in blue. Differences in dive profiles between the two whales are notable. Yellowed area indicates daytime until sunset, while greyed area indicates nighttime (information about local diurnal cycles was obtained from the US Naval Observatory, <https://www.usno.navy.mil/USNO>).

The accelerometer and magnetometer data were decimated to 10 Hz before analysis. In order to coincide tag data axes with body axes of the whale, data was corrected by rotating each three-element vector by a direction cosine matrix derived from the tag orientation using periods of known orientation, such as when the whale surfaces (Johnson and Tyack, 2003; Zimmer et al., 2005). Pitch, roll and heading (animal orientation) was calculated using custom-written MATLAB scripts (Johnson and Tyack, 2003). To determine the continuous whale speed, we used the flow noise from hydrophones (Goldbogen et al., 2006). Flow noise root mean square (RMS) is regressed against periods

of orientation-corrected depth rate (OCDR) when pitch > 45 degree and dive is deeper than 10 m (Fig. 13)(Miller et al., 2004). Acceleration rate (jerk) was also calculated, and it was computed as the norm of the difference of successive accelerometer samples for all three axes of the accelerometer (Simon et al., 2012). Jerk, given in units of  $m/s^3$ , is a valuable indicator of fast movements of a tagged whale because it expresses the rapid changes in orientation and acceleration while removing the slowly changing mean orientation.

Kinematic signatures from tag data were used to detect lunge feeding events (Fig. 14). These include (Cade et al., 2016; Goldbogen et al., 2013):

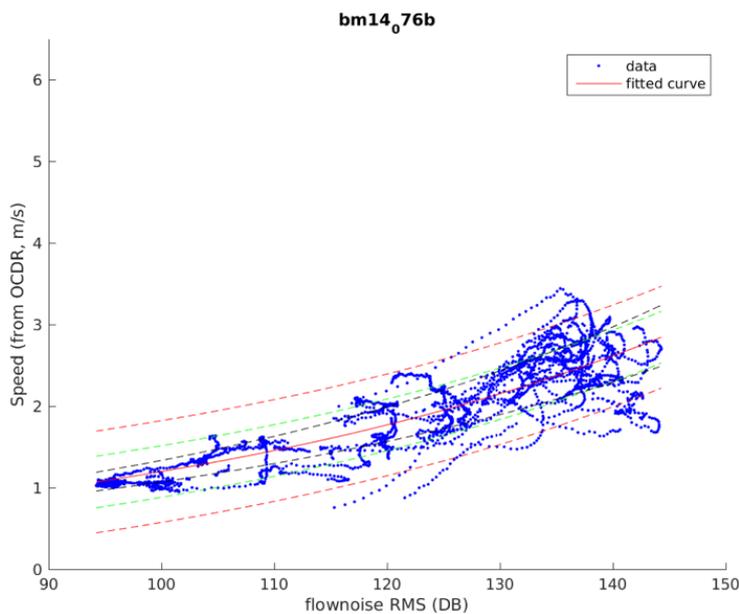
- pitch and roll (degrees);
- intense fluking leading to rapid acceleration ( $>3m/s$  in Chilean blue whales), also observed as high values of jerk and flow noise;
- rapid deceleration immediately when the mouth opens.

For statistic calculations of lunges per dive, we considered a dive only when the animal reached at least the depth of 25 m.

### 2.3.2 Prey abundance & distribution

Acoustic backscatter data were processed using Myriax ECHOVIEW software and MATLAB. Following Reiss's method (Reiss et al., 2008), to ensure patches were composed of krill, patches were identified as being from krill from the 200 kHz, when the difference in volume backscattering coefficient ( $S_v$ ) was 2–18 dB higher than that measured at 38 kHz. A specific range of krill length (12– 20 mm range), obtained from measures of krill captured from net tows during the cruise, was used to determine the dB difference window, although there were occasionally smaller (8–10 mm) larval krill. The dB difference algorithm filtered out non-krill scatterers that were occasionally encountered. According to their scattering characteristics, these were usually small groups or multiple individuals of near-bottom fish. Post-processing of acoustic backscatter data consisted of filtering raw data for noise, subtracting background noise, and removing regions from analysis, including near the surface where bubbles may occur and near the seafloor (Caruso et al., 2021). 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 and MacLennan, 2008). The center-of-mass depth 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). This study analyzed acoustic measures of prey distribution and abundance for four tagged blue whales (bm16\_049a; bm16\_054a; bm17\_063a; bm17\_063b). These deployments were selected as case studies because the echosounder data overlapped well both spatially and temporally with the deployment of tags that included both day and nighttime.

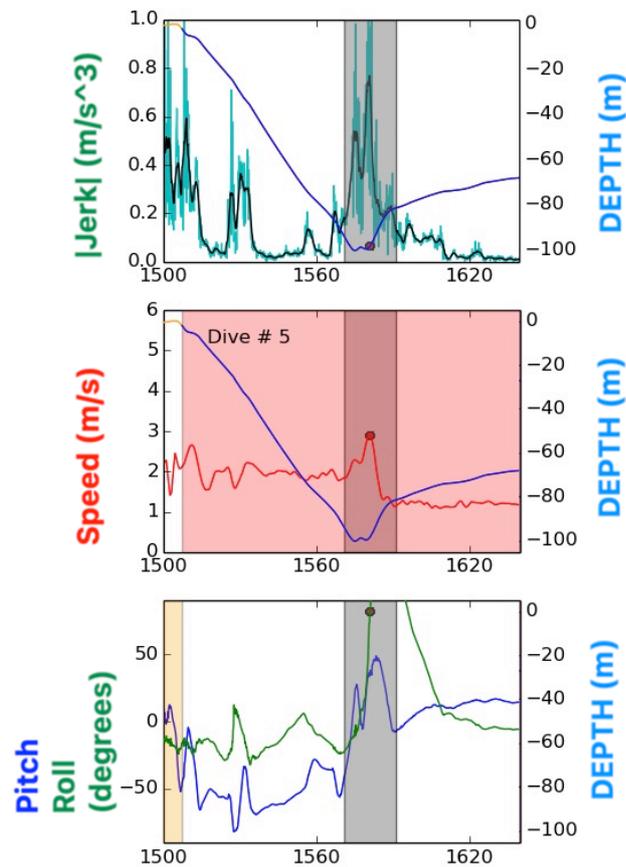


**Figure 13:** Flow noise regressed against periods of orientation-corrected depth rate (OADR) when  $|\text{pitch}| > 45$  deg.

