UNIVERSIDADE FEDERAL DE JUIZ DE FORA
INSTITUTO DE CIÊNCIAS BIOLÓGICA
PROGRAMA DE PÓS GRADUAÇÃO EM BIODIVERSIDADE E CONSERVAÇÃO DA NATUREZA

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COMPORTAMENTO DE MERGULHO DE BALEIAS JUBARTE (*MEGAPTERA NOVAEANGLIAE*) AO LONGO DE SEU CICLO MIGRATÓRIO NO OCEANO ATLÂNTICO SUL OCIDENTAL

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DIVING BEHAVIOR OF HUMPBACK WHALES (MEGAPTERA NOVAEANGLIAE) THROUGHOUT THEIR MIGRATORY CYCLE IN THE WESTERN SOUTH ATLANTIC OCEAN

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Dissertação apresentada ao Instituto de Ciências biológicas da Universidade Federal de Juiz de Fora como requisito parcial à obtenção do título de Mestre Biodiversidade e Conservação da Natureza.

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Título: Diving behavior of humpback whales (*Megaptera novaeangliae*) throughout their migratory cycle in the Western South Atlantic Ocean

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ATWG/SORP

À minha família por sempre terem me apoiado
em cada decisão durante todo esse tempo,
e por sempre acreditarem no meu sonho.
Que me inspiram, me auxiliam
e por ser meu maior exemplo de vida.

To my family for always supporting me
in every decision during that time,
and for always believing in my dream.
That inspires me, help me
and for being my greatest example in life.

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“The sea, once it casts its spell, holds one in its net of wonder forever.”

Jacques-Yves Cousteau.

RESUMO

É pouco conhecido como o comportamento de mergulho durante o ciclo migratório das baleias jubarte *Megaptera novaeangliae* é afetado por características ambientais de seus habitats sazonais e seus papéis sociais. Neste estudo, tags satelitais do sistema Argos foram implantadas na costa do Brasil em 32 baleias jubarte no sudoeste do Oceano Atlântico. Os tags relataram dados de ~ 44 dias (máx = 124 dias) e 92,058 mergulhos. A análise estatística mostrou que a profundidade média de mergulho variou entre os habitats, sendo mais rasa na área de reprodução (BA, 22,6 m), intermediária durante a migração (MI, 30,26 m) e mais profunda na área de alimentação (FA, 35,16 m). Os mergulhos classificados como profundos (> 80 m), foram mais predominantes durante a migração. Em FA, os mergulhos noturnos foram mais rasos e curtos do que os realizados durante o dia, em BA os mergulhos feitos durante o dia foram mais profundos do que em todas as outras fases diárias. Não encontramos diferenças claras na profundidade e duração do mergulho entre as classes sociais. As fases da lua tiveram um efeito claro em BA, mas não em MI e FA, sendo mais rasos na lua cheia. Também vimos que as formas (U, V, Quadrado), apresentaram diferenças na profundidade do mergulho e entre habitats. Nossos dados fornecem os primeiros novos insights sobre os comportamentos de mergulho de indivíduos da mesma população ao longo de seu ciclo migratório, realizando diferentes comportamentos de mergulho, diferentes padrões de classe social, formas, alcance de profundidade, fases do dia e da lua. Além disso, essas descobertas e a compreensão dos padrões de mergulho em seus impulsionadores têm implicações importantes para a modelagem ecológica e as políticas de conservação.

Palavras-chave: Baleia-jubarte. Comportamento de mergulho. Oceano Atlântico. Telemetria satelital.

ABSTRACT

Is poorly known how the diving behavior during the migratory cycle of humpback whales *Megaptera novaeangliae* is affected by environmental characteristics of their seasonal habitats and their social roles. In this study, archival Argos satellite tags were deployed off the coast of Brazil in 32 humpback whales from the South Western Atlantic Ocean. Tags reported data for ~44 days (max = 124 days) and 92,058 dives. Statistical analysis showed that average dive depth varied between habitats, being shallower in the breeding area (BA, 22.6 m), intermediate during the migration (MI, 30.26 m), and deeper in the feeding area (FA, 35.16 m). The dives classified as deep (>80 m), were more predominant during migration. At FA, dives during the night were shallower and shorter than those performed during the day, at BA dives made during the day were deeper than all other diel phases. We have not found clear differences in dive depth and duration between social classes. The moon phases had a clear effect within BA but not within MI and FA, being shallower at full moon. We also saw that the shapes (U, V, Square), showed differences in dive depth and among habitats. Our data provide the first novel insights into the dive behaviors of individuals from the same population throughout their migratory cycle, performing different diving behaviors, different patterns of social class, shapes, depth range, diel and moon phase. Moreover, these findings and the understanding diving patterns in its drivers have important implications for ecological modelling, conservation policies.

Keywords: Humpback whale. Dive behavior. Atlantic Ocean. Satellite telemetry.

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LIST OF ABBREVIATIONS AND ACRONYMS

BA	Breeding area
BR	Brazil
F	Female with calf
FA	Feeding area
IWC	International Whaling Commission
M	Male
MI	Migration
MMA	Ministry of the Environment
SGSSI	South Georgia and the South Sandwich Islands

SUMMARY

CHAPTER I

GENERAL INTRODUCTION CONCERNING HUMPBACK WHALES

1. HUMPBACK WHALE - GENERAL CHARACTERISTICS

1.1. MORPHOLOGY AND LIFE HISTORY

The humpback whale, *Megaptera novaeangliae*, belongs to the group of the "rorqual whales" (Order Cetartiodactyla, Suborder Mysticeti, Family Balaenopteridae) (Figure 1), *megaptera*, its Latin name, means great wings, referring to its long pectoral fins, which can reach one-third of its total length.

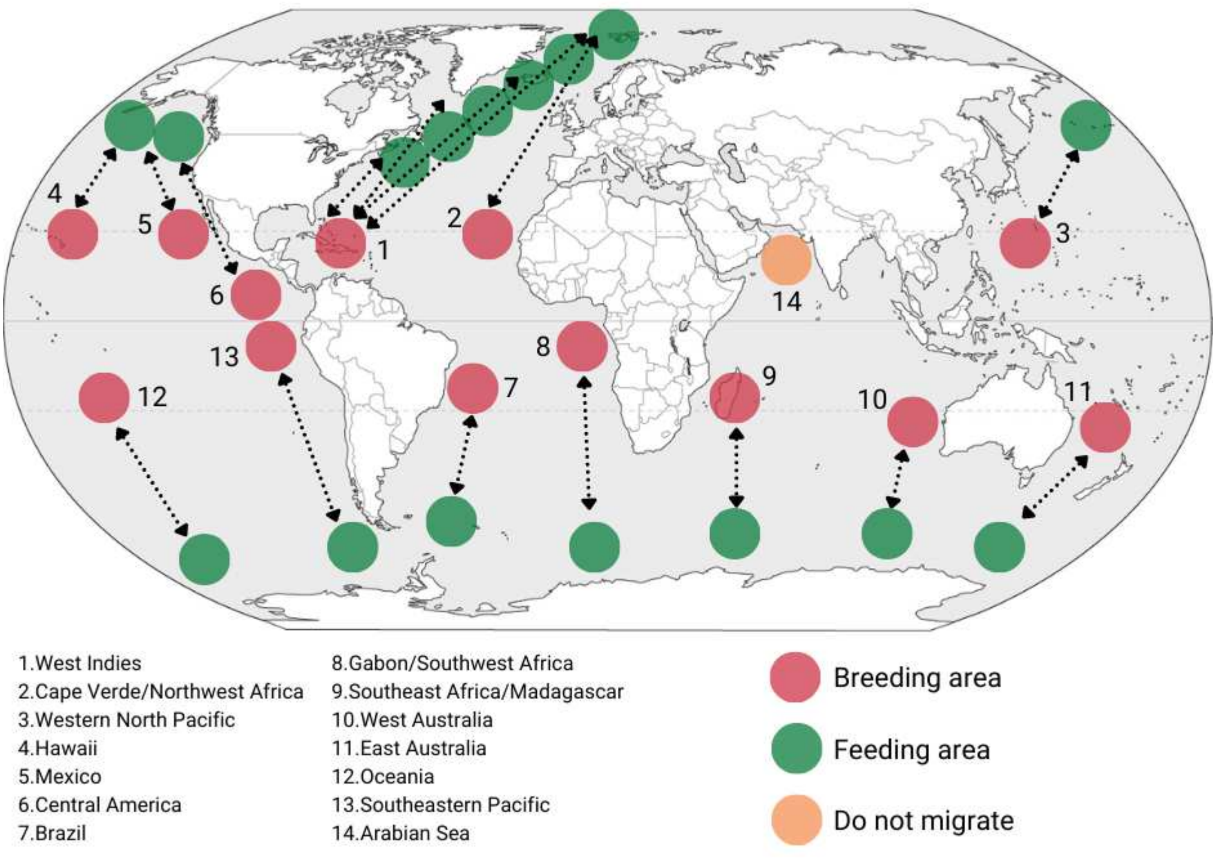
Figure 1 - Humpback whale

Reference: stickpng.com

Humpbacks are about 10 to 16 meters long and females are on average about one meter larger than males (CHITTLEBOROUGH, 1965), weighing 40 tons. The humpback whales also have unique morphological and behavioral adaptations that distinguish them from other whales, such as disproportionally large pectoral fins which allow for faster maneuvers and with greater impulse (WOODWARD et al., 2006). The dorsal fin is relatively small and slightly falcate and is located at the second third of the animal's body (LEATHERWOOD, 1988). The color varies from black to white and can vary within individuals that can often cover the ventral side of the body and the pectoral fin, with some showing grey/white spots (KATONA & WHITEHEAD, 1981). Individual identification can be done through photo identification of the ventral side of the tail or fluke. Each humpback whale has a different pigmentation pattern and trailing edge. The coloration of the fluke ranges from mostly black to mostly white (KATONA & WHITEHEAD, 1981).

Humpback whales are cosmopolitan, inhabiting both hemispheres (JEFFERSON et al., 1993, WINN & REICHLEY, 1985). During the summer they are generally found in high latitudes where they feed and, in the winter, most animals migrate to subtropical and tropical regions in search of warmer, shallow waters for breeding and calving (KATONA & WHITEHEAD, 1981) (Figure 2).

Figure 2 - Global map of the distribution of humpback whale populations and their migratory routes.



Reference: Elaborated by the author (2021)

During the feeding season, the whales store energy in the form of blubber, (CHRISTIANSEN et al., 2013) to sustain winter fasting until they return to the feeding area again. The first to leave the feeding area are females nursing their calf born in the previous breeding season, followed by juveniles, adult males, and other females (non-lactating or pregnant), and finally pregnant females (CLAPHAM, 1996). During the migration back, the process is reversed, the first ones to leave are the pregnant females, and the ones that have calves of the season are the last ones to leave. Gestation lasts between 10 to 12 months. Mothers typically give birth to a single calf, which measures 4.5 to 5 meters at birth (WINN & REICHELEY, 1985) and weighs around 1,000 kg. Calves grow relatively fast and will reach lengths of 8 to 10 meters after a year (CLAPHAM et al., 1999). The calves remain with the lactating mother for up to one year of age, although they may start feeding independently on solid food at six months of age (WINN & REICHLEY, 1985, VAN LENNEP & VAN UTRETCHT, 1953, CHITTLEBOROUGH 1958, CLAPHAM & MAYO 1987).

Because of this long migratory cycle, humpback whales must optimize the use of their fat reserves (CRAIG et al., 2003). Some studies have shown that sporadic feeding behaviors may occur during migration, by observation of bubble feeding (BARAFF et al., 1991) or feeding behavior (SWINGLE et al., 1993, ALVES et al., 2010), besides telemetry studies (LAGERQUIST et al., 2008; FOSSETTE et al., 2014; TRUDELLE et al., 2016; GARRIGUE et al., 2015; FÉLIX & GUZMÁN, 2014) and by feeding based on stomach contents found from a humpback whale stranded (DANILEWICZ et al., 2009). This behavior may be an alternative to supplement the energy demand in periods of fasting and low food availability.

1.2. CHARACTERISTIC BEHAVIORS DURING MIGRATORY CYCLE

In the breeding grounds, humpback whales usually form stable and small social groups, most commonly they are solitary individuals, pairs, or triads (MOBLEY & HERMAN, 1985). The large groups that are observed in this period are called “competitive” groups, which bring together several males and a female with or without a calf. Males typically compete to gain access to the female and may display aggressive behavior towards their competitors (CLAPHAM et al., 1992). Another behavior typical of the reproductive period is the long and complex singing performed for hours or days by the males. Songs are thought to draw the attention of the females (TYACK, 1981), to delimit territorial areas (FRANKEL et al., 1995), or to establish cooperation (DARLING et al., 2006). These songs vary over time, but when looking at each population separately the songs are more similar or have the same themes among themselves (PAYNE & MCVAY, 1971).

In general, the populations of humpback whales do great migrations in a long-distance between the feeding area and breeding area, and they have the longest migration for any mammal (RASMUSSEN et al., 2007, STEVICK et al., 2011). They can travel distances of ~8.000, -8.500km (e.g., STONE et al., 1990, RASMUSSEN et al., 2007), and can last 49 days in distances of 6,236 km (LAGERQUIST et al., 2008). As they move into migration, some reproductive behaviors may remain, such as the male songs (WINN & WINN, 1978; TYACK, 1981; FRANKEL et al., 1995; DARLING et al., 2006; SMITH et al., 2008), as well as the competitive groups that are regularly observed on the east coast of Australia (BROWN & CORKERON, 1995; NOAD 2002). They are known to swim constant course tracks during migrations, with remarkable navigational precision. The whales of WSA (western South Atlantic Ocean) showed that they can have 1º precision during the route, despite the effects of weather events, magnetic field parameters, sea-surface currents, and positions of the sun, showing extreme directional precision across wide expanses of the open ocean (HORTON et al., 2011). These migratory routes don't appear to have changed in the last 50 years, at least for the population of the WSA, keeping up with changes in environmental, geomagnetic, and oceanographic conditions (HORTON et al., 2020). Also, during migration, some whales in other populations like New Caledonia interrupted their migratory route during this period in seamounts. They are undersea mountains (STAUDIGEL et al., 2010, KIM & WESSEL 2011), having a large number of biodiversity, and have a strong influence on the distribution of a wide range of species and thought their life cycle (WORM et al., 2003, TSUKAMOTO 2006, MORATO et al., 2008, 2010, CLARK et al., 2010). These areas are known to have an important environment for some cetaceans to foraging (JOHNSTON et al., 2008, MOULINS et al., 2008, SKOV et al., 2008), and maybe to breeding, resting, and navigational landmarks (GARRIGUE et al., 2015).

In the feeding grounds, the common prey for the humpback whales can be euphausiids (including krill, *Euphausia spp.*), herring (*Clupea spp*.), capelin (*Mallotus villosus*), and sand lance (*Ammodytes spp.*) (MATTHEWS, 1937; TOMILIN, 1967; OVERHOLTZ & NICOLAS, 1979; ICHII & KATO, 1991). In the Southern Hemisphere, humpback whales feed primarily on the Antarctic krill (*Euphausia superba*) (MATTHEWS, 1937). To feed they can form large aggregations to cooperate to corral their prey, sometimes creating a "bubble net", in which bubbles are exhaled during the dive and form a curtain up to the surface where prey is captured (JURASZ & JURASZ, 1979; WATKINS & SCHEVILL, 1979; HAIN et al., 1982; FRIEDLAENDER et al., 2011; BRYNGELSON & COLONIUS 2020).

1.3. THE WESTERN SOUTH ATLANTIC POPULATION OF HUMPBACK WHALES

The population of WSA humpback whales was extremely hunted from the 1830s onwards (MORAIS et al., 2017), they were hunted mainly on breeding grounds until 1900 when the population was relatively stable. From then on, whaling expanded into the feeding areas, reaching the collapse of the population (FINDLAY 2001). The population dropped from an average of 24,700 in 1904 to around 700 in 1926. The smallest abundance was in 1958 when they had only about 440 individuals (PI = 198-1400) (ZERBINI et al., 2019). The population started to recover as soon as the whaling ended. The moratorium on whaling was decided by the International Whaling Commission (IWC) members in 1966, and implementation in Brazil was in 1985. Besides that, the IWC recognizes in the Southern Hemisphere seven breeding stocks labeled “A” to “G” (IWC, 2012).

The population from Brazilian waters inhabiting the WSA forms the stock "A", that migrates from the feeding area near South Georgia and the South Sandwich Islands (British overseas territory in the South Atlantic Ocean) in the summer, to the Brazilian breeding area in the winter. The breeding season lasts from April to December, with the peak of whales in August and September (MARTINS et al., 2001). The main breeding ground is located near the Abrolhos Bank, Brazil, where nearly 80% of the population occurs (BORTOLOTTO et al., 2017), but as this population recovers, other habitats to the north and the south of Abrolhos are currently being used (ANDRIOLO et al., 2010; MARTINS et al., 2001; PIZZORNO et al., 1998; DANILEWICZ et al., 2009; ZERBINI et al., 2004, 2011). At the end of the breeding season, WSA humpback whales migrate through open ocean routes towards high latitudes to their feeding grounds (ZERBINI et al., 2006, 2011, ENGEL & MARTIN 2009). Satellite telemetry has revealed that whales start to arrive in the feeding grounds in October and leaving in May or June, suggesting that the feeding season lasts 8-9 month (ZERBINI et al., unpublished data), which is consistent with the duration of the feeding season for other populations (e.g., Gulf of Maine humpback whales - CLAPHAM et al., 2003).

2. HUMPBACK WHALE DIVING BEHAVIOR

2.1. EVOLUTION OF TELEMETRY STUDY IN CETACEANS

Cetaceans are highly mobile species, migrating over great distances, and spending the majority of their time underwater. Hence, cetaceans are hard to locate and study, resulting in little understanding and knowledge about their distribution. Data loggers and monitoring devices have been used for more than 80 years to remotely track animals to obtain information on their movements and behavior at sea (SCHOLANDER, 1940**;** COOKE et al., 2004; MATE et al., 2007; ROPERT- COUDERT & WILSON, 2005). The first bio-logging tags were deployed on cetaceans in 1930 and were capillary manometers, providing a unique data point recording the deepest dive depth (SCHOLANDER, 1940).