## 2.4 Statistical analysis

The data analyzed from pressure, accelerometer, and magnetometer sensors showed a non-normal distribution, so a non-parametrical test (Mann-

Whitney U test) was applied to compare the behavior of Chilean blue whales between day and nighttime foraging events.



**Figure 14.** Example kinematic signatures to detect feeding lunge from a Chilean blue whale deployment of DTAG (bm16\_49a). The lunge is marked by the red dots, a rapid acceleration rate (jerk) to reach the peak in speed (around 3 m/s), and a mouth opening leading to rapid deceleration.

**Table 1.** Deployment information including date, start time of data acquisition (local time GMT-3), on-animal time (duration tag was attached) and deployment duration (day and night).

Whale ID	Date	Start (local)	On-Animal	Duration (min)	
		hr:min	hr:min	Day	Night
bm14_076a	17-Mar-14	13:15	00:07	7	ND
bm14_076b	17-Mar-14	18:36	05:04	94	210
bm14_082a	23-Mar-14	13:00	03:51	231	ND
bm14_082b	23-Mar-14	13:59	01:22	82	ND
bm14_083a	24-Mar-14	13:22	10:10	396	214
bm15_048a	17-Feb-15	18:39	24:44	866	618
bm15_050a	19-Feb-15	13:21	06:53	413	ND
bm15_053a	22-Feb-15	11:55	09:00	535	5
bm15_054a	23-Feb-15	15:58	10:18	290	328
bm15_057a	26-Feb-15	11:19	03:31	212	ND
bm15_064a	05-Mar-15	20:39	10:17	ND	617
bm16_049a *	18-Feb-16	17:48	12:45	189	576
bm16_050a	19-Feb-16	14:37	06:52	378	34
bm16_054a *	23-Feb-16	13:58	08:48	411	117
bm16_057a	26-Feb-16	16:00	00:16	17	ND
bm16_059a	28-Feb-16	17:01	00:42	42	ND
bm16_062b	03-Mar-16	10:51	09:05	545	ND
bm17_060a	01-Mar-17	15:49	00:22	22	ND
bm17_063a *	04-Mar-17	09:26	01:35	95	ND
bm17_063b *	04-Mar-17	12:28	01:17	77	ND

## **Chapter 3: Results**

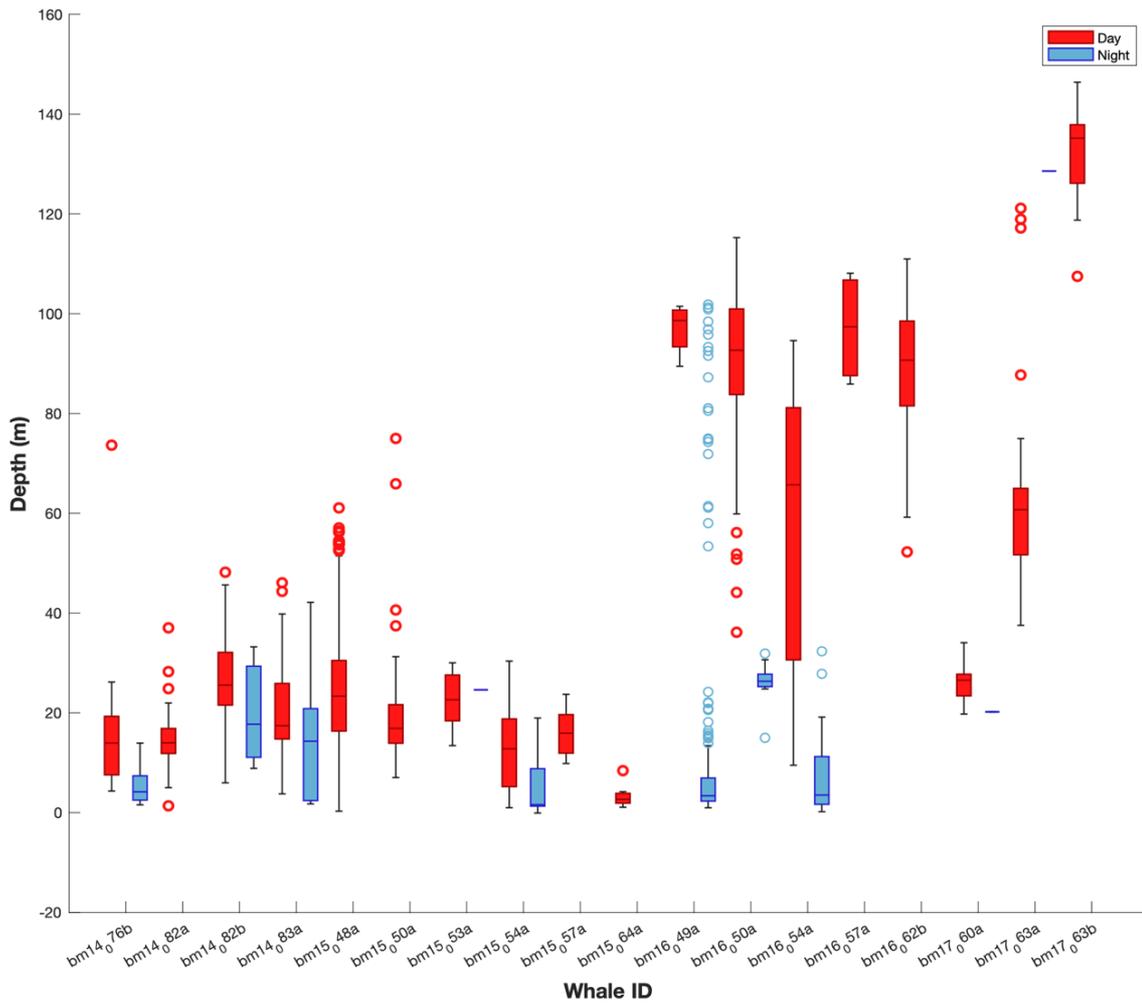
### **3.1 Characterization of foraging events**

During this four-year study, 18 Chilean blue whales have been tagged, acquiring about 126 hours of deployments. We recorded 681 dives (deeper than 25 m) and 1,767 foraging events, called lunges (both deep and shallow lunges were considered). For the characterization of lunges, we analyzed the depth at which these events occur, the whales' speed and pitch, and the difference in time between lunges (Inter-Lunge Interval). Then, a comparison between day and night was applied to verify the differences on the daily timescale. Foraging events (lunges) were correlated to prey distribution and biomass (NASC). Differences between deployments from different years were also analyzed.

#### **3.1.1 Depth analysis**

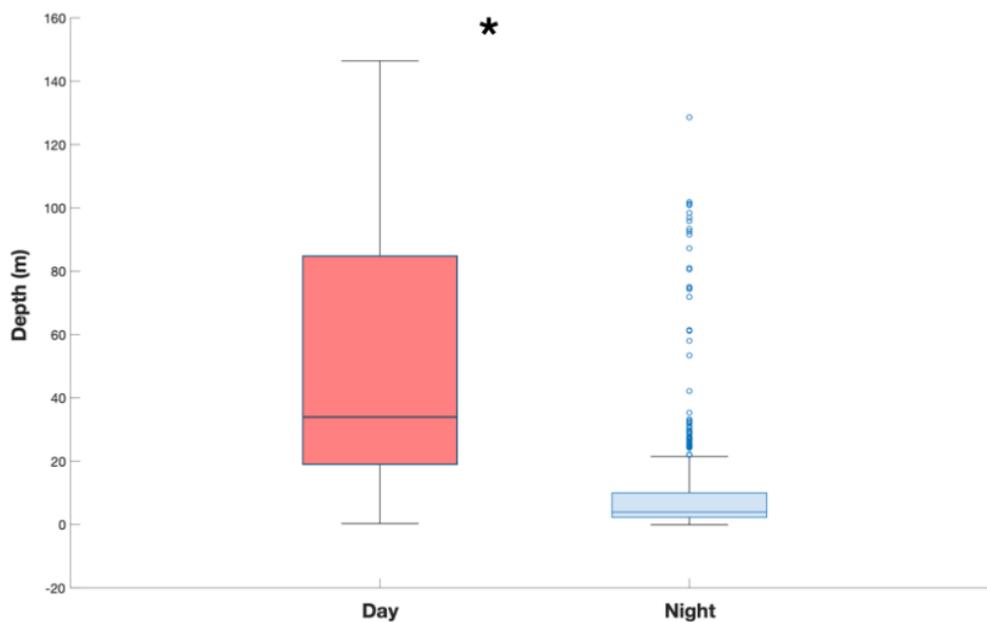
For all the whales with lunge events detected during day and night, there is a noticeable difference in depth at which lunges occur. Deeper lunges were reported during daytime, and shallower feeding events during night hours (Fig. 15). However, within whales, we can see differences in lunge depth ranges mainly during day hours (e.g., bm14\_076b, day median depth = 14 m with data

extremes [4.3 26.2]; bm16\_054a, day median depth = 67 with data extremes [9.5 94.6]).



**Figure 15.** Lunges depth ranges (m) of each of the 18 tagged whales during daytime (red) and nighttime (blue). The central mark indicates the median depth, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. The whiskers extend to the most extreme data points not considered outliers, and the outliers are plotted individually.

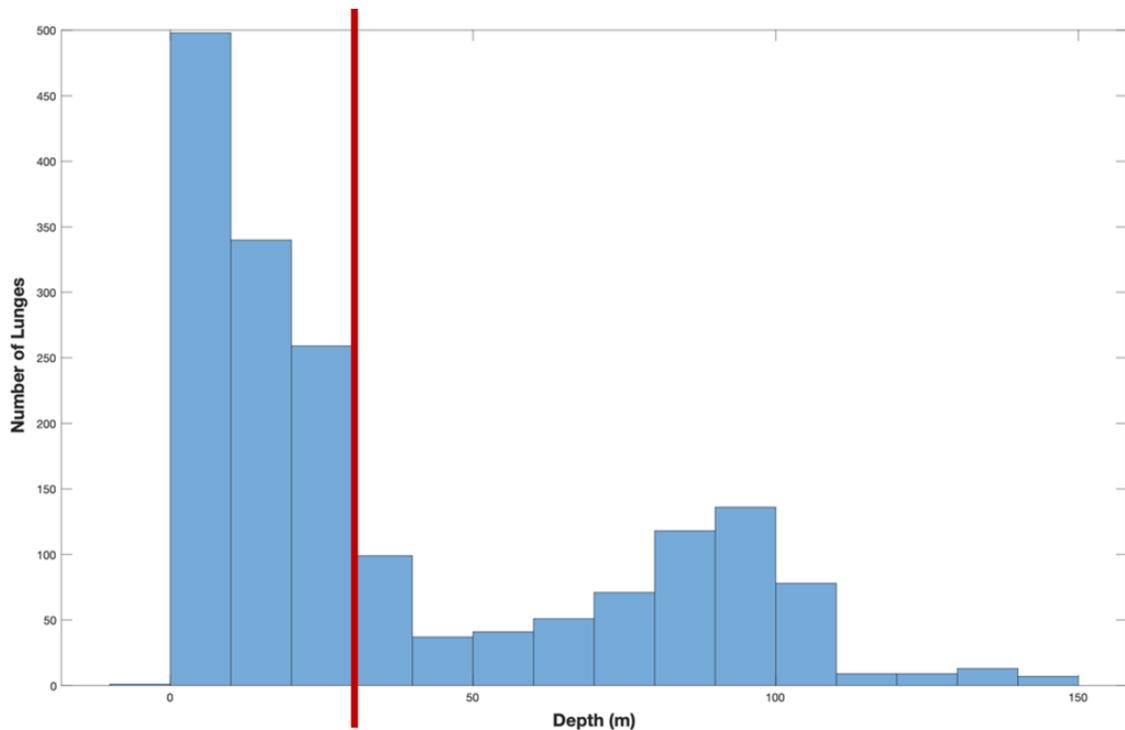
The foraging events detected during day hours (n = 1182) were compared with the night foraging events (n = 585). A significant difference is observed between the depth of lunges during the day and night (Mann-Whitney U-test,  $p < 0.05$ ), with median day depth of 33.9 m and a median night depth of 3.9 m (Fig. 16).