Since then, it has taken several decades for the improvement of instruments and the advent of VHF transmitters, digital depth recorders, and satellite-linked transmitters (ANDREWS et al., 2019). The tags were bigger at the beginning and the electronic components were placed outside the body, not being retained for long. The miniaturization and implantation of electronics within the body helped in increasing the duration of the tag, obtaining data from months (MATE et al., 2007). With this constant evolution of the tracking technology over the years, it has become possible not only to collect geographic positions but also to obtain behavioral data (e.g., dive depth and duration) and environmental conditions (e.g., temperature). Compared to other methodologies for observing cetaceans, tags can provide almost continuous data regardless of the observer, which is essential to study how cetaceans behave in all habitats used throughout the life cycle (eg., breeding season, migration, and feeding season), and how they respond to various anthropogenic disturbances, such as noise from commercial vessel traffic, seismic exploration vessels, or naval mid-frequency sonar.

2.2. FORAGING ECOLOGY AND DIVING BEHAVIOR THROUGHOUT CYCLE MIGRATION

The feeding behavior is often inferred from the study of whale diving behavior, with most of these studies being done in the feeding areas. One reason is the interest in understanding how they balance energy costs (DOLPHIN, 1987a b; DIETZ et al., 2002; HEIDE-JØRGENSEN & LAIDRE, 2007; GOLDBOGEN et al., 2008; HAZEN et al., 2009; WARE et al., 2011; TYSON et al., 2012; FRIEDLAENDER et al., 2013). Besides, it is possible to understand if whales of different social classes and age classes adapt their feeding behavior as a function of environmental conditions that influence prey distribution and availability.

A study relating humpback whale foraging dives and energy balance in the fjords of the Western Antarctic Peninsula showed that the energy and time spent in deeper dives are higher, due to the foraging activity (ACEVEDO-GUTIERREZ et al., 2002). This diving behavior during foraging is driven by the balance between the energy gain through the prey and the energy expenditure spent during the dive (GOLDBOGEN et al., 2013). Over the coast of California (GOLDBOGEN et al., 2008), it was observed that the foraging dives occurred at the upper limit where the dense aggregations of krill were located, hence supporting the theory that predicts that the predator's optimal foraging depth is always shallower than the prey depth

(MORI, 1998). In this study, they also observed that dives in search of prey that had more lunges at greater depths were associated with a longer duration of diving, and it has also been observed that the deeper the dives the greater the number of lunges (WARE et al., 2011).

In addition, whales appear to adapt foraging dives to the diel cycle. Satellite tracking of humpback whales in the Western Antarctic Peninsula showed exploratory deep dives before sunset, interspersed with deep dives with foraging and becoming increasingly deeper approaching sunset and becoming shallower at night (FRIEDLAENDER et al., 2013). This diving pattern is consistent with the vertical migration pattern of krill in the water column (ZHOU & DORLAND, 2004; NOWACEK et al., 2011). At night, prey forms dense aggregations close to the surface, and are more efficiently consumed by whales than during the day when they are located deeper. Whales also showed a greater resting behavior at the surface during the day, probably digesting food from the previous night (FRIEDLAENDER et al., 2013).

Although feeding occurs for the most part in feeding grounds, sporadic foraging has also been reported during migration and over breeding grounds. One of the first records was in the Dominican Republic in 1989 through the observation of bubble feeding performed several times (BARAFF et al., 1991), as well as the observation of feeding over the coast of Virginia (SWINGLE et al., 1993) and Brazil (ALVES et al., 2010). Some other studies have also shown that these sporadic feeding events can occur during migration and in breeding areas, inferring feeding from the stomach content of a humpback whale stranded off the coast of Brazil (DANILEWICZ et al., 2009). Also, telemetry studies suggesting this sporadic feeding behavior by conducting behavioral segmentation of the tracks into transit-like movement and area restricted search movement (ARS). Whales slowed and followed winding paths in specific areas during their migration route, sometimes related to seamounts. This type of movement may be indicative of foraging, but also resting or social interactions (LAGERQUIST et al., 2008; FOSSETTE et al., 2014; TRUDELLE et al., 2016; GARRIGUE et al., 2015; FÉLIX & GUZMÁN, 2014). This behavior during migration may be an alternative to supplement the energy demand in this period.

Fewer studies have investigated diving behavior during migration and breeding areas (HAMILTON et al., 1997; BAIRD et al., 2000; HERMAN et al., 2007; VIDESEN et al., 2017; DERVILLE et al., 2020). Whales are expected to perform shallower and shorter dives during their migration back to the feeding grounds, as they have been fasting for a long time and would need to minimize the energy spent on the route until they reach the feeding area. On the other hand, whales can also dive deeper during migration, probably being related to foraging behavior, for example in the migratory corridor in Hawaii, the deepest dives of humpback whales were usually at night (HENDERSON et al., 2018), and at the migratory corridor of the east coast of Australia, the diving pattern was strongly influenced by depth. Although the study was done in shallow water (up to 60 m), it was clear that the animals tended to dive for longer in the deepest waters (KAVANAGH et al., 2017). However, studies in other deeper locations are important to understand if this pattern would hold.

In the breeding grounds, a study carried over of Maui, Hawaii, through telemetry and bioacoustics, showed that the peak of the males singing was at night and that in general males remained at shallower depths when singing (BAIRD et al., 2000, HERMAN et al., 2007). Mothers with calf remained close to the surface most of the time due to nursing/suckling (VIDESEN et al., 2017). In New Caledonia, South Pacific, where humpback whales have been tracked in both their coastal and pelagic movements, mothers did not dive significantly shallower than other adult whales, even reaching a maximum depth of 336 m (DERVILLE et al., 2020).

2.3. UNDERSTANDING DIVING BEHAVIOR HAS IMPLICATIONS FOR CONSERVATION

The collisions between whales and vessels, and the interactions with fisheries occur worldwide and are the biggest threats to baleen whales (BLONDIN et al., 2020, PIROTTA et al., 2019, SOLDEVILLA et al., 2017, KNOWLTON & KRAUS 2001, LAIST et al., 2001, READ et al., 2006, THOMAS et al., 2016). For instance, ship strikes are the main cause of mortality of blue whales (*Balaenoptera musculus*), humpback whales, and fin whales (*Balaenoptera physalus*) over the US west coast (ROCKWOOD et al., 2017, CARRETTA et al., 2015). Understanding how whales use the water column can help mitigate anthropogenic threats, especially collisions with vessels.

Most mortality estimates are based on stranded animals, hence many casualties from ship strikes remain unreported causing the actual number of deaths to be underestimated (ROCKWOOD et al., 2017, WILLIAMS et al., 2011). Therefore, there are still some doubts, not having a complete understanding of the problem, for example, what is the exact number of whales that die. Also, there is difficulty in implementing priority areas, as each species would need a specific area for it, and with different priorities (ROCKWOOD et al., 2017). Satellite tracking of whales in areas of intense marine traffic can support ship strike risk assessments

To date, the behavior of diving with humpback whales has never been studied at an individual level throughout a complete migratory cycle that covers the area of breeding, migration, and feeding. Whales are hypothesized to make shorter dives in shallow depths during the breeding and migration season, sporadically deeper and longer dives during migration, and deeper and longer dives during the feeding season. Furthermore, that the males dive deeper than the females, that the U-dives are deeper than the V and Square-shapes, concerning the moon phase, that it influences the dives between habitats, mainly in the feeding area and with shallow dives by day in the breeding and migration area, and deep dives by night in the feeding area.

Understanding diving behavior about habitat use and bioenergetics can provide fundamental data to contribute to the conservation of humpback whales.

CHAPTER II

DIVING BEHAVIOR OF HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) THROUGHOUT THEIR MIGRATORY CYCLE IN THE WESTERN SOUTH ATLANTIC OCEAN

ABSTRACT

Is poorly known how the diving behavior during the migratory cycle of humpback whales *Megaptera novaeangliae* is affected by environmental characteristics of their seasonal habitats and their social roles. In this study, archival Argos satellite tags were deployed off the coast of Brazil in 32 humpback whales from the South Western Atlantic Ocean. Tags reported data for ~44 days (max = 124 days) and 92,058 dives. Statistical analysis showed that average dive depth varied between habitats, being shallower in the breeding area (BA, 22.6 m), intermediate during the migration (MI, 30.2 m), and deeper in the feeding area (FA, 35.1 m). The dives classified as deep (>80 m), were more predominant during migration. At FA, dives during the night were shallower and shorter than those performed during the day, at BA dives made during the day were deeper than all other diel phases. We have not found clear differences in dive depth and duration between social classes. The moon phases had a clear effect within BA but not within MI and FA, being shallower at full moon. We also saw that the shapes (U, V, Square), showed differences in dive depth and among habitats. Our data provide the first novel insights into the dive behaviors of individuals from the same population throughout their migratory cycle, performing different diving behaviors, different patterns of social class, shapes, depth range, diel and moon phase. Moreover, these findings and the understanding diving patterns in its drivers have important implications for ecological modelling, conservation policies.

Keywords: Humpback whale. Dive behavior. Atlantic Ocean. Satellite telemetry.

1. INTRODUCTION

Cetaceans are highly mobile animals that move through extensive areas and typically spend 90% of their time underwater. For this reason, monitoring their behavior throughout their ranges can be difficult, therefore, limiting our ability to track their behavior during their life cycle. Understanding behavior has important implications for ecological modeling and conservation strategies. For example, whales spend a great deal of time closer to the surface or at rest, being more often at night, which can lead to overlap with ships, making them more vulnerable to ship strikes at night than during the day (OWEN et al., 2016, IZADI et al., 2018, CALAMBOKIDIS et al., 2019). Also, with the deeper feeding behavior of some species, there is a potential risk of entanglement in nets, impacting behaviors across a range of timescales (VAN DER HOOP et al., 2017, SOLDEVILLA et al., 2017). These diving patterns vary by region, sex, age, and reproductive condition. They also need to balance energy expenditure during the dives in an optimized way according to their needs in each habitat and social class, to complete the migratory route and also reproductive season.

Most baleen whales feed at the surface up to depths of typically 400 m (GOLDBOGEN et al., 2013, FRIEDLAENDER et al., 2013, 2020), but their diving behaviors are extremely variable between and within species as animals have to adapt to forage in different prey and different environments. For example, the Bryde's whale (*Balaenoptera edeni/brydei*) was shown to have the maximum depth of the dive-related when they were feeding, foraging dives were deeper than non-foraging dives (IZADI et al., 2018). When analyzing the diving behavior of humpback whales mothers and southern-right-whales mothers (*Eubalaena australis*) with their calves, it was observed that they are synchronized (TABER & THOMAS 1982, THOMAS & TABER 1984, SZABO & DUFFUS 2008, TYSON et al., 2012), mainly after giving birth, being a strategy to protect the offspring (LENT 1974, TYSON et al., 2012). In the feeding area in southeastern Alaska, humpback whale mothers modify their diving behavior, decreasing depth and time, to minimize separation time (SZABO & DUFFUS 2008, TYSON et al., 2012). As the season passes, the mother begins to become less responsible for the calf and forces him to make deeper and longer dives (SZABO & DUFFUS 2008, TYSON et al., 2012). Therefore, the diving patterns are complex and are affected by many factors.

Diving behavior will also change over the course of the day as prey responds to changes in luminosity (e.g., night versus day time) and moon phases (PANIGADA et al., 1999, 2003, FRIEDLAENDER et al., 2009, 2015, CALAMBOKIDIS et al., 2009, DONIOL-VALCROZE et al., 2011, BURROWS et al., 2016, KEEN et al., 2019, OWEN et al., 2019). For example, humpback whales in the western Antarctic Peninsula showed a distinctive dial pattern when feeding, which was performed mainly at night with deeper foraging dives around sunset and sunrise (FRIEDLAENDER et al., 2013). Fin-whales in Southern California change their dives in response to lunar cycles as these cycles are known to influence the vertical migration of euphausiids (BENOIT-BIRD et al., 2009), with, for instance, migration closer to the surface occurring more frequently during a new moon rather than the full moon (KEEN et al., 2019).

Humpback whales are known as one of the animals that perform the longest migrations (DULAU et al., 2017), in some cases, they can cover distances between 8.000-8.500km (STONE et al., 1990, RASMUSSEN et al., 2007, ROBBINS et al., 2011) between two migratory destinations. Understanding diving behavior during these long-distance migrations is important to better understand whale ecology as they transition between breeding and foraging habitats. Dive patterns are expected to change as these animals move through habitats with different oceanographic and physiographic characteristics during their migratory cycle. Understanding diving behavior may also have conservation implications as they could be used to evaluate areas where whales tend to spend more time close to the surface and be at higher risk of ship strikes. Studies on diving behavior about humpback whales are more common in feeding grounds (DOLPHIN 1987a b, 2009, DIETZ et al., 2002, HEIDE-JØRGENSEN & LAIDRE 2007, GOLDBOGEN et al., 2008, 2012, HAZEN et al., 2009, BOCCONCELLI 2010, WARE et al., 2011, TYSON et al., 2012, STIMPERT et al., 2013, FRIEDLANDER et al., 2013, TYSON 2014, WITTEVEEN et al., 2015, KIRCHNER et al., 2018, CALAMBOKIDIS et al., 2019) but information on diving patterns in the breeding (CHU 1988, BAIRD et al., 2000, VIDESEN et al., 2017, DERVILLE et al., 2020) and migratory corridors (HAMILTON et al., 1997, KAVANAGH et al., 2016) is much more limited.

In general, during the feeding season, humpback whales tend to perform deeper and longer dives to gain access to their prey (GOLDBOGEN et al., 2008, WARE et al., 2011). In the breeding ground, humpback whales are may perform comparably shallower and shorter dives (VIDESEN et al., 2017, CLAPHAM et al., 1992, BAIRD et al., 2000, HERMAN et al., 2007) which are likely associated with the need to reproduce and/or nursing and calving (CLAPHAM et al., 1992, HERMAN et al., 2007, VIDESEN et al., 2017). But some exceptions have been documented. For example, with a shorter duration, deep and long dives have been documented in low latitudes of the western South Pacific, (DERVILLE et al., 2020). There are some hypotheses as to why they perform such deep dives in these areas, which can be a form of guidance during navigation (VAN HAREN, 2015), of communication between members, and can also be of interactions during the mating competition (HERMAN et al., 2007), also, it can be a form of opportunistic feeding (BARAFF et al., 1991; ALVES et al., 2010; DANILEWICZ et al., 2009; GENDRON & R, 1993; ANDREWS-GOFF et al., 2018; CERCHIO et al., 2016; TRUDELLE et al., 2016). During migration back to the feeding area, whales may perform relatively shallow dives because they have been fasting for an extended period, and would need to reconcile the energy spent en route to the feeding areas, where they can replenish the energy spent during the reproductive cycle. Especially females with calves, they have a great decrease in body condition due to nursing since the breeding season (BEJDER et al., 2019), so they can also be expected to perform shallower and shorter dives to save energy. However, sporadic deep dives may occur as an alternative to supplement the energical demands during the migration (BARAFF et al., 1991, SWINGLE et al., 1993, MATE et al., 2007, LAGERQUIST et al., 2008, DANILEWICZ et al., 2009, DE SÁ ALVES et al., 2009, FOSSETTE et al., 2014, FÉLIX & GUZMÁN 2014, GARRIGUE et al., 2015, TRUDELLE et al., 2016), but more evidence is necessary to assert this behavioral pattern (JÖNSSON & JONSSON 1997, DOLPHIN 1987a, GOLDBOGEN et al., 2008, FRIEDLAENDER et al., 2013).

The ability to document cetacean diving behavior began with Evans' pioneering radio telemetry research on dolphins, and Watkins and Schevill on whales (EVANS 1971, WATKINS & SCHEVILL 1977, 1979, WATKINS et al., 1978, WATKINS & TYACK 1991). Over the last several decades, the miniaturization of electronics and the development of longer-term satellite transmitters allowed for sampling of dive patterns at broader temporal scales (weeks to months, MATE et al., 2007, DERVILLE et al., 2020). In this study, long-term satellite tracking data is used to characterize the diving patterns of humpback whales in the WSA during their southbound migration to evaluate potential differences in dive behavior and habitat use in breeding and feeding grounds as well as migratory corridors. Information on dive depth, dive duration is integrated with habitat, individual social class at the time of tagging, shape, diel phases, and moon phases to assess hypotheses about potential changes in diving behavior as they go through different habitats during their migration. We hypothesize that dive depths and durations will vary across each habitat and will be influenced by sex, shape, and moon and diel phases. Also, that the dives carried out in each habitat will be at different depths, becoming deeper from the breeding area, migration, and finally into the feeding area. Furthermore, that the males dive deeper than the females, also that the U-dives are deeper than the V and Square-shapes, concerning the moon phase, that it influences the dives among habitats, mainly in the feeding area and with shallower dives by day in the breeding and migration area, and deeper dives by night in the feeding area.

2. MATERIAL AND METHODS

2.1 DATA COLLECTION

Adult humpback whales were tagged between 2016 and 2019 (Table 1) in September, October, or November at their breeding grounds in the region of Banco dos Abrolhos (Southern Bahia State). Overall, 22 females with a calf at the time of tagging, and 10 males were instrumented. Fieldwork was carried out on days without rain and with a Beaufort Sea state less than or equal to 4. Type C archival satellite transmitters (ANDREWS et al., 2019) (Figure 3) in a SPLASH 10 configuration (Wildlife Computers, Redmond, WA, USA) were deployed using a custom-made compressed air rifle (ARTS) (HEIDE-JØRGENSEN et al., 2001) at the dorsal surface of the whale's body, near the dorsal fin. SPLASH 10 tags carry a pressure sensor capable of determining dive parameters such as depth and duration.

Table 1 - Summary of tags deployments.