**Figure 16.** Lunge depth ranges (m) of all lunges during day hours (red) and night hours (blue) of all the DTAG deployments. Mann-Whitney U-test ( $p \leq 0.05$ ; \*).

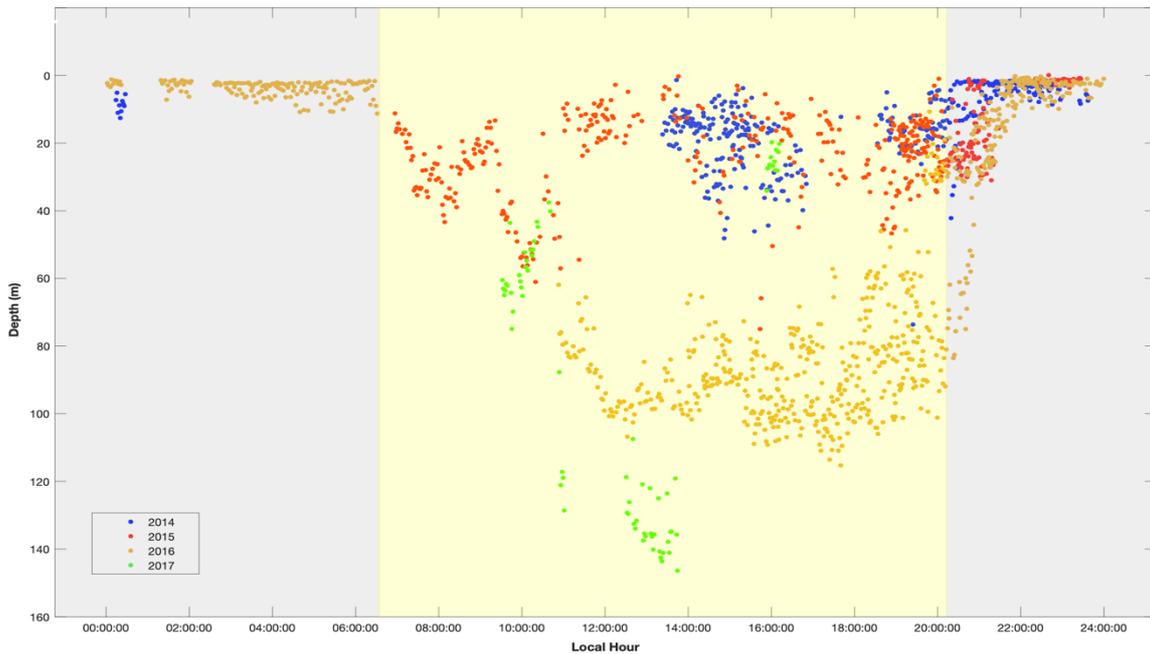
Considering the limit of very shallow waters at 30 m of depth, two peaks are represented by the total number of lunges. For shallow waters (0-30 m), the peak is in the range of 0-10 m of depth, where 498 lunges were detected, while for waters at greater depths ( $> 30$  m), the peak is around 90-100 m with 136 lunges detected (Fig. 17). In general, a higher number of lunges in very shallow

waters was reported (1,097 lunges in the first 30 m against 670 lunges between 30-150 m).



**Figure 17.** Lunges at different depths (meters). Values are represented as the total amount of events detected at a specific range of depth (bins of 10 m). The red line divides the data into lunges detected in very shallow waters and not (>30 m).

Throughout the four years of the study (2014-2017), it was observed a noticeable change in depth at which the whales fed during daytime (Fig. 18). Mode values (Mv) of day lunge depth of each year are: 2014 (blue dots), Mv = 10-20 m; 2015 (red dots), Mv = 20-30 m; 2016 (yellow dots), Mv = 80-100 m; 2017 (green dots), Mv = 120-150 m. During nighttime, depth mode values have no significant difference over the four years.

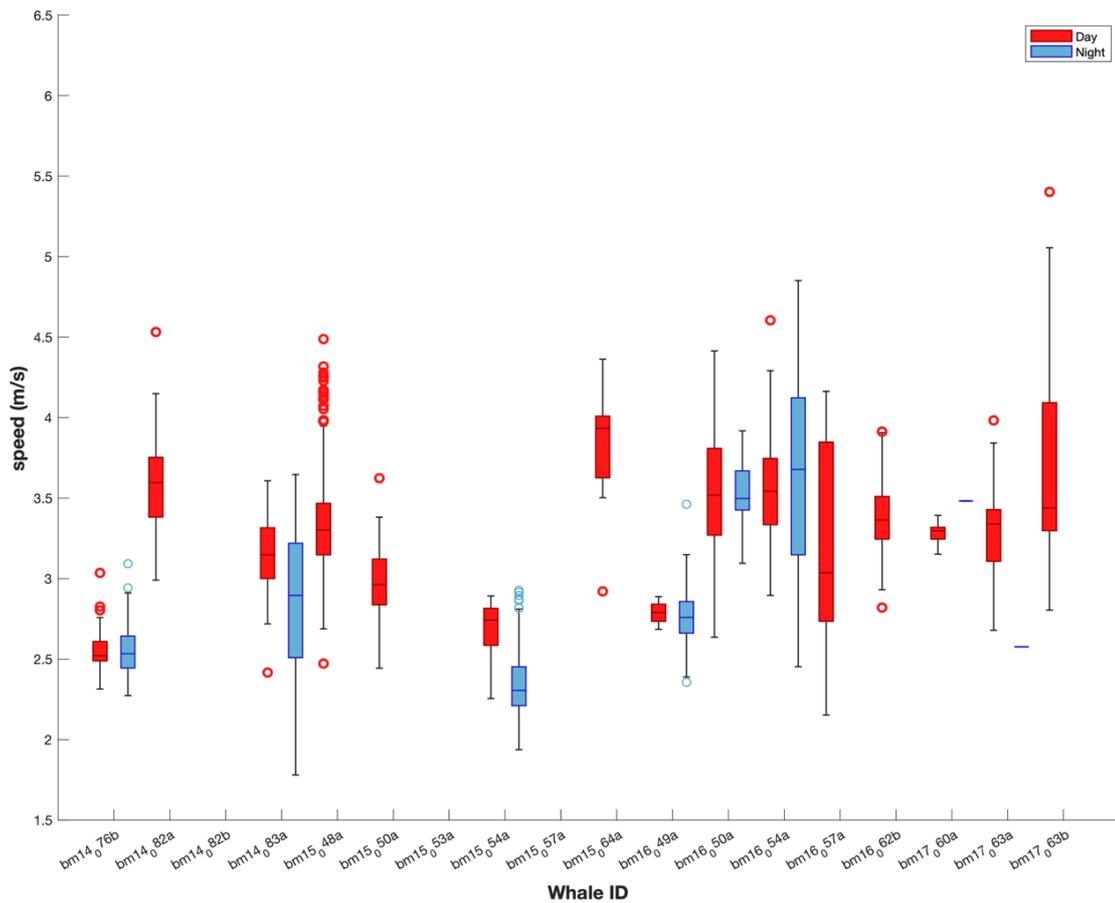


**Figure 18.** Distribution of all feeding events (1,767) of the 18 tagged whales during the four-year study (2014: blue; 2015: red; 2016: yellow; 2017: green). Each point represents a lunge at a specific local time (x-axis) and depth (y-axis). The gray areas represent nighttime (information about local diurnal cycles was obtained from the US Naval Observatory, <https://www.usno.navy.mil/USNO>).

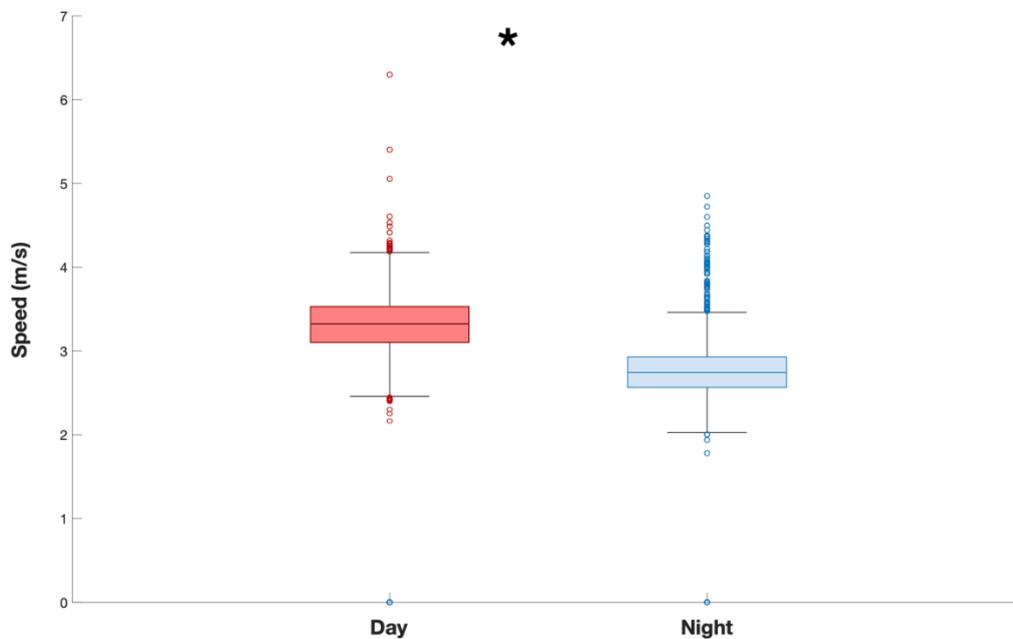
### 3.1.2 Speed analysis

The animal speed was measured during each lunge, as the whale reaches its maximum speed right before opening the mouth during feeding and then decelerates. Figure 19 shows differences within whales, with median values of speed ranging from 2.3 m/s to 3.9 m/s for night lunges and 2.5 m/s to 3.6 m/s during the day. However, while comparing all speeds of day-lunges with night-

lunge, a statistical difference is reported (Mann-Whitney U-test,  $p < 0.05$ ; day median: 3.3 m/s; night median: 2.7 m/s) (Fig. 20).