Whale ID	**Class**	**Year**	**Tag deployment**	**Last emission**	**Latitude**	**Longitude**
111868	F	2016	10/24/16	11/06/16	-20.3977	-39.9437
120942	F	2017	10/07/17	11/14/17	-18.059792	-39.102626
111870	M	2017	10/07/17	02/05/18	-18.060838	-39.110631
120947	F	2017	10/07/17	11/13/17	-18.080733	-39.089412
87777	F	2017	10/07/17	11/13/17	-18.07506	-39.053996
84485	M	2017	10/07/17	11/04/17	-18.000995	-39.133732
112696	F	2017	10/07/17	10/30/17	-18.007974	-39.063934
172002	F	2017	11/09/17	03/09/18	-18.090852	-39.14133
172001	F	2017	11/10/17	03/15/18	-18.038011	-39.058721
171997	M	2017	11/10/17	11/26/17	-18.125971	-39.044471
172000	M	2017	11/13/17	01/19/18	-18.079757	-39.030604
121191	F	2017	10/16/17	11/22/17	-18.020567	-39.09808
87780	F	2017	10/15/17	11/03/17	-18.009464	-39.075723
121206	F	2017	10/15/17	11/04/17	-17.982761	-39.18944
121203	M	2017	10/16/17	02/03/18	-18.141115	-39.021026
123226	F	2017	10/16/17	11/24/17	-18.15569	-39.010609
120937	M	2017	10/16/17	01/17/18	-18.157974	-39.000332

112728	F	2017	10/19/17	11/03/17	-18.05036	-39.122676
120943	M	2017	10/24/17	11/21/17	-18.132944	-39.137698
172004	F	2017	11/17/17	12/16/17	-18.038628	-39.061774
84484	F	2017	11/10/17	01/13/18	-18.037794	-39.059066
111868	F	2018	09/30/18	11/04/18	-18.063508	-39.180534
84484	F	2018	09/30/18	10/30/18	-18.030795	-39.208695
111870	F	2018	10/06/18	11/16/18	-18.067163	-39.167549
112696	F	2018	10/15/18	12/06/18	-17.992826	-39.169175
87640	F	2018	10/18/18	11/14/18	-17.953919	-39.086253
120938	M	2018	10/23/18	12/08/18	-18.011117	-39.027134
120942	M	2018	10/23/18	12/13/18	-17.991824	-39.050272
171994	M	2018	10/23/18	12/22/18	-17.960551	-39.045978
121191	F	2018	10/29/18	01/16/19	-18.002099	-39.009143
194593	F	2019	10/12/19	10/31/19	-18.034982	-39.082895
194601	F	2019	10/20/19	12/07/19	-18.044545	-39.085893

Reference: Elaborated by the author (2021). Whale ID = unique tag number. Class = Social class (F = female with calf, M = Male). Tag deployment = data of deployment. Last emission = last day of data emission. Latitude and longitude = location of deployment.

Figure 3 - Humpback whale (left) equipped with a SPLASH10 satellite tag (right).

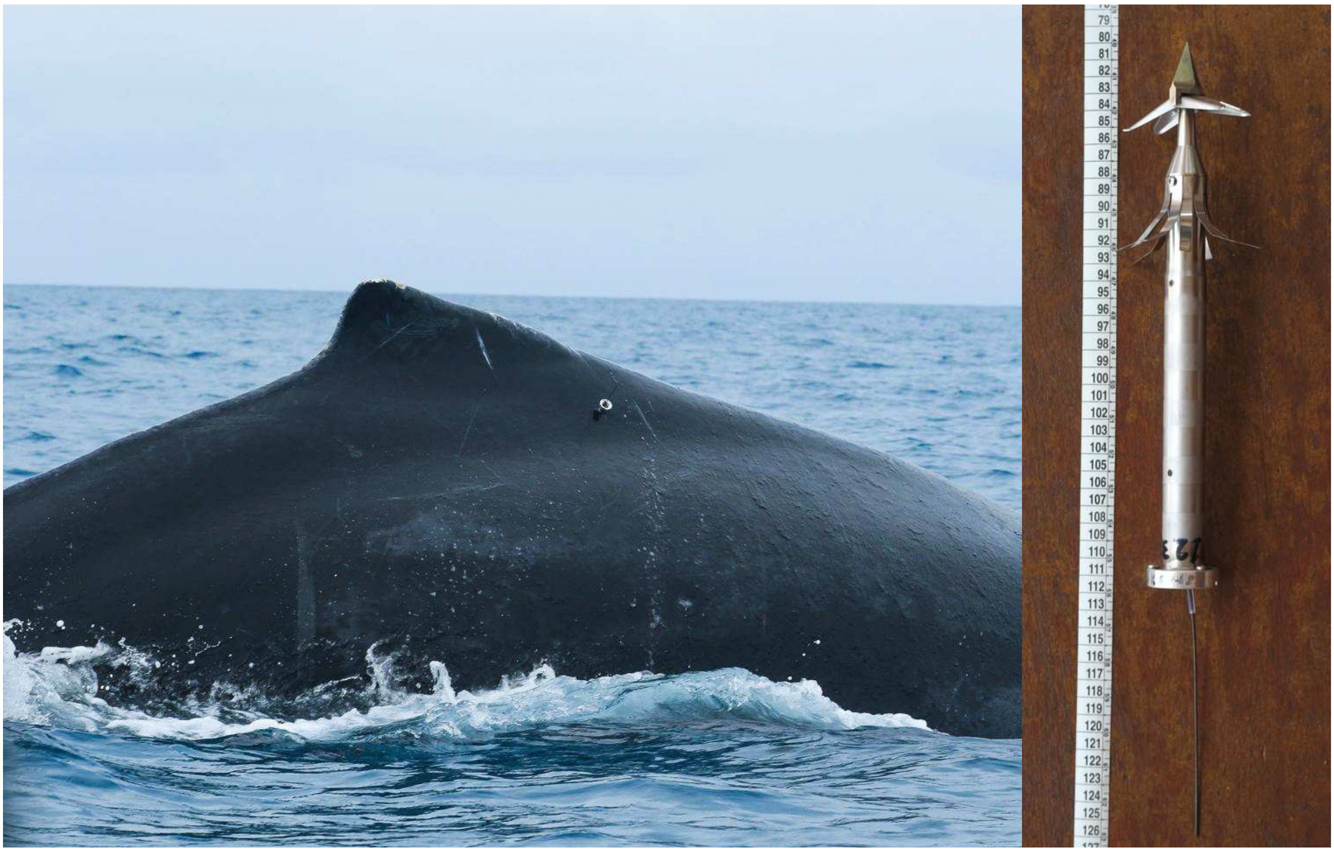


Photo credit: Anne Elise and Mario Angelo

Transmitters were programmed to collect and archive information about dives every 1 second. A dive event was defined as any dive more than 10 meters deep and more than 5 seconds long. The locations are estimated by the ARGOS System with six levels of quality, coded as A, B, 0, 1, 2, or 3 in increasing order of precision, A and B do not have accuracy and Z corresponds to an invalid location (ARGOS, 1990).

Data collection begins to be collected the moment the tag is in contact with the water and transmitted as a message to satellites in polar orbits of the ARGOS system when the transmitter is exposed to the air. In addition to geographic positions, calculated based on the radio transmissions of the tag. Information on dive behavior computed using the “behavioral mode” tool is also transmitted by the tag. This tool provides the minimum and maximum dive depth (margin of error), the minimum and maximum duration of the dive, the interval between one dive and another, and the shape of the dive (“U”, “Square”, and “V”). Generally, the shapes in "U" is associated with foraging behavior being deeper, as well as "V", and this one also is associated with traveling/migration or exploratory behavior (GOLDBOGEN et al., 2008, ALVES et al., 2010, PARKS et al., 2011, GOLDBOGEN et al., 2013, HEIDE-JØRGENSEN et al., 2013, GOLDBOGEN et al., 2017)

2.2 ANALYSIS OF LOCATION DATA

Location data was filtered and corrected in the *R* software (R version 3.5.1) according to the methodology used by Derville (2020). Z locations were removed, along with locations implying speeds above 18 km/h (ZERBINI et al., 2015), locations on land, and duplicate locations. When the track was interrupted for more than 24 hours, it was split into two or more segments as needed. The trajectories were projected in the Atlantic Centered Mercator coordinate system. The *crawl* package version 2.2.1 (JOHNSON, et al., 2008) was used to adjust a model to the observed Argos positions and produce predicted locations every 6 hours using a Continuous-time Correlated Random Walk model (CRW).

The CRW movement model is based on two parameters: first, β, where autocorrelation of velocity occurred, and second, σ, the velocity of variation. With this, it was possible to determine the position of the predicted animal at any time, from the initial to the end of the original track. As for the errors that exist in the ARGOS positions, they were incorporated as ellipses, semi-minor, and semi-major axis errors, together with deployment positions included with the logarithmic error of the ellipses defined as 0. The parameter β was constrained between - 3 and 4, and in addition, it was optimized using the previous normal distribution with mean - 0.15 and standard deviation of 1.5. Regarding the parameter σ, it was not restricted but optimized from an initial value of log (10).

2.3 DIVE BEHAVIOR ANALYSIS

The data collected were divided into (1) dive depth (the maximum dive depth for each dive, computed as the average of the minimum and maximum values measured by the sensor), (2) dive duration (the average duration computed from the minimum and maximum values reported by the tag for each dive), (3) dive shape (“U”, “Square” and “V” shapes). Dives were also divided into “shallow” (< 80m) and “deep” (> 80m), based on the relation between dive deep as described by Derville et al., (2020).

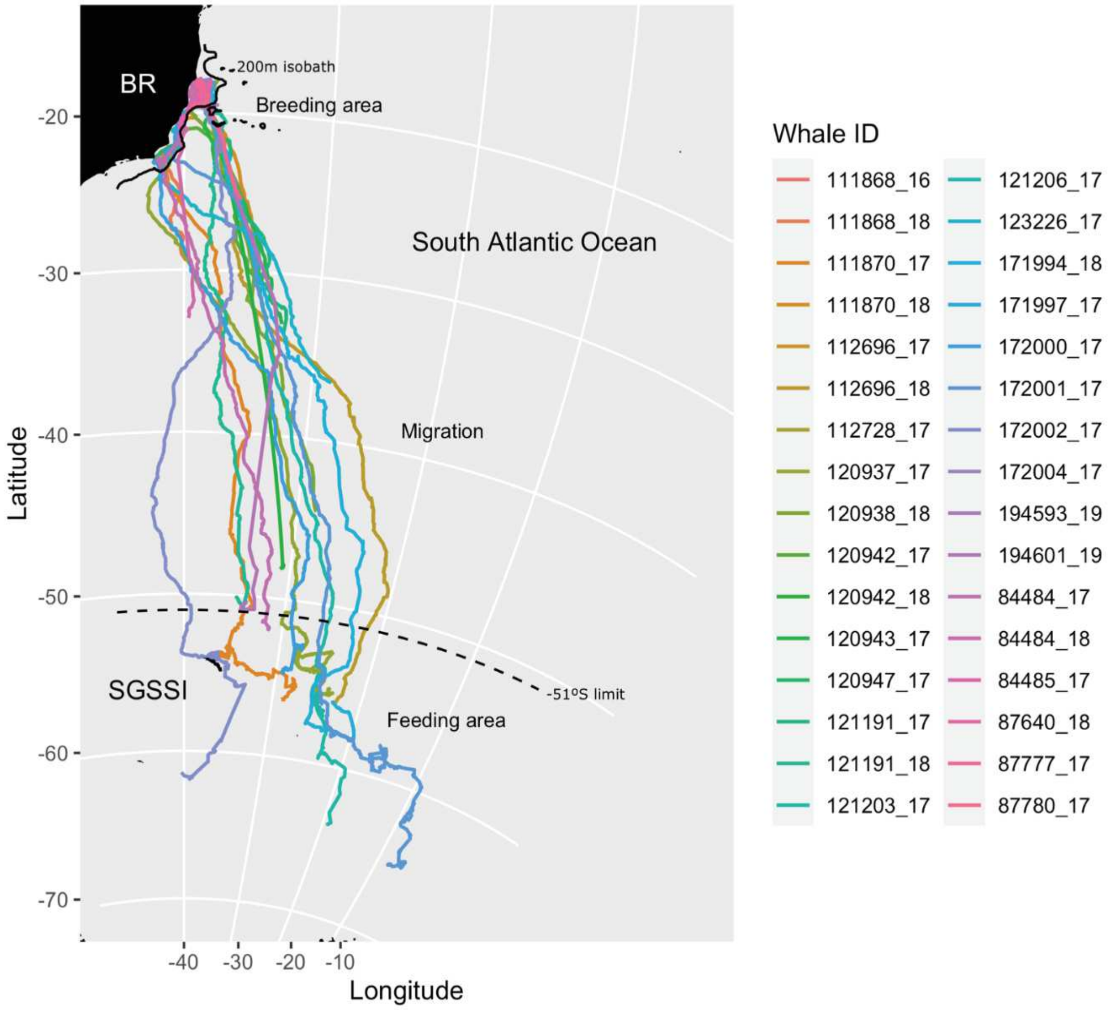
Three presumably aberrant deep dives of 663.7 m, 1079.7 m, and 1495.7 m were observed for the same individual. These data points were censored because they appeared to be extreme outliers. Thus, dives deeper than 600m, shallower than 10m (⅔ to ¾ of the body length of an adult), and lasting more than 30min were removed based on the methodology used by Derville et al., (2020).

2.4 ENVIRONMENTAL CONDITIONS PREDICTORS OF MOVEMENT AND DIVING BEHAVIOR

2.4.1 Habitats

Dives were separated into three habitats, breeding grounds, migratory routes, and feeding areas, according to specific parameters (Figure 4). The breeding ground was defined as any area along the coast of Brazil within the 200m isobath based on the *marmap* package version 1.0.2 (PANTE & SIMON-BOUHET, 2013). Dives occurring in areas deeper than 200m were considered as part of the breeding area if whales moved offshore but returned within that isobath before initiating the migration. The feeding areas were defined as the area south of 51ºS, the approximate limit of the Antarctic Convergence in the South Atlantic Ocean (DEACON, 1984; ZERBINI et al., 2011). The migratory corridor was defined as the region between the breeding and feeding habitats.

Figure 4 - Study site map indicating the three different habitats (Breeding area, Migration, and Feeding area) and their limits.



Reference: Elaborated by the author (2021). BR = Brazil, SGSSI = South Georgia and South Sandwich Islands. Whale ID = unique tag number and their tracks.

2.4.2 Daylight illumination and moon phases

Differences in dive parameters were examined concerning daylight illumination and moon phases to assess whether these variables influenced the whales' dive behavior. The time of the dives, originally recorded in UTC, was adjusted to local time before integration of the telemetry and the illumination data.

Information on solar elevation was obtained from the *oce* package version 1.1-1 1 (KELLEY & RICHARDS, 2019). These data were used to categorize the predicted whale locations into four groups: (1) "dawn" was defined as solar elevation from - 12 to + 6 degrees in relation to the horizon during sunrise, (2) "dusk" was defined as solar elevation from + 6 to

- 12 degrees at sunset, (3) “day” was defined as elevation greater than + 6 degrees, and (4) “night” as elevation less than - 12 degrees (FALCONE et al., 2017).

Table 2 - Daylight illumination phases.

Solar elevation in degrees in relation of the horizon	
Dawn	- 12 to +6
Sunrise	+ 6 to -12
Dusk	> +6
Sunset	< -12

Reference: Elaborated by the author (2021)

Lunar phases were obtained from the *suncalc* package, version 0.5.0 (THIEURMEL & ELMARHRAOUI, 2019). Moon luminosity value was extracted for each location based on the predicted latitude, longitude, and time of the day. The values of moon luminosity were categorized into four phases: 0 - 0.25 new moon, 0.25 - 0.5 first quarter, 0.5 - 0.75 full moon and 0.75 - 1 last quarter.

Table 3 - Moon phases.

Moon phases categorically	
First quarter	0.25 to 0.49
Full moon	0.5 to 0.74
Last quarter	0.75 to 1
New moon	0 to 0.24

Reference: Elaborated by the author (2021)

2.5 STATISTICAL ANALYSIS

We tested the effect of the habitats on dive depth and dive duration using Linear Mixed effects models (LMM), through the *lme4* package (BATES et al., 2015). LMMs were chosen because observations (dive depths and duration) are correlated in space and time and because they are nested within individuals (whales). Therefore, whale identity was included as a random effect by assuming that the intercept varies randomly among whales. We included the variables longitude, bathymetry, diel phase, shape, and social class to control for their effects. However, a moderate temporal autocorrelation remained in models' residuals (~ 0.5), so we adopted a more conservative significance level (effects with $p < 0.0001$ were considered significant). We opted to adopt a conservative significance level instead of including an auto-regressive model because the dataset is already large (so the degrees of freedom are still large even with dependence between observations) and because it has a lower computational cost than including an auto-regressive model. Moreover, the random effects already account for an amount of the dependence between observations on the same whale over time and the effects of the other predictors were also taken into account.

We also used LMMto estimate the effects of social class, habitats, shape, depth range, diel phases, moon phases, bathymetry, and latitude and longitude on dive depth and dive duration within each habitat. We used the *lme* function from the *nlme* package (PINHEIRO J, et al., 2020) to fit the LMMs and incorporate the ARMA (auto-regressive moving average model) to model the temporal correlation in the models's residuals. The ARMA structure takes into account that the observations are nested within whales. Here we opted to include ARMA because we have many predictors within each habitat, reducing the available degrees of freedom, and because the computational cost of including ARMA was lower in this case than with the model with the whole data (effects of habitats).

The continuous predictors were transformed by centering and scaling actual values to zero mean and unit variance. We applied a logarithmic transformation in all response variables to achieve residual normality and homoscedasticity. Model residuals were absent of spatial auto-correlation (SAC) as verified by Moran's I test (evaluated through random samples to reduce computational costs). Multicollinearity was checked by a variance inflation factor (VIF) and Pearson correlation. We excluded latitude from the model because it was correlated with habitat (VIF > 4).

We computed the pairwise comparisons between levels of the predictors through the estimated marginal means from the fitted models. The *lmerTest* was used to calculate the denominator degrees of freedom (KUZNETSOVA, BROCKHOFF, & CHRISTENSEN, 2017). SAC and temporal auto-correlation were calculated using the *ncf* and *forecast* packages, respectively (BJØRNSTAD, 2018; HYNDMAN & KHANDAKAR, 2008; HYNDMAN et al., 2019). The *MuMIn* package (BARTÓN, 2018) was used to obtain the marginal R^2 (variance explained by the fixed effects) (NAKAGAWA & SCHIELZETH, 2013). Pairwise comparisons between levels were obtained through the *emmeans* package (LENTH et al., 2018), to analyze which levels differ from which, pair by pair. Graphics were produced using the *ggplot2* package (WICKHAM, 2016).

3. RESULTS

3.1 TAG DEPLOYMENT DATA

The average transmission duration of the SPLASH10 satellite tags was 44 days (median = 35, SD = 34.88, min = 4 days, max = 124 days) (Table 4). A total of 92,058 dives were obtained and 136 were excluded by the three aberrant dives values, bad locations, and time duration exceeding 30 min.

The average depth along the whole tracks (all three habitats combined) was 38.2 m (SD = 31.63, median = 26.7) and the maximum dive depth was 464 m. Average dive and maximum dive durations were 3.7min (SD = 3.14) and 29 min, respectively.

Table 4 - Summary of raw tag deployments.