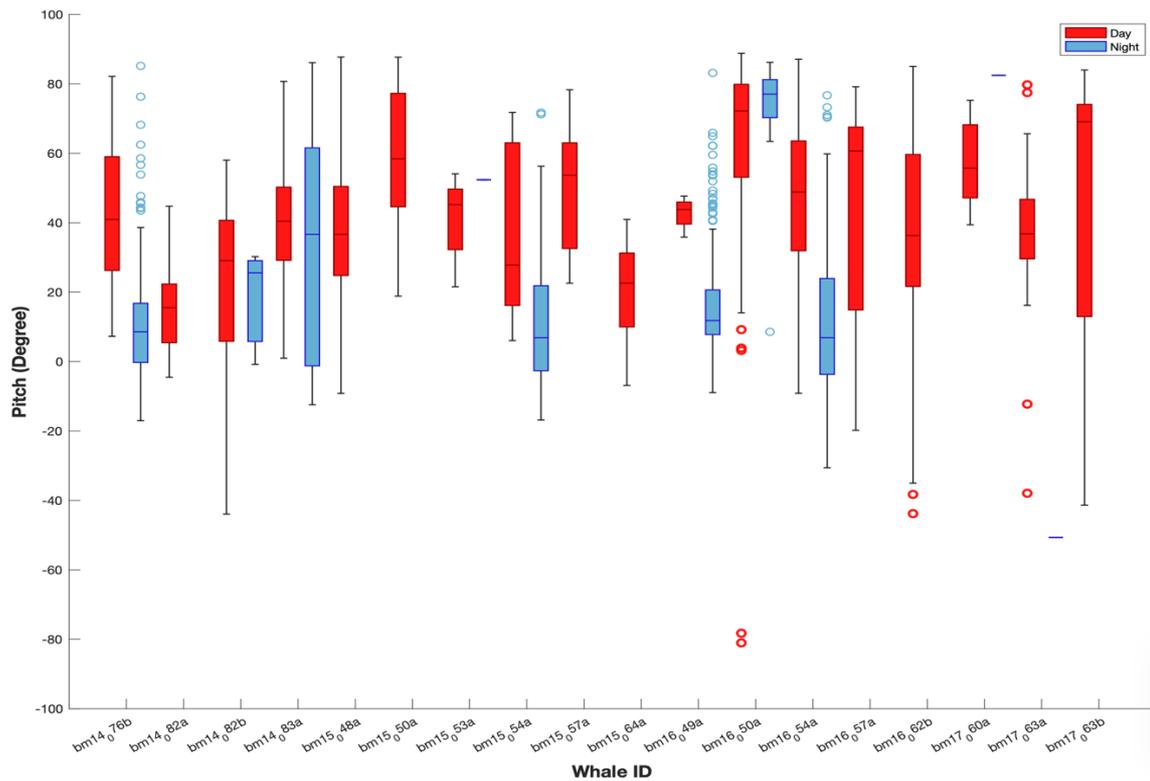
**Figure 19.** Lunges speed range (m/s) of the 18 tagged whales during daytime (red) and nighttime (blue). The central mark indicates the median speed, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. The whiskers extend to the most extreme data points not considered outliers, and the outliers are plotted individually.



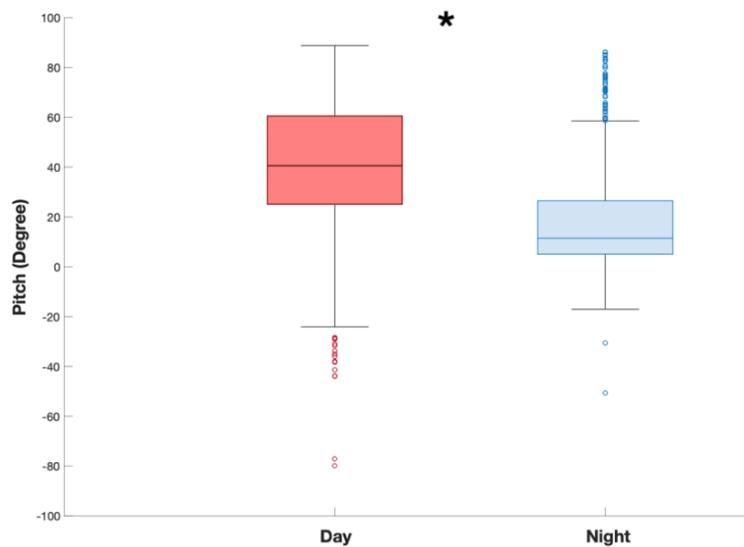
**Figure 20.** Speed of lunges (m/s) during day hours (red) and night hours (blue) of all the DTAG deployments. Mann-Whitney U-test ( $p \leq 0.05$ ; \*).

### 3.1.3 Pitch analysis

As for depth and speed, pitch values (degrees of rotation around the side-to-side axis is called “pitch”) during feeding events, vary among whales and between day- and night-lunges, with relatively higher values during daytime (Fig. 21). A positive pitch value ( $> 0^\circ$ ) was also reported for more than 95% of lunges, having all the median values higher than  $7^\circ$  degrees. Median values of daytime and nighttime pitches are  $40.6^\circ$  and  $11.4^\circ$ , respectively (Mann-Whitney U-test,  $p < 0.05$ ) (Fig. 22).