				Dives				
		Tag			Depth (m)		Duration (min)	
Whale ID	Class	Deployment	Duration (days)	n. º	Mean	Max.	Mean	Max.
111868_16	F	10/24/2016	12.3	427	40.9	91.7	5.4	22.7
120942_17	F	10/07/2017	37.4	1055	22.8	175.7	1.9	7.5
111870_17	M	10/07/2017	120.3	7028	46.5	319.7	3.7	24.3
120947_17	F	10/07/2017	36.4	2630	34.7	143.7	4.3	17.0
87777_17	F	10/07/2017	6.5	462	23.6	57.7	4.0	18.3
84485_17	M	10/07/2017	27.4	1773	29.0	77.7	4.8	19.2
112696_17	F	10/07/2017	22.3	1291	28.5	155.7	3.4	12.3
172002_17	F	11/09/2017	119.3	6815	36.9	279.7	3.1	15.7
172001_17	F	11/10/2017	124.4	15502	36.8	279.7	2.6	22.7
171997_17	M	11/10/2017	15.2	551	25.0	73.7	5.3	18.7
172000_17	M	11/13/2017	66.3	4603	35.8	327.7	4.6	24.6
121191_17	F	10/15/2017	37.5	3170	44.3	287.7	3.5	18.0
87780_17	F	10/15/2017	18.2	642	41.7	147.7	3.5	12.6
121206_17	F	10/15/2017	19.3	1251	36.2	223.7	3.6	13.7
121203_17	M	10/16/2017	109.2	5837	38.5	391.7	2.9	22.9
123226_17	F	10/16/2017	38.3	2110	39.9	215.7	4.3	16.9
120937_17	M	10/16/2017	92.3	7001	41.1	279.7	3.9	28.2
112728_17	F	10/19/2017	14.3	1004	26.7	103.7	4.4	16.5
120943_17	M	10/24/2017	27.4	797	39.3	235.7	3.7	15.0
172004_17	F	11/17/2017	28.3	519	36.6	167.7	5.0	12.1
84484_17	F	11/21/2017	52.7	3793	34.1	243.7	4.3	13.8
111868_18	F	09/30/2018	34.4	2111	42.6	367.7	6.1	20.7
84484_18	F	09/30/2018	28.9	1614	21.4	175.7	2.6	14.9
111870_18	F	10/06/2018	40.3	1270	33.2	235.7	5.1	17.2
112696_18	F	10/15/2018	51.4	4295	44.9	243.7	4.3	25.6
87640_18	F	10/18/2018	26.3	1767	25.2	103.7	5.3	20.7
120938_18	M	10/23/2018	45.4	1244	37.1	463.7	4.5	23.7

120942_18	M	10/23/2018	50.4	225	40.2	327.7	3.5	14.1
171994_18	M	10/23/2018	59.3	5424	42.2	295.7	3.8	29.0
121191_18	F	10/29/2018	78.3	4206	45.9	287.7	4.1	18.4
194593_19	F	10/12/2019	18.5	1310	36.4	271.7	5.1	19.7
194601_19	F	10/20/2019	47.4	335	35.8	195.7	3.8	14.2
		Mean	47.05	2876.81	38.2	38.5	3.7	3.7
		SD	33.34	3124.52	31.63	31.99	3.14	3.14
		Max.	124.4	15502	463.7	463.7	29	29
		Total	1505.9	92058				

Reference: Elaborated by the author (2021). Whale ID = unique tag number. Class = Social class (F = female with calf, M = Male). Tag Deployment = day at deployment tag, Tag Duration (days) = number of days when data were received. Dives n. º = number of dives recorded.

3.2 DIVE DEPTHS AND DURATION BY HABITATS

In general dive depth and duration in the three main habitats are summarized in Table 5. In the breeding area, there were a total of 32 animals transmitting data, during the migration, there were 29, and only nine animals transmitted in the feeding area. The depths and durations of the dives were statistically different across habitats (Figure 5, Table S1). In the breeding area, the average depth was the lowest, 22.6 m with a maximum depth of 244 m. During migration, the average depth dive was 30.2 m and the maximum was 464 m. Finally, in the feeding grounds, the mean and maximum dive depth was, respectively, 35.1 m and 320 m.

The dive duration at the breeding area had an average of 2.6 min, during migration with the higher average, of 3.1 min, and then at the feeding area had the lowest average, of 2.4 min (Figure 5, Table 5).

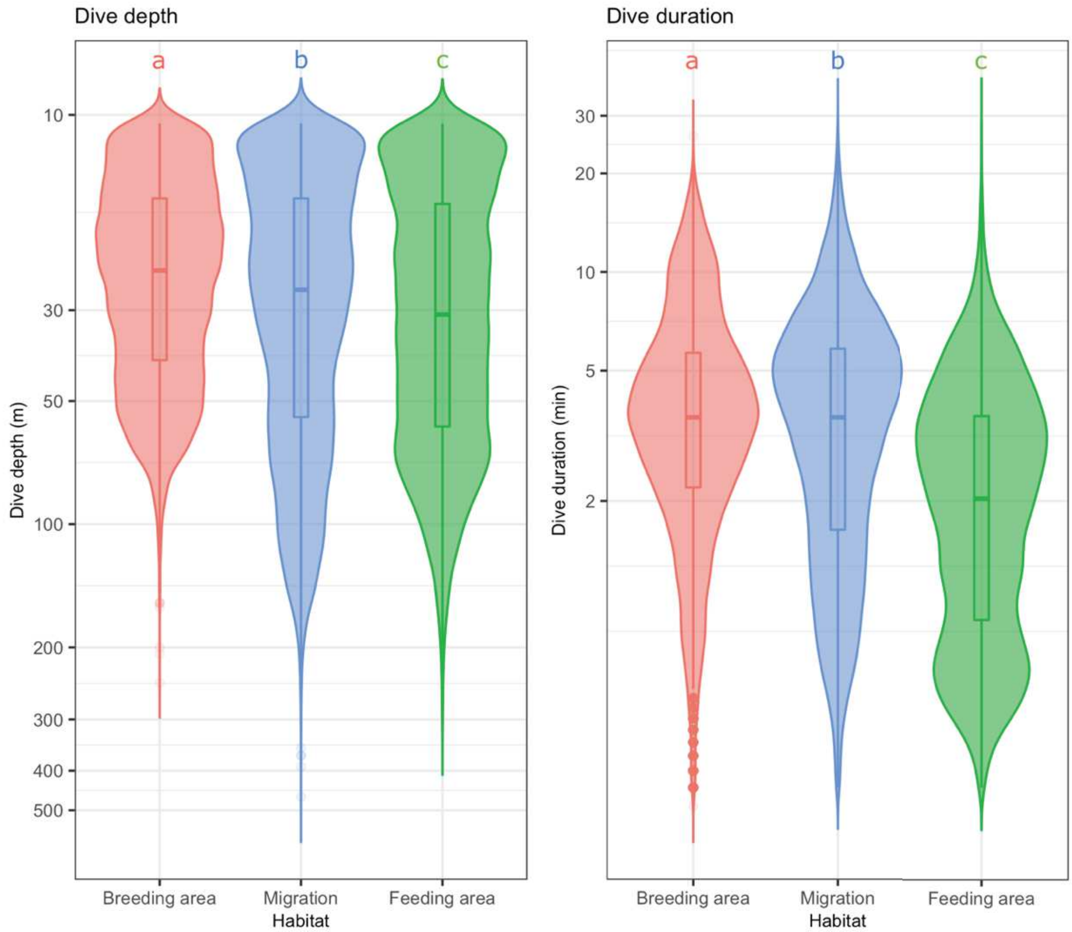
Table 5 - Summary of dive depth and duration within each habitat.

			Tag	**Dives**		
			Duration (days)	**n. º**	**Depth (m)**	**Duration (min)**
Habitats	**BA**	**Mean**	14.78		22.6	2.6
		SE ±	8.76		1.03	1.04
		Max.	37		244	26
		Total	473	26025		
	MI	**Mean**	22.13		30.2	3.1
		SE ±	12.89		1.03	1.04
		Max.	42		464	29
		Total	642	35384		

	FA	**Mean**	39.11		35.1	2.4
		SE ±	28.25		1.03	1.04
		Max.	77		320	28.9
		Total	352	30650		

Reference: Elaborated by the author (2021). Summary of dive depth and duration in each habitat. Dive and duration mean of dives, and summary of duration and number of dives registered. The averages were estimated from a linear mixed effects model accounting for the random effect of whale. BA = Breeding area, MI = Migration, FA = Feeding area. Tag Duration (days) = number of days when data were received. Dives n. º = number total of dives registered for each habitat.

Figure 5 - Dive depth and dive duration within each habitats.

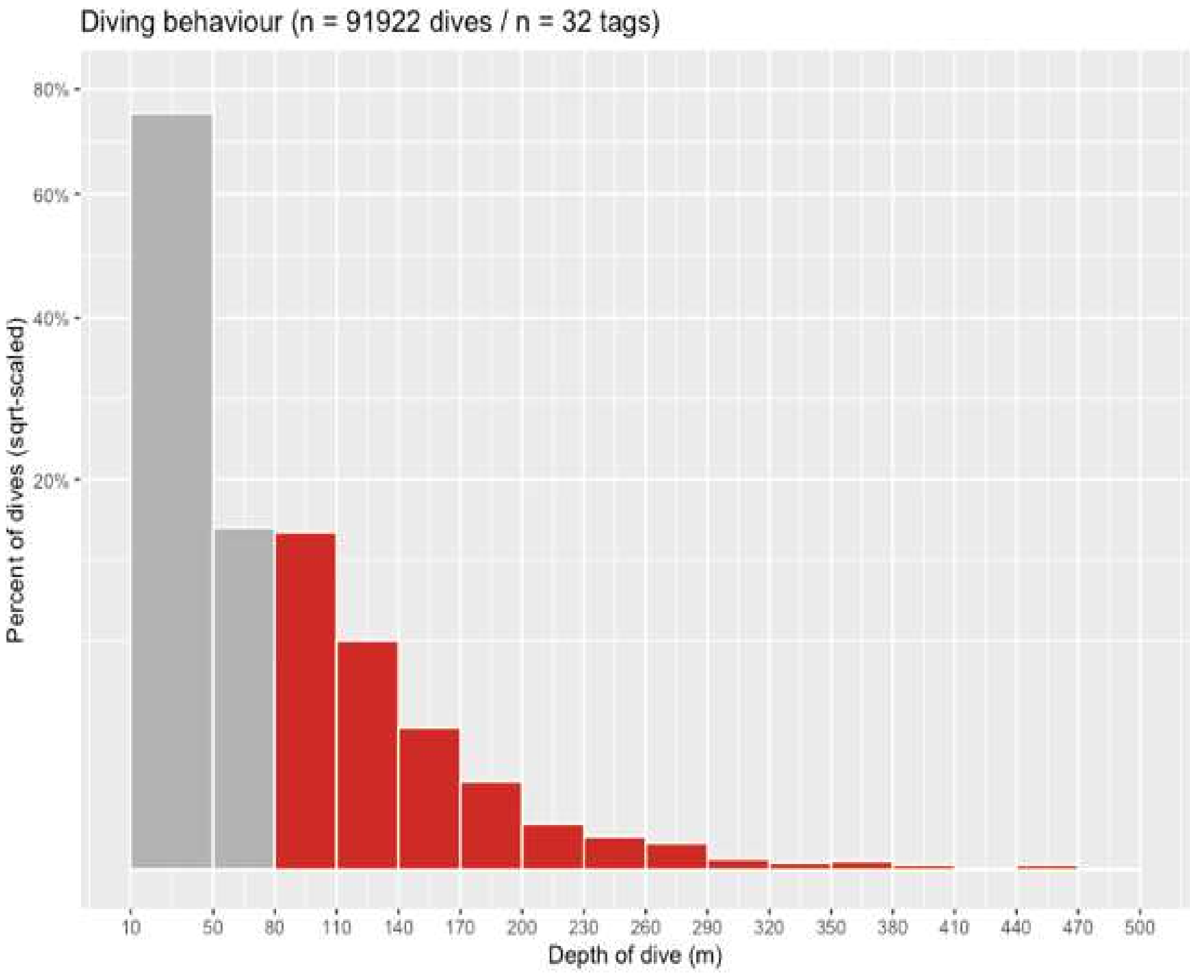


Reference: Elaborated by the author (2021). Dive depth and duration by habitats. Mean dive and duration from the observed data. The statistical differences (letters) were estimated from a linear mixed effects model. The letters show when a given mean is statically different ($p < 0.001$) from each other.

3.3 DEPTH RANGE PER HABITAT

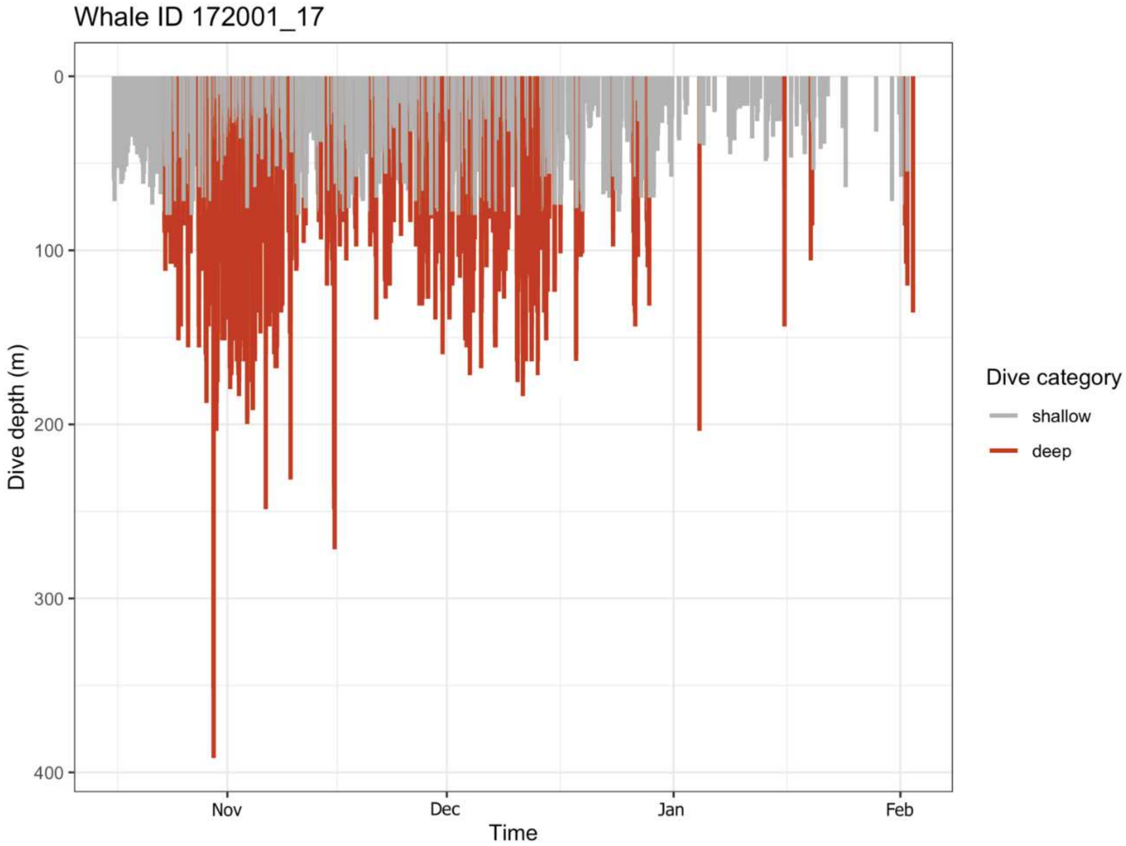
A total of 90.5% of the dives were classified as shallow (<80 m). Only 9.5% of the dives were classified as "deep" (>80 m) (Figure 6, 7). The highest average depth of deep dives was made during the migration (14%) and they were also more predominant in this habitat (Table 6). The location where the deepest dive (464 m) occurred were associated with the Rio Grande Elevation, a chain of seamounts located at 4,473 m of depth, at 2,370.48 km east of the state of Rio Grande do Sul - BR and of Uruguay at latitudes ranging from 28° and 34° S, and longitudes from 28° and 40° W (Figure 8, 9, Table S2) (CAMBOA & RABINOWITZ 1984).

Figure 6 - Percent of shallow and deep dives.



Reference: Elaborated by the author (2021).

Figure 7 - Dive depths of whale ID 172001_17 (female) along the course of tracking. Dives were considered deep when > 80 m.



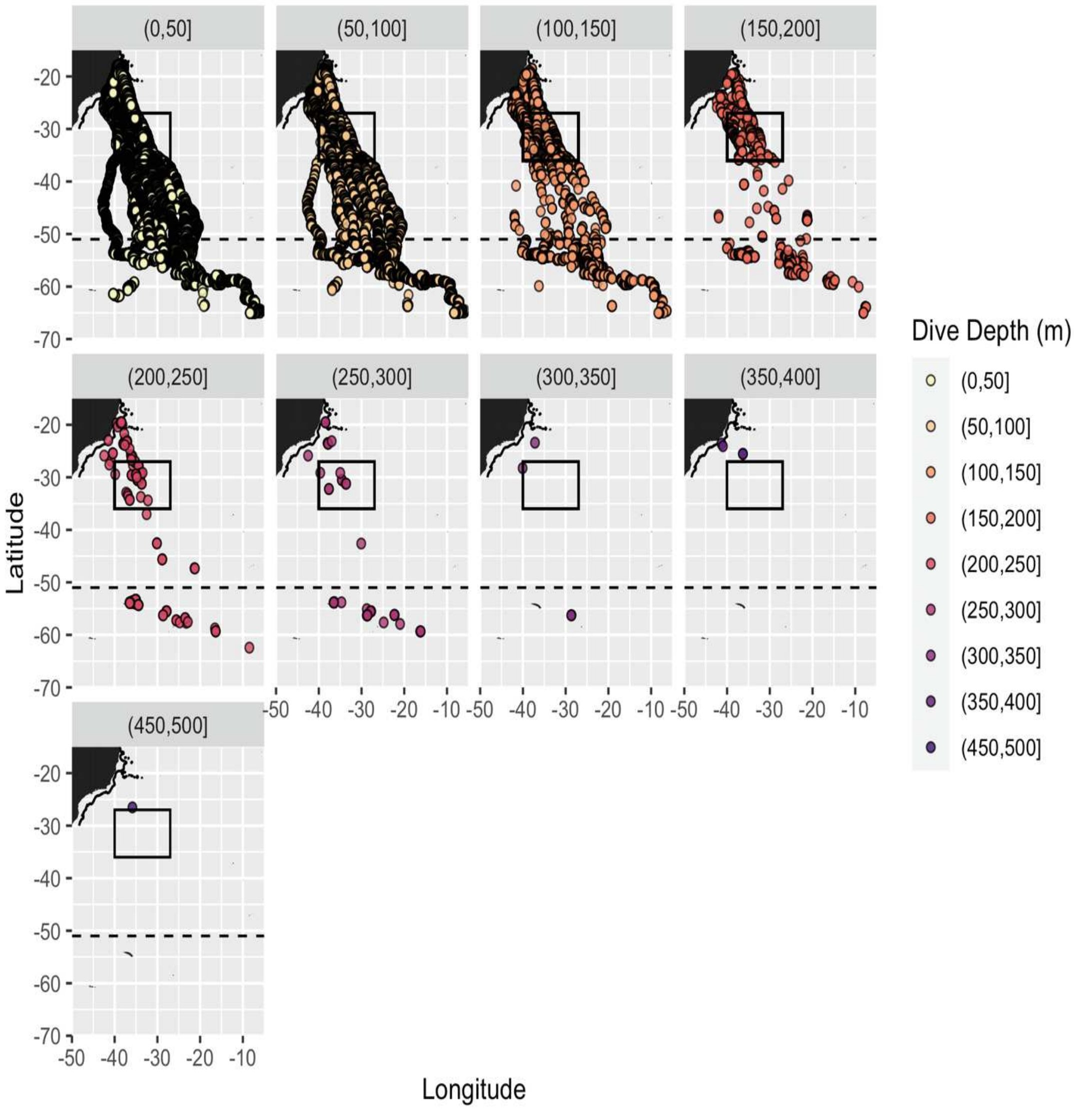
Reference: Elaborated by the author (2021).