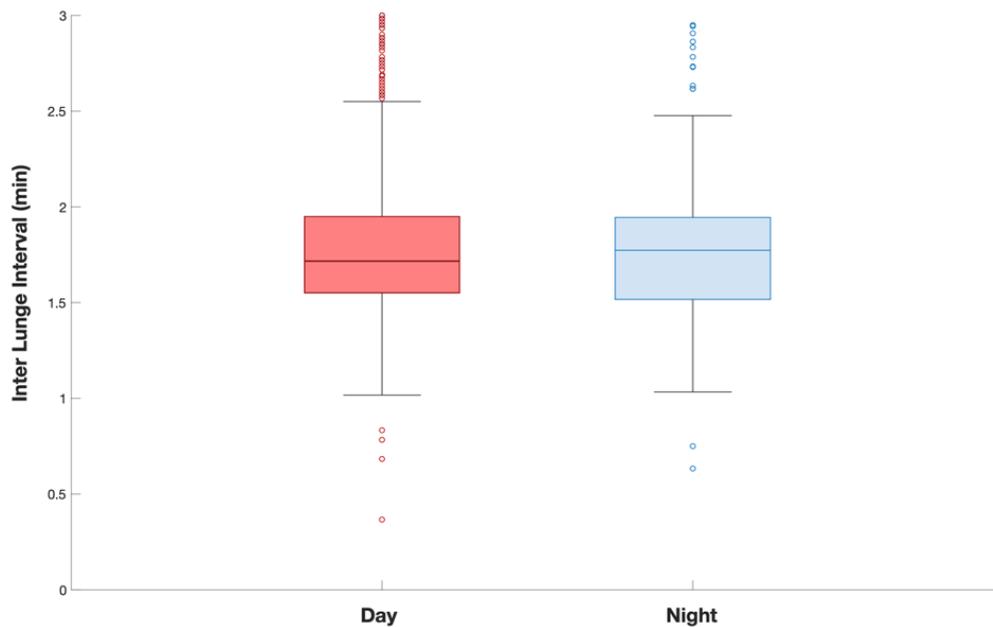
**Figure 21.** Whales pitch during feeding events of the 18 tagged whales during daytime (red) and nighttime (blue). The central mark indicates the median speed, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. The whiskers extend to the most extreme data points not considered outliers, and the outliers are plotted individually.



**Figure 22.** Whales' pitch during feeding events at daytime (red) and nighttime (blue) of all the DTAG deployments. Mann-Whitney U-test ( $p \leq 0.05$ ; \*).

### 3.1.4 Inter-Lunge Interval (ILI)

While for all three previous features a significant difference has been shown between day and nighttime, no significant difference was reported for the Inter-Lunge Interval values between day and night (day median = 1.71; night median = 1.77; Mann-Whitney U-test,  $p < 0.05$ ) (Fig. 23). The time limit between lunges was fixed as 3 minutes of resting time on the surface and the period of searching for prey was excluded.



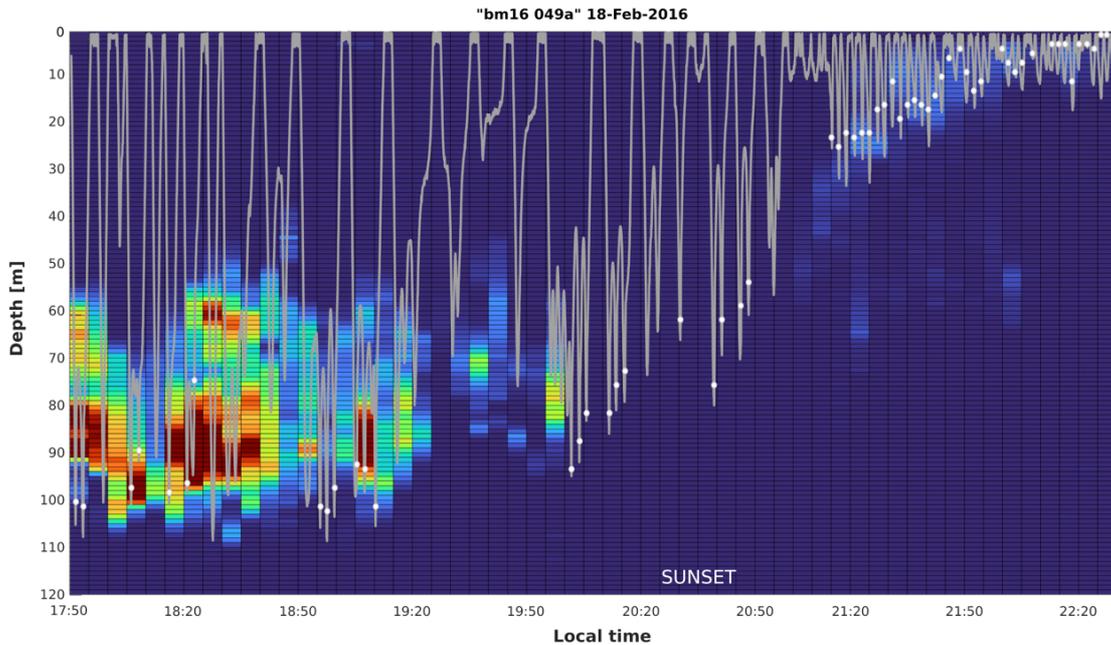
**Figure 23.** ILI time (min) of daytime lunges (red) and nighttime lunges (blue) of all the DTAG deployments. Mann-Whitney U-test ( $p \leq 0.05$ ; \*).

### 3.2 Prey mapping

Results of prey distribution reveal a strong overlap between dive depth, lunges, and the presence of acoustically measured krill biomass (Fig. 24). 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 foraging events 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 foraging 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 between the location of the krill layer (as measured by NASC) and the foraging depth of tagged whales (Table 1; Fig. 24).

Figure 24 shows a direct observation of the diurnal pattern of transition from the deep daytime of krill distribution and deep lunges by blue whales to the shallow nighttime distribution of krill and shallow/surface lunges by whales. Most of our survey effort in this study took place during daylight hours to locate, tag, and 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 daytime to night (as shown in Fig. 24).



**Figure 24.** An echogram of unprocessed 200 kHz backscatter shows the location of krill scattering layers, with the dive profile of a tagged blue whale (bm16\_049a, gray line) and feeding events (white dots). Volume backscatter ( $S_v$ ) is proportional to krill abundance or biomass.

Whale ID	Date	On-Animal (hr:min)	Lunge depth [m] (mean $\pm$ SD)	NASC depth [m] (mean $\pm$ SD)
bm16_049a	18-Feb-16	12:45	39.9 $\pm$ 38.7	55.5 $\pm$ 29.9
bm16_054a	23-Feb-16	08:48	41 $\pm$ 32.4	62 $\pm$ 21.5
bm17_063a	04-Mar-17	01:35	65.9 $\pm$ 24.1	84 $\pm$ 7.2
bm17_063b	04-Mar-17	01:17	132.5 $\pm$ 8.8	90.4 $\pm$ 6.4

**Table 1.** Relation between lunge depth and krill layer depth (NASC) for the deployments where prey distribution data were co-located with tagged whales.