Table 6 - Depth range within each habitat.

Habitat	Depth range	Dive mean	*p* value	%
Breeding area	**Shallow**	22.0	<.0001	99
	Deep	86.4		1
Migration	**Shallow**	25.2	<.0001	86
	Deep	111.0		14
Feeding area	**Shallow**	29.3	<.0001	89
	Deep	80.6		11

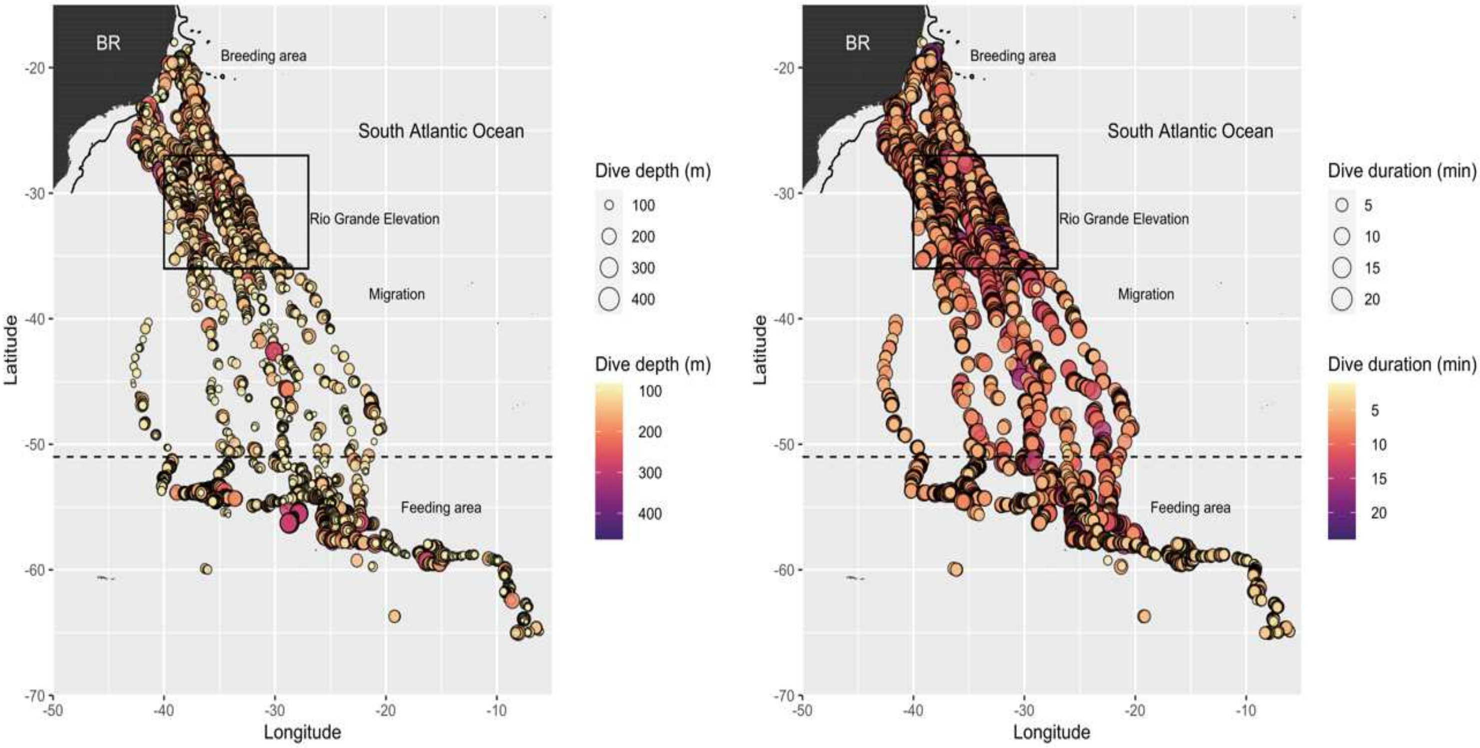
Reference: Elaborated by the author (2021). Dive mean = dive depth mean (m) of dives registered for each depth range and habitat. Depth range Shallow = < 80 m. Depth range Deep = > 80 m. % = percentage of dives.

Figure 8 - Map of dives per depth range (50m bins).



Reference: Elaborated by the author (2021). The line on the coast of Brazil is the limit of the breeding area by 200m of bathymetry. The square represents the approximate area of the Rio Grande Elevation. The dashed line is the 51ºS limit, the border between the migratory route and the feeding grounds.

Figure 9 - General map showing deep dives (>80m) and dive duration.



Reference: Elaborated by the author (2021). General map showing deep dives (>80 m, left) and dive duration (right) on a continuous color scale (size of point is proportional to depth and duration). BR = Brazil. The line on the coast of Brazil is the limit of the breeding area by 200m of bathymetry. The dashed line is the -51oS limit, where the feeding area starts.

Longitude significantly had a negative effect on dive depth ($p < 0.001$); as long increases the longitude, shallower is the depth of diving. The bathymetry had a positive effect ($p < 0.001$), as the dive depth increased in deeper waters.

3.4 DIVE PATTERNS BY SOCIAL CLASS WITHIN EACH HABITAT

Out of the 32 animals that transmitted in the breeding grounds, 22 were females and 10 were males. In the migratory corridor, they were, respectively, 19 and 10. Finally, in the feeding grounds, data were received for 4 females and 5 males.

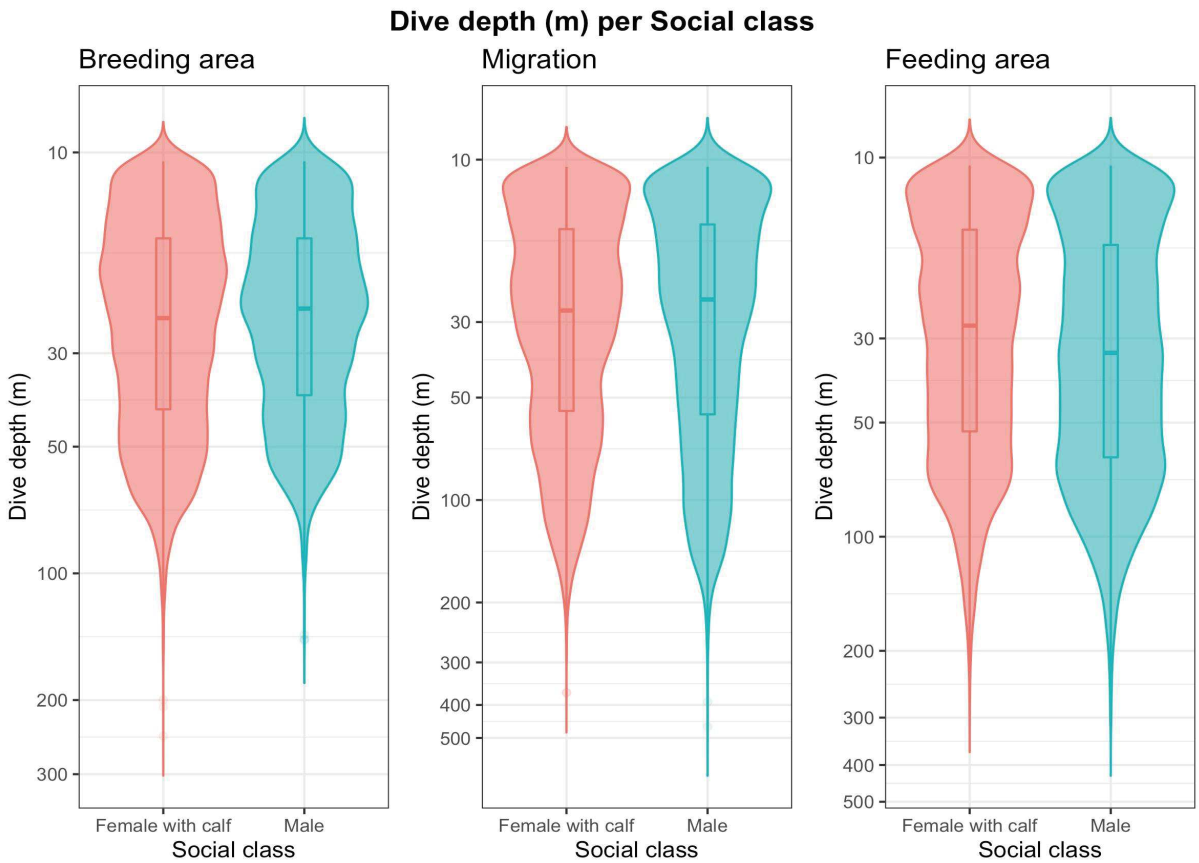
Within the same habitat, we have not found strong evidence for the effects of social class on dive depth (p = 0.85, estimate = -0.0121), and on dive duration (p = 0.85, estimate = 0.0158) (Figure10; Table 7, Table S3).

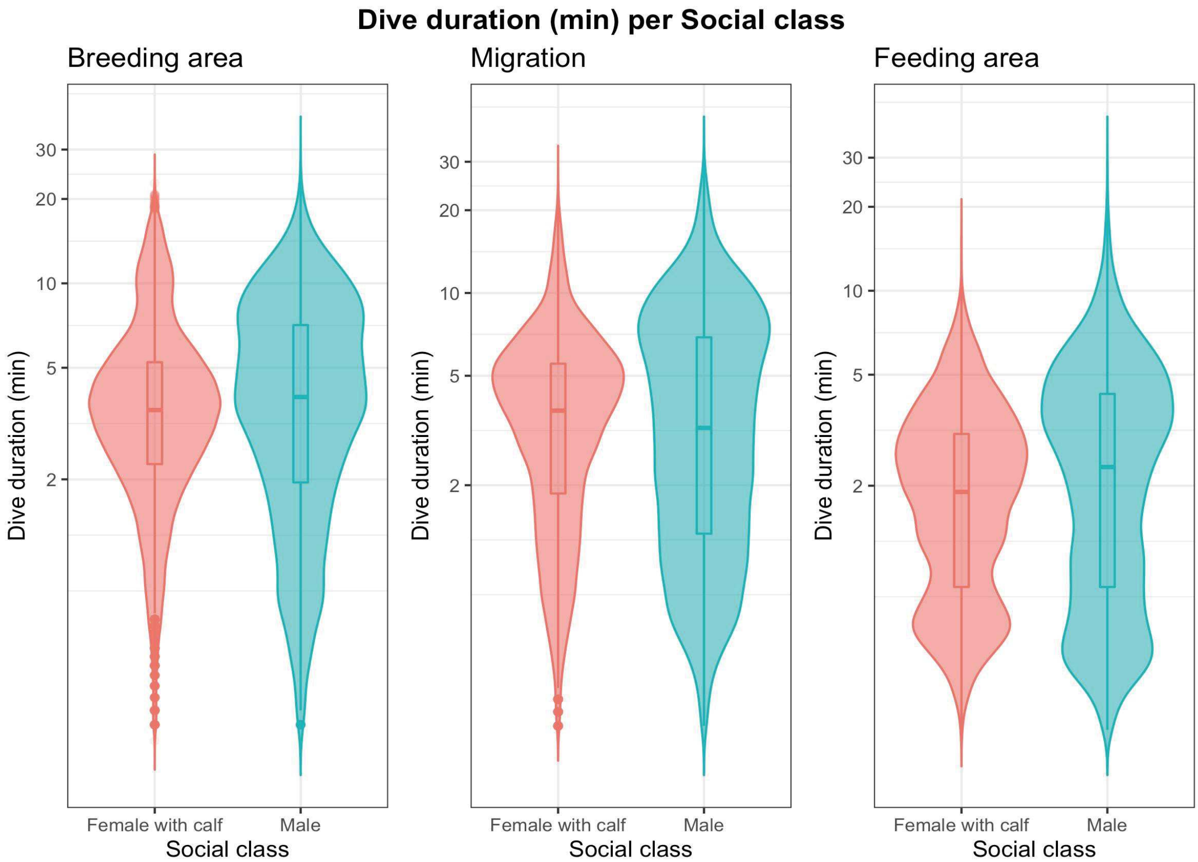
Table 7 - Summary of dive depth and duration per social class within each habitat.

		Dives							
		Depth (m)				Duration (min)			
Habitats	Class	Mean	Max.	*p*	SE ±	Mean	Max.	*p*	SE ±
BA	F	26.3	244	0.6380	1.03	3.1	22.8	0.4375	1.04
	M	25.5	144		1.05	3.3	26		1.07
MI	F	28.7	280	0.3900	1.04	3.1	25.6	0.3478	1.06
	M	31.1	464		1.07	3.5	29		1.10
FA	F	32.1	280	0.9938	1.07	2.3	15.8	0.2051	1.10
	M	32.1	320		1.06	1.9	29		1.09

Reference: Elaborated by the author (2021). Summary of dive depth and duration per social class in each habitat. The statistical differences were estimated from a linear mixed effects model accounting for the random effect of whale. BA = Breeding area, MI = Migration, FA = Feeding area. Class = Social class (F = female with calf, M = Male).

Figure 10 - Dive depth and dive duration by social class within each habitat.





Reference: Elaborated by the author (2021). Mean dive and duration from the observed data. The statistical differences were estimated from a linear mixed effects model. There was no significant difference between any with significance level of 0.001.

A total of 92% of the dives by females were classified as shallow (<80 m), and 11% were deep (> 80m), while for males these proportions were 89 and 11%, respectively. No statistical differences were found concerning depth range between males and females at deep (p = 0.99, estimate deep = -0.00726) and shallow dives (p = 0.89, estimate shallow = 0.03504) (Table S4).

No difference in the average depth of shallow and deep dives was found between males and females in the breeding and feeding areas (Table 8, Table S5). However, in the migratory routes, the average depth of deep dives was greater for males (101.4 m) than females (120.3 m) (p = 0.0061) (Table 8, Table S5). There was no statistical difference in the average depth of shallow dives across sexes.

Table 8 - Depth range per social class within each habitat.

Habitat	Depth range	Class	Dive mean	SE ±
BA	**Shallow**	**F**	25.2	1.03

		M	24.5	1.05
	Deep	**F**	85.6	1.06
		M	90.0	1.10
MI	**Shallow**	**F**	26.3	1.02
		M	24.2	1.04
	Deep	**F**	101.4	1.03
		M	120.3	1.04
FA	**Shallow**	**F**	28.5	1.04
		M	30.2	1.03
	Deep	**F**	82.2	1.05
		M	79.0	1.04

Reference: Elaborated by the author (2021). Dive mean = dive depth mean (m) of dives registered for each depth range and habitat. Habitat BA = Breeding area, Habitat MI = Migration, Habitat FA = Feeding area. Class F = female with calf. Class M = male. Depth range Shallow = > 80 m. Depth range Deep = > 80 m.

3.5 DIVES SHAPES PER HABITAT

Overall, we found strong evidence for the effects of dive shapes on dive depth ($p < 0.0001$) and dive duration ($p < 0.0001$). The V-shape dives were the deepest on average, followed by the U-shape, and the Square-shape dives (Table S6). The proportion of Square-dives seems to be bigger in the breeding area than in the other habitats. Interestingly the average U-shape depths were equal during migration and feeding area, this has also happened for the average Square-shape depths, being equal in these two habitats. The Square-shape dives were the longest in duration, followed by V-shape, and U-shape (Table 9). A similar pattern was found within each habitat separately (Figure 11, Table 9, Table S7). The mean diving depth of the different dive shapes consistently increased across habitats, with the shallowest dives occurring in the breeding habitats and the deepest dives in the feeding areas.

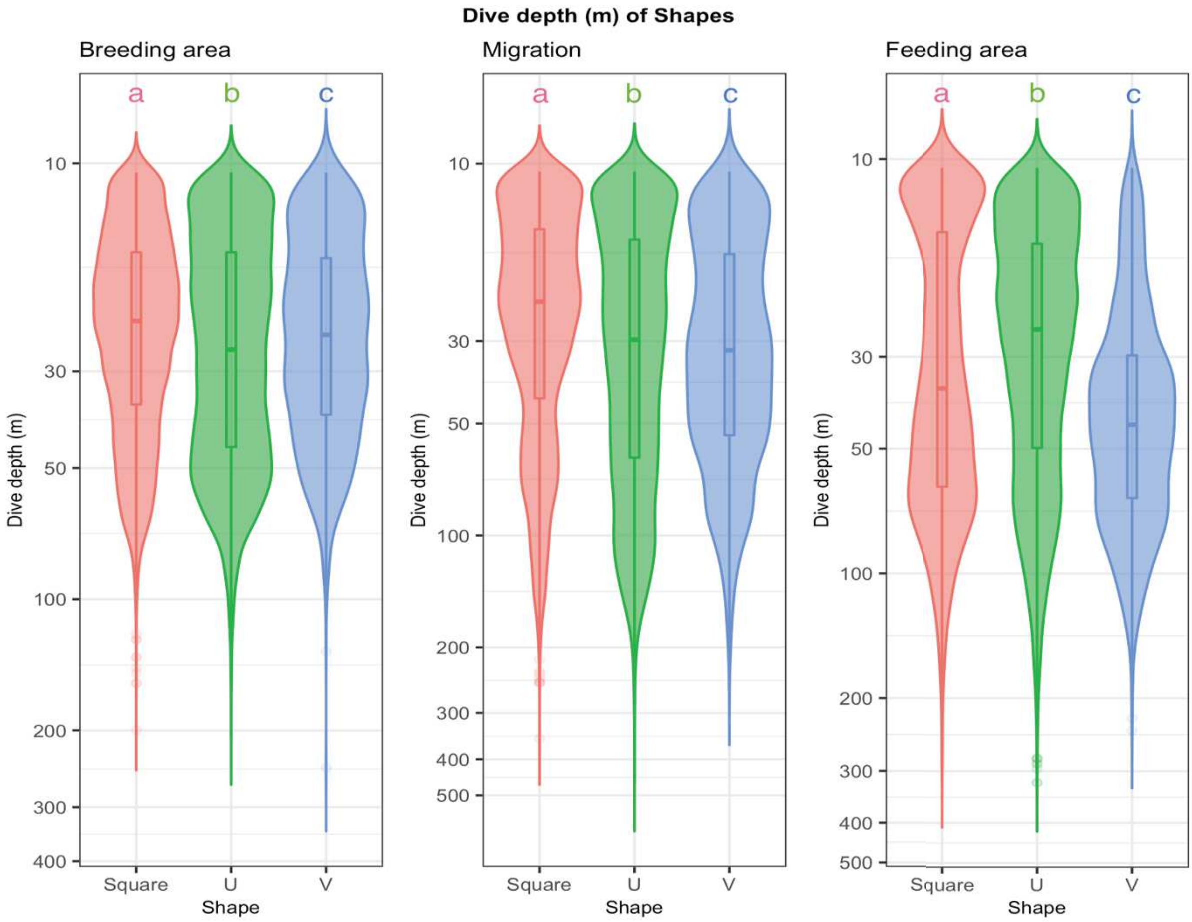
Table 9 - Summary of dive depth and duration per shape within each habitat.