## Chapter 4: Discussions

The foraging behavior of Chilean blue whales (*Balaenoptera musculus chilensis*) is shaped by various challenges. As air-breathing diving animals, they should adopt an energetically efficient mode of locomotion and minimize the use of oxygen during deep foraging dives (Williams et al., 1999). Even though they are big animals, foraging dive time is limited due to the high energetic costs of drag associated with their lunging technique to capture prey (Goldbogen et al., 2007). In general, baleen whales depend on prey density to maximize the amount of prey captured in a single feeding event, and the foraging effort tracks the diel vertical movement of krill (Friedlaender et al., 2013). The density of krill patches varies largely with depth during vertical excursions, having denser aggregations at depths during the day, then migrate towards the sea surface and disperse at night (Hewitt and Demer, 2000).

In the northern Chilean Patagonia, Caruso et al. (2021) showed that blue whales perform shallower dives close to the surface during the night to reach the vertically-migrating krill. Consequentially, a diurnal pattern of habitat preference of krill and foraging dives of whales was directly observed (Caruso et al., 2021). In this study, we characterized the kinematics of foraging behavior to better understand the feeding strategies of Chilean blue whales. The analyses indicated that their kinematics is significantly modified in response to the diel

vertical migration of krill. We found different kinematics and feeding strategies among the 18 tagged whales analyzed. By measuring depth, pitch, roll, and speed, Chilean blue whales exhibited more acrobatic maneuvers when foraging on deep, high-density, more sparsely distributed krill aggregations, contrary to what has been described by Goldbogen et al. (2015) in a different region.

In contrast, blue whales maneuvered less when foraging on shallow, low-density krill patches. While we did not observe any significant difference in roll maneuvers among lunges at different depths, we reported higher speeds and steepest pitches when feeding at higher depths. By executing lunges at depth, the increasing speed, and changing body orientation with steep pitch can have higher energetic costs with respect to a more linear trajectory lunge (Wilson et al., 2013).

According to the optimal foraging theory (Doniol-Valcroze et al., 2011), the energetically costly strategy should be balanced with prey quality and quantity, which in our case, can be confirmed with more dense patches at higher depths. The results showed no significant difference in time between consecutive lunges during deeper foraging dives compared to shallow ones. The tagged whales continued to forage until the energetic gain for consumption outweighs the search time, capture, and handling of prey (Pyke, 1984). Moreover, the results showed that the overall feeding rates were higher during

the night on shallow patches, while they tended to decrease during the day when the whales targeted denser and deeper krill aggregations. Even so, the maximum numbers of lunges per dive were reported with increasing krill density and depth.

Although we did not have prey mapping data for each of the 18 tagged whales, it was possible to predict the density and quality of patches reflected by the number of feeding events during a dive, following the previous hypothesis (Goldbogen et al., 2008). Given the overall in feeding rates, it suggests that Chilean blue whales indeed prefer to forage when krill are closer to the surface. Here, the krill is less dense but expands both horizontally and vertically. By foraging in shallow patches with less distance between krill and the central place (sea surface), the search time to detect and locate prey decreases while the probability of finding it increases.

Furthermore, Chilean blue whales should benefit from searching on shallow water volumes and being close to the surface; they should be able to optimize oxygen management by minimizing dive duration. Foraging close to the surface has another advantage to air-breathing filter feeders, allowing simultaneous foraging and breathing on the surface simultaneously, and thus permitting whales to forage continuously. This result suggests that foraging in more dense but sparse patches at high depth cannot be as efficient as waiting

for krill to migrate closer to the surface. In contrast to shallow foraging events, deep foraging dives require more energy, consume higher levels of oxygen, and have a longer recovery time on the surface. As shown in this study, Chilean blue whales exhibit more energetically costly maneuvers (pitch and speed) when executing deeper lunges.

## Chapter 5: Conclusions

Intensive hunting of whales - which started in the late 19th century - had brought many species to the brink of extinction by the 1960s. Blue whales are slowly recovering thanks to the laws of the International Whaling Commission (Clapham, 2009). Nonetheless, there is still a long way to go before the species is secure. As according to the IUCN Red List of threatened species, the blue whale is still listed as 'Endangered'. The species is facing various direct threats from anthropogenic activities, such as a high risk of ship collision (Caruso et al., 2021), entanglement and underwater noise (Fleming et al., 2011), and indirect threats such as the decline in krill due to climate change, overfishing and fish farming with potentially negative impacts on the whales.

Foraging is a primary need for wild animals to grow and reproduce. Southern Chile is an important region where different number of baleen whales (e.g., blue, humpback, and minke whales) take refuge to feed. Due to increasing on marine traffic and fish farming (especially salmon farming), the population of blue whales are facing greater threats. As showed by Caruso et al. (2021), in southern Chile, marine traffic occurs with higher rate during night. This study showed that, since deep lunges require more energetically costly maneuvers, search time, and recovery time, blue whales prefer feeding at a higher rate

during the night on shallow, low-density krill patches. Thus, they have a higher risk of ship collisions during feeding at night. These findings provided valuable and useful information, although they are subject to limitations due to the limited sample size associated with studying free-ranging and large whales. Vessel strike is a dramatic threat since whales concentrate their energies on feeding during the night since millions of years, so it will be difficult for them to switch their foraging strategy towards a higher energy cost activity.

Recent advances in bio-logging tags have permitted the collection of novel data about marine animal behavior and physiology and their habitat. Future challenges involve analyzing bio-logging data to understand individual behavior, predict population processes, and optimize species monitoring and conservation programs. Furthermore, the acquisition of long-term movement datasets on large whales is the current scientific goal for studying population dynamics and the impact of human activities.

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