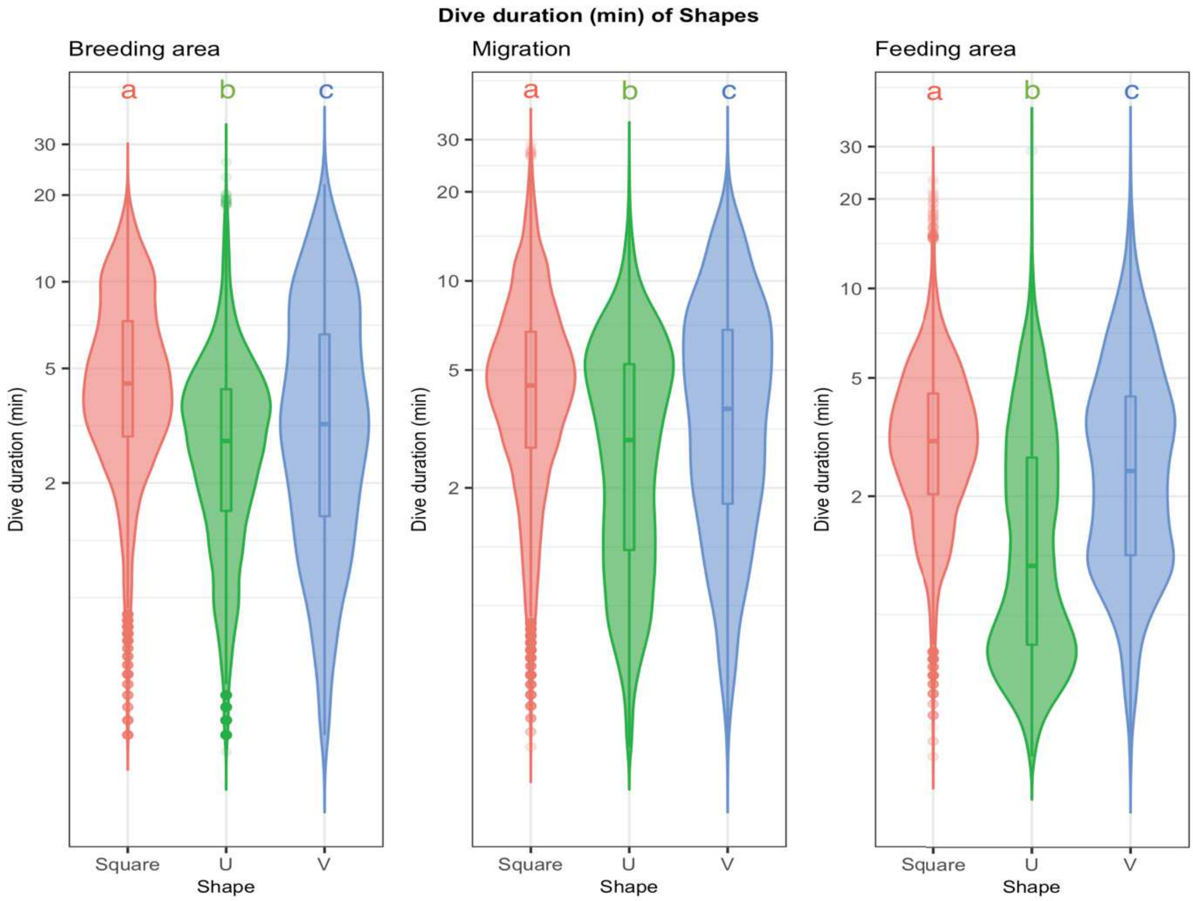
	Dives	
	Depth (m)	**Duration (min)**

Habitat	Shape	n. º	%	Mean	Max.	SE ±	Mean	Max.	SE ±
BA	Square-shape	13449	51.9	25.3	200	1.03	4.2	22.9	1.04
	U-shape	11123	42.9	25.9	208	1.03	2.6	26	1.04
	V-shape	1331	5.1	26.5	244	1.03	3.1	21.8	1.04
MI	Square-shape	12806	36	28.2	352	1.04	3.9	29	1.06
	U-shape	20077	57	30.5	464	1.04	2.7	24.7	1.05
	V-shape	2483	7	33.1	249	1.04	3.4	23.3	1.06
FA	Square-shape	10192	33	28.2	296	1.05	2.4	23.23	1.07
	U-shape	17320	57	30.5	320	1.05	1.7	29	1.07
	V-shape	3141	10	38.1	240	1.05	2.2	26.4	1.07

Reference: Elaborated by the author (2021). Summary of dive depth and duration per shape in each habitat. The averages were estimated from a linear mixed effects model accounting for the random effect of whale. Habitat BA = Breeding area, Habitat MI = Migration, Habitat FA = Feeding area. n. º= Dives registered. % = percentage of dives.

Figure 11 - Dive depth and dive duration of shapes within each habitat.





Reference: Elaborated by the author (2021). Dive depth of shapes per habitat. Dive mean from the observed data. The statistical differences (letters) were estimated from a linear mixed effects model accounting for the random effect of whale. The letters show when a given mean is statistically different ($p < 0.001$) from each other within the same habitat.

There were differences in dive depths for dives classified as "shallow" across the different dive shapes within each habitat. In the breeding areas, Square-shaped dives were significantly shallower than U-shape and V-shape dives (*p-value* Square-shape U-shape = <.0001, *p-value* Square-shape V-shape = 0.0480). In the migratory corridors, average dive depth was different across all dives shapes (*p-value* Square-shape U-shape = <.0001, *p-value* Square-shape V-shape = <.0001, *p-value* U-shape V-shape = <.0001), with Square-shape dives being the shallowest and V-shaped dives being the deepest. Finally, in the feeding area, V-shape dives were significantly deeper than square-shape and U-shape dives (*p-value* Square-shape V-shape = <.0001, *p-value* U-shape V-shape = <.0001) (Table 10, Table S8).

For dives classified as "deep", there was no statistical difference across dive shapes in the breeding areas. On the other hand, U-shape dives were deeper in the migratory routes (*p-value* U-shape V-shape = <.0001, *p-value* Square-shape U-deep = <.0001) and in the feeding habitats (*p-value* U-shape V-shape = 0.0001, *p-value* Square-shape U-shape = 0.0002) (Table 10, Table S8).

Table 10 - Depth range per shape within each habitat.

Habitat	Depth range	Shape	Dive mean	SE ±
Breeding area	**Shallow**	Square	24.2	1.03
		U	25.2	1.03
		V	25.2	1.03
	Deep	Square	84.7	1.06
		U	88.2	1.06
		V	95.5	1.14
Migration	**Shallow**	Square	22.6	1.02
		U	25.0	1.02
		V	28.7	1.02
	Deep	Square	111.0	1.03
		U	120.3	1.02
		V	101.4	1.04
Feeding area	**Shallow**	Square	26.8	1.03
		U	27.3	1.03
		V	34.8	1.03
	Deep	Square	79.0	1.03
		U	85.6	1.03
		V	77.4	1.03

Reference: Elaborated by the author (2021). Dive mean = dive depth mean (m) of dives registered for each depth range and habitat. Depth range Shallow = < 80 m. Depth range Deep = > 80 m.

3.6 DAYLIGHT DISTRIBUTION

Significant dial variation was observed in the average dive depths in all habitats (Table 9). Dives at dawn and day were slightly deeper than those at dusk or night, but still statistically different between dawn and day only in the breeding grounds. However, in the feeding habitats, deeper dives were observed during the day and dusk (Table 11, Figure 12, Table S9).

Average dive duration was also different across periods of the day in the three regions examined. Longer dives were observed at dusk and night in the breeding area. In the migratory corridors the dives made at day were shorter, and at night longer (Table 11). In the feeding area, dive duration was significantly greater during the day and the shortest at night (Table 11, Figure 12, Table S10).

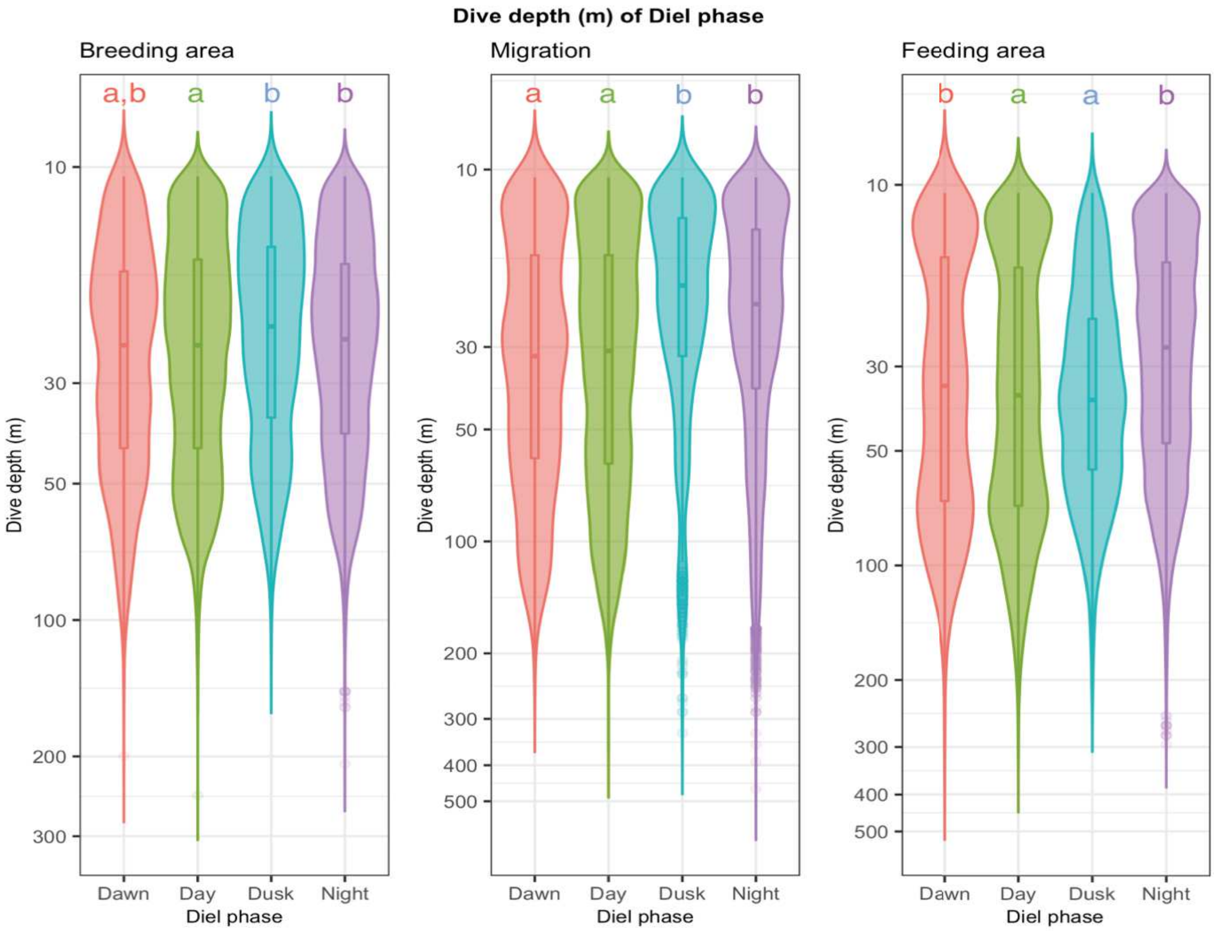
Table 11 - Summary of dive depth and duration per dial phase within each habitat.

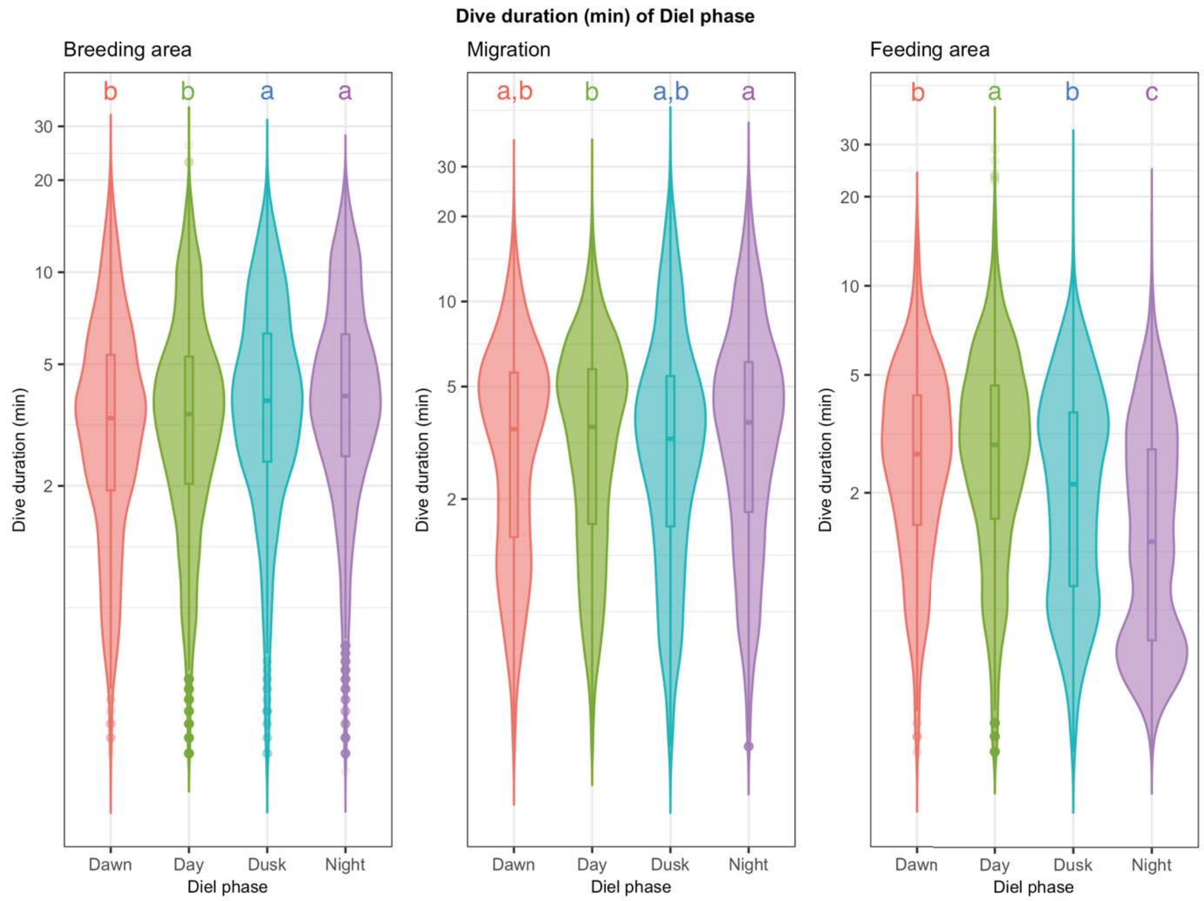
	Dives		
		Depth (m)	**Duration (min)**

Habitat	Diel phase	%	n. º	Mean	Max.	SE ±	Mean	Max.	SE ±
BA	**Dawn**	7.9	2044	26.4	200	1.03	2.9	20.9	1.04
	Day	54.1	14001	26.5	244	1.03	3.1	26	1.04
	Dusk	6.2	1606	25.2	116	1.03	3.4	20.2	1.05
	Night	31.9	82552	25.6	208	1.03	3.5	20.7	1.04
MI	**Dawn**	8.5	3000	32.4	244	1.04	3.2	23.2	1.06
	Day	59.9	21200	32.5	368	1.04	3.2	27.3	1.05
	Dusk	5.5	1959	27.6	328	1.04	3.3	28.3	1.06
	Night	26	9207	27.7	464	1.04	3.4	29	1.06
FA	**Dawn**	4.7	1436	29.8	320	1.05	2.1	15.2	1.07
	Day	36	11025	34.9	320	1.05	2.6	29	1.07
	Dusk	6.9	2101	34.8	216	1.05	2.0	20.8	1.07
	Night	52.5	16091	29.1	296	1.05	1.7	17.9	1.07

Reference: Elaborated by the author (2021). Summary of dive depth and duration per dial phase in each habitat. The averages were estimated from a linear mixed effects model accounting for the random effect of whale. Habitat BA = Breeding area, Habitat MI = Migration, Habitat FA = Feeding area. n. º= Dives registered. % = percentage of dives.

Figure 12 - Dive depth and duration of diel phase within each habitat.





Reference: Elaborated by the author (2021). Dive depth of diel phase per habitat. Dive mean from the observed data. The statistical differences (letters) were estimated from a linear mixed effects model accounting for the random effect of whale. The letters show when a given mean is statistically different ($p < 0.001$) from each other within the same habitat.

When dives classified as deep and shallow are considered, no differences across periods of the day were observed in the breeding grounds (Table S11). In the migratory routes, dive depths were lower at dusk and night for the shallow dives and deep dive depth was greater for dives performed at dusk (Table S11). In the feeding areas, shallow dives were significantly deeper at dusk and day and deep dives were deeper during the day (Table 12, Table S11).

The shallow dives at the feeding area had a statistical difference between dusk and day, dawn and night, also, the day had a difference with dusk, dawn, and night. The dives during dusk were deeper than the day, and dawn and night. Concerning the deep dives at the feeding area, dives made during the day showed to be different to dawn, dusk, and night, also night different between day, dawn, and dusk. The dives made at day were deeper (93.6 m) than during night (69.4 m) (Table 12, Table S11).

Table 12 - Depth range per diel phase within each habitat.

Habitat	Depth range	Diel phase	Dive mean	SE ±
BA	Shallow	Dawn	25.2	1.03
		Day	25.2	1.03
		Dusk	24.2	1.03
		Night	24.7	1.03
	Deep	Dawn	83.0	1.08
		Day	81.4	1.06
		Dusk	104.5	1.17
		Night	90.0	1.07
MI	Shallow	Dawn	26.8	1.02
		Day	27.1	1.02
		Dusk	23.5	1.02
		Night	24.0	1.02
	Deep	Dawn	101.4	1.03
		Day	104.5	1.02
		Dusk	129.0	1.05
		Night	109.9	1.03
FA	Shallow	Dawn	26.8	1.03
		Day	29.6	1.03
		Dusk	33.4	1.03
		Night	27.9	1.03
	Deep	Dawn	79.0	1.04
		Day	93.6	1.03
		Dusk	81.4	1.04
		Night	69.4	1.03

Reference: Elaborated by the author (2021). Dive mean = dive depth mean (m) of dives registered for each depth range and habitat. Habitat BA = Breeding area. Habitat MI = Migration. Habitat FA = Feeding area. Depth range Shallow = < 80 m. Depth range Deep = > 80 m.

3.7 MOON PHASES DISTRIBUTION

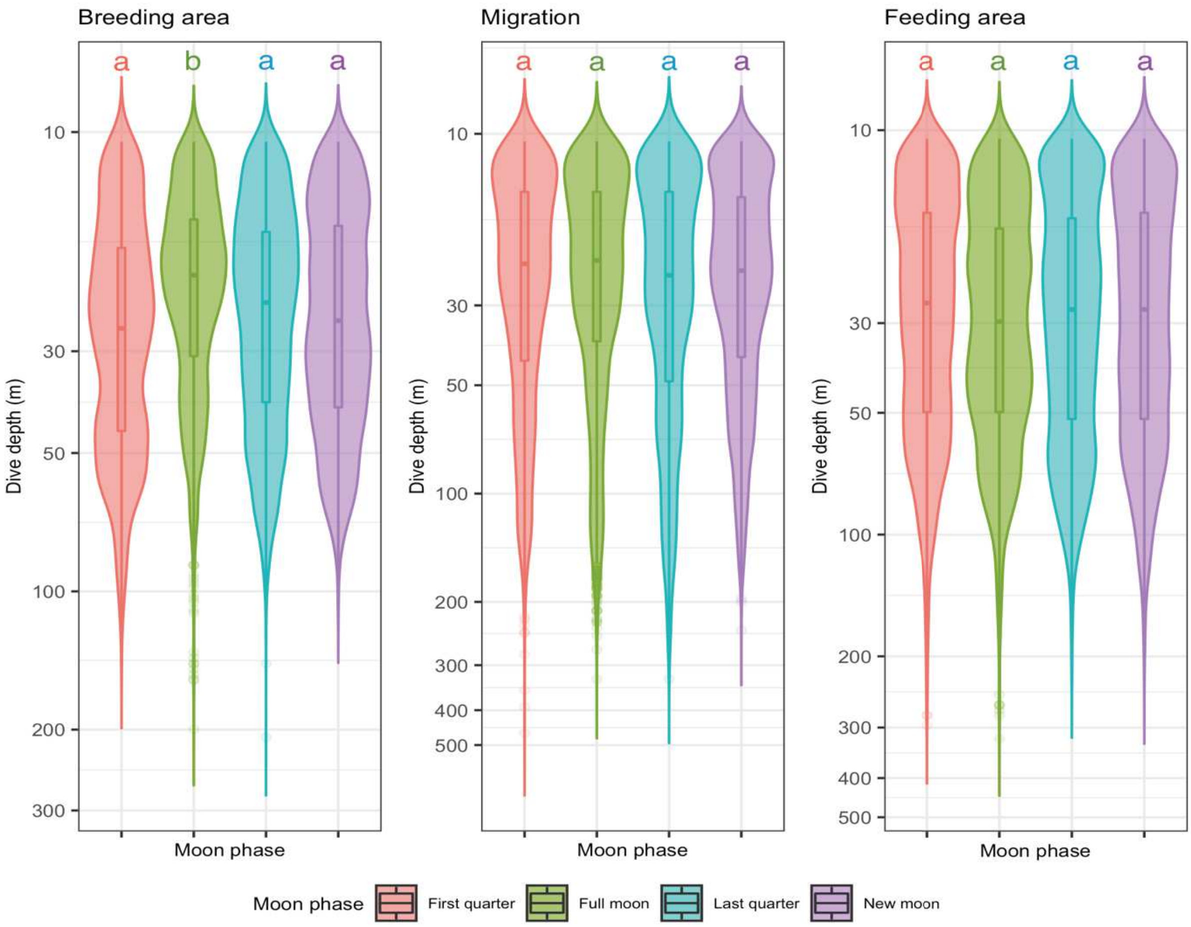
Average dive depth was significantly shallower in the breeding grounds, but similar across the other moon phases. No statistical difference was observed in the average depths of dive in any of the other habitats (Figure 13, Table 13, Table S12). Mean dive duration did not differ across moon phases in the breeding grounds and the migratory corridor. However, depth duration was greater during the full moon in the feeding grounds (Figure 13, Table 13, Table S13).

Table 13 - Summary of dive depth and duration per moon phase within each habitat.

		Dives							
				Depth (m)			**Duration (min)**		
Habitat	**Moon phases**	**%**	**n. º**	**Mean**	**Max.**	**SE ±**	**Mean**	**Max.**	**SE ±**
BA	**Last quarter**	27.8	3318	25.5	208	1.03	3.3	26.0	1.05
	Full moon	27.88	2530	22.1	200	1.03	3.2	20.7	1.06
	First quarter	20.7	2464	25.8	244	1.04	3.7	20.9	1.06
	New moon	30.16	3590	26.4	118	1.03	3.4	22.9	1.05
MI	**Last quarter**	27.04	3831	29.1	328	1.04	3.3	25.9	1.05
	Full moon	23.63	3348	29.6	368	1.04	3.5	28.3	1.06
	First quarter	21.66	3069	27.6	464	1.04	3.1	26.6	1.05
	New moon	27.66	3918	28.0	240	1.04	3.2	29.0	1.06
FA	**Last quarter**	27.07	5314	38.4	240	1.06	2.0	29.0	1.07
	Full moon	24.42	4793	38.4	320	1.06	1.8	17.9	1.07
	First quarter	27.39	5376	38.8	296	1.06	2.2	26.4	1.07
	New moon	21.12	4145	38.0	296	1.06	1.9	22.4	1.07

Reference: Elaborated by the author (2021). Summary of dive depth and duration per moon phase in each habitat. The averages were estimated from a linear mixed effects model accounting for the random effect of whale. Habitat BA = Breeding area, Habitat MI = Migration, Habitat FA = Feeding area.

Figure 13 - Dive depth and duration of moon phases within each habitat.


Breeding area
a
b
a
a
10
30
50
100
200
300
Dive depth (m)
Moon phase
Migration
a
a
a
a
10
30
50
100
200
300
400
500
Dive depth (m)
Moon phase
Feeding area
a
a
a
a
10
30
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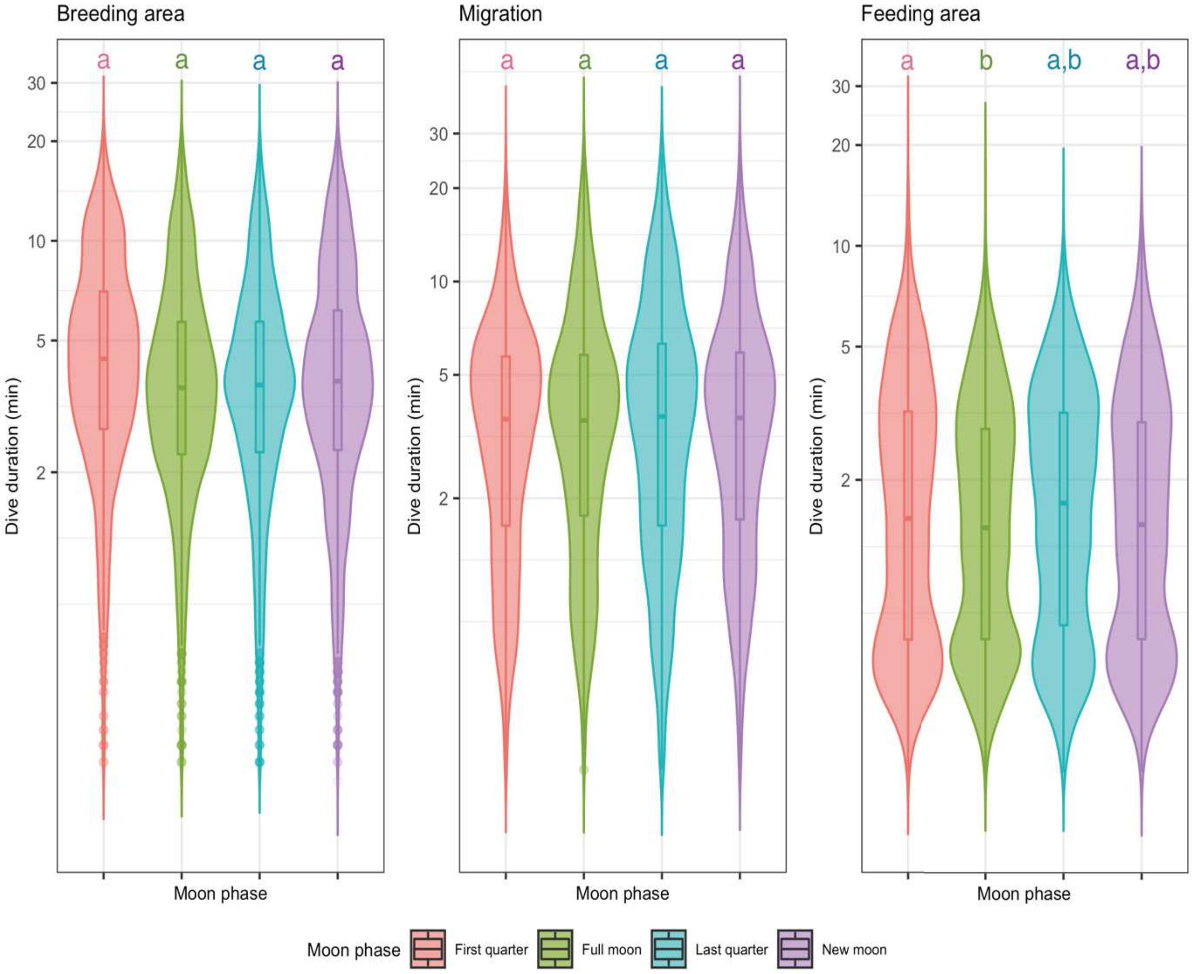
300
400
500
Dive depth (m)
Moon phase
Moon phase
First quarter
Full moon
Last quarter
New moon



Reference: Elaborated by the author (2021). Dive depth of moon phases per habitat. Dive mean from the observed data. The statistical differences (letters) were estimated from a linear mixed effects model accounting for the random effect of whale. The letters show when a given mean is statistically different ($p < 0.001$) from each other within the same habitat.

In the shallow dives made at the breeding area, we found a significant difference from full moon to all the other phases, the deep dives did not show a difference among them. During migration and at the feeding area, the shallow and deep dives also did not show differences among them (Table 14, Table S14).

Table 14 - Depth range per moon phase within each habitat.

Habitat	Depth range	Moon phase	Dive mean	SE ±
BA	Shallow	**Last quarter**	25.7	1.03
		Full moon	21.7	1.03
		Last quarter	24.7	1.03

		New moon	26.3	1.03
	Deep	**Last quarter**	93.6	1.07
		Full moon	86.4	1.10
		Last quarter	75.9	1.08
		New moon	87.3	1.12
MI	**Shallow**	**Last quarter**	23.3	1.02
		Full moon	22.1	1.02
		Last quarter	23.8	1.02
		New moon	24.2	1.02
	Deep	**Last quarter**	104.8	1.05
		Full moon	113.2	1.05
		Last quarter	116.7	1.05
		New moon	104.5	1.05
FA	**Shallow**	**Last quarter**	26.8	1.05
		Full moon	27.9	1.05
		Last quarter	27.3	1.04
		New moon	26.8	1.05
	Deep	**Last quarter**	70.8	1.05
		Full moon	71.5	1.05
		Last quarter	70.8	1.05
		New moon	74.4	1.05

Reference: Elaborated by the author (2021). Dive mean = dive depth mean (m) of dives registered for each depth range and habitat. Habitat BA = Breeding area. Habitat MI = Migration. Habitat FA = Feeding area. Depth range Shallow = < 80 m. Depth range Deep = > 80 m.

4. DISCUSSION

4.1 DIVE DEPTH AND DURATIONS

To analyze and characterize the diving behaviors of humpback whales in the WSA, relatively long-term transdermal satellite transmitters were deployed and the results demonstrate a general effect of habitat in the species dive behavior. We found that diving depth and duration among the three habitats differed. For dives categorized as shallow (< 80 m), the lowest average depth in the breeding area may be related to the parental care by the mother towards the calf (VIDESEN et al., 2017), from the behavior of singing males (TYACK, 1981) or by activities near the surface typical of competitive groups (BAIRD et al., 2000, HENDERSON et al., 2018). The diving behavior of females with calves and males did not show differences within the same habitat. The results presented here for females with calves are consistent with observations in other regions. In Western Australia, it was observed that nursing behavior was performed between 1.1 m and 19.2 m, and half of them were above 2.5 m (VIDESEN et al., 2017), with the maximum depth of the nursing was relatively close to the observed average of females with calves in our study site, that is, 26.3 m.

In the Western South Pacific, the dive depths were in general greater than in our study area (DERVILLE et al., 2020). Females accompanied by calves made dives of 36.2 m on average, which is 10 m more than the females with calves present in this study. For males, an average dive depth of 51.1 m was documented (DERVILLE et al., 2020), nearly twice the averages seen here. These lower averages in our study may be related to differences in the main habitat across the two regions. The main humpback whale breeding grounds off Brazil, and the area where whales were tagged in this study, corresponding to a region known as the Abrolhos reef complex (SICILIANO, 1995, MARTINS et al., 2001, ANDRIOLO et al., 2010). This region is characterized by volcanic islands, shallow banks, canals, and coral reefs, with an average depth of 30 m and a maximum depth of 70 m at the edge of the reef (LEÃO, 1999), in contrast, the depths in New Caledonia where had deeper dives the seabed varied from 200 m to more than 2,000 m.

In this study, the highest average dive of deep dives, and the longer average duration of diving occurred during migration. These results were unexpected to some extent as it would be expected that shallower dives may help minimize energy costs during an energetically demanding period (the migration) particularly after whales were fasting in the breeding grounds. It is yet unclear why whales of both sexes/classes would show deeper dives during the migration. One possible explanation is that these dives could represent attempts to forage during the migration. Even though it is not known as a habitual feeding area for this population, the concentration of these deepest dives was associated with the Rio Grande Elevation region, where the record dive, of 464 m at the limit of this area, which may be also an indication of foraging behavior, as this behavior usually occurs below 100 m (GOLDBOGEN et al., 2008). Concerning the Rio Grande Elevation has a length of ~ 480,000 km², comprising three areas that rise from 1.5 km to 3.5 km above the seabed with surrounding complex seabed (PEREZ et al., 2018). There are reports of fish called alfonsino (*Beryx splendens*) living in the seamounts in the Northern Section of the Mid-Atlantic Ridge (VINNICHENKO 1997) and Nazca and Sala y Gómez in the Eastern Central Pacific (PARIN et al., 1997, DUBOCHKIN & KOTLYAR, 1989), these seamounts are similar of Rio Grande Elevation. The *B. splendens* feed on pelagic prey, such as euphausiids, usually close to the water column, due to vertical migration (VINNICHENKO 1997). As well in these seamounts had euphausiids, we can suppose that they may also have in the Rio Grande Elevation and that the humpback whales may be feeding as a complementary way of supplying the energy spent on the journey to the breeding and the energy spent at that time in the return to the feeding area.

The shortest average duration of diving in the feeding area may be an indication that, as they are in the usual feeding area, they do not need to spend more time during foraging dives, as the prey is more abundant.

4.2 DIVE PATTERN AND SHAPES

In the breeding area, the lowest average of shallow dives in Square-shape and also the longest average dive duration among habitats may be related to the behavior's characteristic of breeding areas, such as the singing male dives, mating behavior, swimming followed by rest, or parental care. During the migration, U-shape dives were the deepest among all dive categories. These U-dives may be another indicator that foraging behavior may be occurring. In other studies, U-shape dives are related to foraging behavior (GOLDBOGEN et al., 2008, 2013, 2017, HEIDE-JØRGENSEN et al., 2013). Coincidentally, these U- dives were associated with the location of the Rio Grande Elevation. In the feeding area, the pattern of the shortest duration, with the lowest average of deep dives among habitats, also with the higher average of deep dives in U-shape, may be related to being in the usual feeding area, without having to dive deeply and for a long time looking for the prey, since the prey has a larger concentration in that area.

4.3 DIVE DAYLIGHT AND MOON CORRELATIONS

In the breeding area, due to the deeper dives performed during the day, and the shorter duration of diving during dawn and day, we can suggest that maybe whales prefer to perform the characteristics behaviors of the breeding season with sunlight, and also it seems that the bigger proportion of dives were during the day. Another possibility for these deeper dives during the day can be due to the high temperature in the tropics in the hottest hours of the day in which can overheat with the dark color of the skin and for staying a long time on the surface, thus they can dive deeper to perform thermoregulation (SCHOLANDER & SCHEVILL 1955). Meantime, the lower average depths and the longer duration of diving during dusk and night may indicate that they are resting in shallower depths (SOLDEVILLA et al., 2017, CALAMBOKIDIS et al., 2019) and for longer durations in these periods (IZADI et al., 2018).

During migration, whales may prefer to swim along this course at greater depths during daylight due to the deeper dives made at dawn and the day, besides it seems to be a bigger proportion of dives made during the day than other diel phases. Also performing supposed resting behaviors at shallower depths in dark periods, due for longer duration and shallower dives at dusk and night, as well in the breeding area. Further, the deeper dives at dusk can be due to the exploratory behavior before foraging, presumably in response to vertically migrating prey.

Diving behavior in the feeding area showed the shortest duration among the habitats and occurred primarily at night. In addition, the lowest average of shallow dives at dawn and night, are consistent with the foraging behavior of humpback whales at the West Antarctic Peninsula (WARE et al., 2011). The evidence that these dives occur mainly at night (FRIEDLAENDER et al., 2013), and also with the vertical migration of euphausiids, performing vertical migrations daily (ZHOU & DORLAND 2004), making access to prey substantially easier for them during this the night, what may explain the deeper dives at feeding area during the day in this study. Furthermore, in the feeding area, the dives made at dusk became shallower until the night, remaining constant in this shallower depth until dawn, and increasing the depth during the day. This pattern did not occur in the breeding area or during migration. The foraging dives at the feeding area, in special for fin-whales (*Balaenoptera physalus*) at Southern California Bight and humpback whales in the Western Antarctic Peninsula, showed also this diel pattern (FRIEDLAENDER et al., 2013, KEEN et al., 2019). Here we saw this pattern happen also with U-shape and V-shape, which in theory, are related to the foraging behaviors. However, interestingly, this variation among the diel patterns also happened for the Square-shape. In particular, Square-shape seems to be a modulatory behavior among habitats, adapting and performing the characteristic behaviors of each habitat in this shape. Having the longest average duration, along with the lowest depth average among all shapes and habitats, can be a form of compensation to save energy during these behaviors' characteristics of each habitat.

Another factor that can also influence the foraging behavior is the vertical migration of prey by the luminosity of the moon (BENOIT-BIRD et al., 2009). During the full moon, animals that perform vertical migrations, such as euphausiids, proved to be sensitive to light levels, remaining at greater depths (CLARKE 1973, HAYS 1995, PINOT & JANSÁ 2001). Migration closer to the surface occurs more often on darker nights (e.g., with a new moon) (KEEN et al., 2019). Light levels at 150 m at full moon were found to be similar to the light levels at 500 m during the day (CLARKE & DENTON 1962). This may explain the higher proportion of shallow dives during the new moon in *B. physalus* in the Southern California Bight (KEEN et al., 2019).

The lowest average depth in the breeding area occurred unexpectedly at the full moon. The reasons for this finding are still unclear. However, studies of dives related to moon phases have been primarily conducted in the feeding area or have been related to foraging dives (OWEN et al., 2019, KEEN et al., 2019, STERLING et al., 2014), thus behavioral patterns need to be better investigated during the breeding season. Average depths and duration during migration and in the feeding area do not seem to be influenced by lunar phases.

5. CONCLUSIONS

We observed that the dives depth and duration made among the three habitats were different. The shallow dive patterns at the breeding area coincide with characteristic reproductive behaviors that may occur near the surface as there may not be a need for deeper dives in search of prey. Dive patterns during migration suggest that feeding behavior may be occurring as whales move towards their primary foraging areas grounds. In the feeding area, the dive pattern coincides with other species' behavioral patterns of foraging. The social classes do not influence the average depths of dive, demonstrating that what can influence are the habitats. The moon phases had a clear effect within the breeding area but not within the migration and feeding area, being shallower at the full moon.

From this, we can observe the first study with an evaluation of the dive behavior of individuals from the same population in these different areas. Where the humpback whales of WSA perform different diving behaviors concerning the use of each habitat, as they pass through different stages of their migratory cycle, with different patterns of social class, shapes, depth range, diel phase, and moon phase. These new insights can be useful to understand the ecology of whales, also, can assist in the mitigation of human activities, which are some of the biggest causes of mortality within cetaceans. Continuous data collection may increase our knowledge of diving behavior in habitats and their environment. Including new variables, for example, chlorophyll, wind, temperature, a distance of shore, temporal variables (years), and individual behavioral variables (surface time and behavioral state) are part of our future goals.

SUPPLEMENTARY MATERIAL

Table S1 - Pairwise differences of dive depth and duration in each habitat.

Pairwise differences of dive depth from habitats

1	estimate	SE	*p*.value
BA - FA	-0.515	0.0149	<.0001
BA - MI	-0.251	0.0132	<.0001
FA - MI	0.264	0.0114	<.0001

Pairwise differences of dive duration from habitats

1	estimate	SE	*p*.value
BA - FA	0.0416	0.0140	0.0081
BA - MI	-0.1889	0.0112	<.0001
FA - MI	-0.2305	0.0101	<.0001

Pairwise differences of dive depth and duration in each habitat. The statistical differences were estimated from a linear mixed effects model accounting for the random effect of whale. BA = Breeding area, MI = Migration, FA = Feeding area.

Table S2 - Pairwise differences of depth range in each habitat.

Pairwise differences of depth range from Breeding area

	estimate	SE	*p*.value
shallow - deep	-1.25	0.0561	<.0001

Pairwise differences of depth range from Migration

	estimate	SE	*p*.value
shallow - deep	-1.47	0.0166	<.0001

Pairwise differences of depth range from Feeding area

	estimate	SE	*p*.value
shallow - deep	-1.01	0.0156	<.0001

Pairwise differences of depth range in each habitat. The statistical differences were estimated from a linear mixed effects model accounting for the random effect of whale. Shallow = < 80 m. Deep = > 80 m.

Table S3 - Pairwise differences of dive depth and duration per social class in each habitat.

Pairwise differences dive depth of social class from Breeding area

	estimate	**SE**	***p*.value**
F - M	0.029	0.061	0.6380

Pairwise differences dive depth of social class from Migration

	estimate	**SE**	***p*.value**
F - M	-0.0736	0.0842	0.3900

Pairwise differences dive depth of social class from Feeding area

	estimate	**SE**	***p*.value**
F - M	0.000772	0.0963	0.9938

Pairwise differences dive duration of social class from Breeding area

	estimate	**SE**	***p*.value**
F - M	-0.0688	0.0874	0.4375

Pairwise differences dive duration of social class from Migration

	estimate	**SE**	***p*.value**
F - M	-0.112	0.118	0.3478

Pairwise differences dive duration of social class from Feeding area

	estimate	**SE**	***p*.value**
F - M	0.194	0.139	0.2051

Pairwise differences of dive depth and duration per social class. The statistical differences were estimated from a linear mixed effects model. Class: F = female with calf, M = male.

Table S4 - Pairwise differences of depth range by social class.

Pairwise differences of sex and depth range			
contrast	**estimate**	**SE**	***p*.value**
F shallow – M shallow	0.03504	0.0503	0.8986
F shallow – F deep	-1,32E+05	0.0152	<.0001
F shallow – M deep	-1,33E+05	0.0526	<.0001
M shallow – F deep	-1,35E+05	0.0525	<.0001
M shallow – M deep	-1,36E+05	0.0159	<.0001
F deep – M deep	-0.00726	0.0518	0.9990

Pairwise differences of depth range by social class. The statistical differences were estimated from a linear mixed effects model. F shallow = Female with calf at shallow dives. F deep = Female with calf at deep dives. M shallow = Male at shallow dives. M deep = Male at deep dives.

Table S5 - Pairwise differences of depth range by social class in each habitat.

Pairwise differences of social class and depth range from Breeding area			
contrast	**estimate**	**SE**	***p*.value**
F shallow - M shallow	0.0231	0.0599	0.9806
F shallow - F deep	-1.2250	0.0538	<.0001
F shallow - M deep	-1.2755	0.1014	<.0001
M shallow - F deep	-1.2481	0.0803	<.0001
M shallow - M deep	-0.0505	0.0822	<.0001
F deep - M deep	-0.0505	0.0947	0.9510

Pairwise differences of social class and depth range from Migration			
contrast	**estimate**	**SE**	***p*.value**
F shallow - M shallow	0.0833	0.0503	0.3478
F shallow - F deep	-1.3468	0.0182	<.0001
F shallow - M deep	-1.5176	0.0534	<.0001
M shallow - F deep	-1.4301	0.0532	<.0001
M shallow - M deep	-1.6009	0.0191	<.0001
F deep - M deep	-0.1708	0.0524	0.0061

Pairwise differences of social class and depth range from Feeding area

contrast	estimate	SE	*p*.value
F shallow - M shallow	-0.0646	0.0611	0.7153
F shallow - F deep	-1.0617	0.0204	<.0001
F shallow - M deep	-1.0177	0.0631	<.0001
M shallow - F deep	-0.9971	0.0640	<.0001
M shallow - M deep	-0.9531	0.0171	<.0001
F deep - M deep	0.0440	0.0639	0.9014

Pairwise differences of depth range by social class in each habitat. The statistical differences were estimated from a linear mixed effects model accounting for the random effect of whale. F shallow = Female with calf at shallow dives. F deep = Female with calf at deep dives. M shallow = Male at shallow dives. M deep = Male at deep dives.

Table S6 - Pairwise differences of dive depth and duration per shape.

Pairwise differences of dive depth from shapes

1	estimate	SE	*p*.value
Square - U	-0.0644	0.00483	<.0001
Square - V	-0.1410	0.00944	<.0001
U - V	-0.0766	0.00930	<.0001

Pairwise differences of dive duration from shapes

	estimate	SE	*p*.value
Square - U	0.587	0.00549	<.0001
Square - V	0.219	0.01031	<.0001
U - V	-0.368	0.01005	<.0001

Pairwise differences of dive depth and duration per shape. The statistical differences were estimated from a linear mixed effects model.

Table S7 - Pairwise differences dive depth by shape in each habitat.

Pairwise differences dive depth of shape from Breeding area

	estimate	SE	*p*.value
Square - U	-0.0235	0.00702	0.0023

Square - V	-0.0444	0.01381	0.0037
U - V	-0.0209	0.01387	0.2880

Pairwise differences dive depth of shape from Migration			
	estimate	**SE**	***p*.value**
Square - U	-0.1669	0.00836	<.0001
Square - V	-0.2317	0.01488	<.0001
U - V	-0.0648	0.01426	<.0001

Pairwise differences dive depth of shape from Feeding area			
	estimate	**SE**	***p*.value**
Square - U	-0.0787	0.00711	<.0001
Square - V	-0.3013	0.01146	<.0001
U - V	-0.2226	0.01067	<.0001

Pairwise differences dive depth by shape in each habitat. The statistical differences were estimated from a linear mixed effects model accounting for the random effect of whale.

Table S8 - Pairwise differences of depth range by shape in each habitat.

Pairwise differences of shape and depth range at Breeding area			
contrast	**estimate**	**SE**	***p*.value**
Square shallow - U shallow	-0.0385	0.00605	<.0001
Square shallow - V shallow	-0.0369	0.01288	0.0480
Square shallow - Square deep	-1.2463	0.05976	<.0001
Square shallow - U deep	-1.2931	0.05444	<.0001
Square shallow - V deep	-1.3732	0.13476	<.0001
U shallow - V shallow	0.0016	0.01292	1.0000
U shallow - Square deep	-1.2078	0.05979	<.0001
U shallow - U deep	-1.2546	0.05442	<.0001
U shallow - V deep	-1.3347	0.13478	<.0001
V shallow - Square deep	-1.2094	0.06090	<.0001
V shallow - U deep	-1.2562	0.05563	<.0001
V shallow - V deep	-1.3363	0.13523	<.0001
Square deep - U deep	-0.0468	0.05215	0.9471
Square deep - V deep	-0.1269	0.13359	0.9333
U deep - V deep	-0.0801	0.12862	0.9894

Pairwise differences of shape and depth range at Migration			
contrast	**estimate**	**SE**	***p*.value**
Square shallow - U shallow	-0.0912	0.00603	<.0001
Square shallow - V shallow	-0.2330	0.01136	<.0001
Square shallow - Square deep	-1.5819	0.01983	<.0001
Square shallow - U deep	-1.6633	0.01499	<.0001
Square shallow - V deep	-1.6633	0.03101	<.0001
U shallow - V shallow	-1.5005	0.01095	<.0001
U shallow - Square deep	-0.1419	0.01968	<.0001
U shallow - U deep	-1.4908	0.01470	<.0001
U shallow - V deep	-1.5721	0.03093	<.0001
V shallow - Square deep	-1.4094	0.02191	<.0001
V shallow - U deep	-1.3489	0.01757	<.0001
V shallow - V deep	-1.4302	0.03219	<.0001
Square deep - U deep	-0.0813	0.01707	<.0001
Square deep - V deep	0.0814	0.03223	0.1166
U deep - V deep	0.1627	0.02960	<.0001

Pairwise differences of shape and depth range at Feeding area			
contrast	**estimate**	**SE**	***p*.value**
Square shallow - U shallow	-0.0159	0.00651	0.1401
Square shallow - V shallow	-0.2589	0.01013	<.0001
Square shallow - Square deep	-1.0825	0.01945	<.0001
Square shallow - U deep	-1.1581	0.01682	<.0001
Square shallow - V deep	-1.0564	0.02418	<.0001
U shallow - V shallow	-0.2430	0.00944	<.0001
U shallow - Square deep	-1.0665	0.01940	<.0001
U shallow - U deep	-1.1422	0.01664	<.0001
U shallow - V deep	-1.0405	0.02410	<.0001
V shallow - Square deep	-0.8235	0.02080	<.0001
V shallow - U deep	-0.8992	0.01820	<.0001
V shallow - V deep	-0.7975	0.02513	<.0001
Square deep - U deep	-0.0757	0.01742	0.0002
Square deep - V deep	0.0260	0.02499	0.9042
U deep - V deep	0.1017	0.02286	0.0001

Pairwise differences of depth range by shape in each habitat. The statistical differences were estimated from a linear mixed effects model accounting for the random effect of whale.

Table S9 - Pairwise differences dive depth by diel phase in each habitat.

Pairwise differences dive depth of dial phase at Breeding area			
	estimate	**SE**	***p*.value**
dawn - day	-0.00384	0.0172	0.9960

dawn - dusk	0.04658	0.0230	0.1780
dawn - night	0.02951	0.0176	0.3371
day - dusk	0.05042	0.0179	0.0254
day - night	0.03335	0.0128	0.0451
dusk - night	-0.01707	0.0183	0.7871

Pairwise differences dive depth of dial phase at Migration			
	estimate	**SE**	***p*.value**
dawn - day	-0.00419	0.0205	0.9970
dawn - dusk	0.16092	0.0284	<.0001
dawn - night	0.15889	0.0213	<.0001
day - dusk	0.16511	0.0226	<.0001
day - night	0.16308	0.0162	<.0001
dusk - night	-0.00203	0.0232	0.9998

Pairwise differences dive depth of dial phase at Feeding area			
	estimate	**SE**	***p*.value**
dawn - day	-0.15873	0.0280	<.0001
dawn - dusk	-0.15734	0.0346	<.0001
dawn - night	0.02371	0.0279	0.8305
day - dusk	0.00139	0.0258	0.9999
day - night	0.18244	0.0213	<.0001
dusk - night	0.18105	0.0258	<.0001

Pairwise differences dive depth by diel phase in each habitat. The statistical differences were estimated from a linear mixed effects model accounting for the random effect of whale.

Table S10 - Pairwise differences dive duration by diel phase in each habitat.

Pairwise differences dive duration of dial phase at Breeding area			
	estimate	**SE**	***p*.value**
dawn - day	-0.0568	0.0259	0.1259
dawn - dusk	-0.1379	0.0347	0.0004
dawn - night	-0.1822	0.0267	<.0001
day - dusk	-0.0811	0.0271	0.0146
day - night	-0.1254	0.0196	<.0001
dusk - night	-0.0443	0.0277	0.3793

Pairwise differences dive duration of dial phase at Migration			
	estimate	**SE**	***p*.value**
dawn - day	0.00599	0.0231	0.9939
dawn - dusk	-0.02616	0.0317	0.8424
dawn - night	-0.05005	0.0240	0.1568
day - dusk	-0.03215	0.0253	0.5813
day - night	-0.05604	0.0188	0.0149

dusk - night	-0.02389	0.0259	0.7920

Pairwise differences dive duration of dial phase at Feeding area			
	estimate	**SE**	***p*.value**
dawn - day	-0.1897	0.0279	<.0001
dawn - dusk	0.0275	0.0344	0.8546
dawn - night	0.2324	0.0278	<.0001
day - dusk	0.2172	0.0257	<.0001
day - night	0.4221	0.0221	<.0001
dusk - night	0.2049	0.0258	<.0001

Pairwise differences dive duration by diel phase in each habitat. The statistical differences were estimated from a linear mixed effects model accounting for the random effect of whale.

Table S11 - Pairwise differences of depth range by diel phase in each habitat.

Pairwise differences of diel phase and depth range at Breeding area			
contrast	**estimate**	**SE**	***p*.value**
dawn shallow - day shallow	0.0025	0.0155	1.0000
dawn shallow - dusk shallow	0.0401	0.0208	0.5298
dawn shallow - night shallow	0.0174	0.0159	0.9576
dawn shallow - dawn deep	-1.1928	0.0796	<.0001
dawn shallow - day deep	-1.1722	0.0598	<.0001
dawn shallow - dusk deep	-1.4196	0.1575	<.0001
dawn shallow - night deep	-1.2717	0.0694	<.0001
day shallow - dusk shallow	0.0376	0.0162	0.2799
day shallow - night shallow	0.0149	0.0119	0.9147
day shallow - dawn deep	-1.1953	0.0797	<.0001
day shallow - day deep	-1.1747	0.0581	<.0001
day shallow - dusk deep	-1.4221	0.1570	<.0001
day shallow - night deep	-1.2742	0.0687	<.0001
dusk shallow - night shallow	-0.0227	0.0164	0.8669
dusk shallow - dawn deep	-1.2329	0.0808	<.0001
dusk shallow - day deep	-1.2123	0.0601	<.0001
dusk shallow - dusk deep	-1.4596	0.1568	<.0001
dusk shallow - night deep	-1.3118	0.0696	<.0001
night shallow - dawn deep	-1.2102	0.0797	<.0001
night shallow - day deep	-1.1896	0.0589	<.0001
night shallow - dusk deep	-1.4370	0.1570	<.0001
night shallow - night deep	-1.2891	0.0680	<.0001
dawn deep - day deep	0.0206	0.0708	1.0000
dawn deep - dusk deep	-0.2267	0.1626	0.8602
dawn deep - night deep	-0.0789	0.0791	0.9750
day deep - dusk deep	-0.2474	0.1534	0.7431
day deep -night deep	-0.0995	0.0613	0.7358

dusk deep - night deep	0.1479	0.1577	0.9824

Pairwise differences of diel phase and depth range at Migration			
contrast	**estimate**	**SE**	***p*.value**
dawn shallow - day shallow	-0.00807	0.0152	0.9995
dawn shallow - dusk shallow	0.12601	0.0209	<.0001
dawn shallow - night shallow	0.10225	0.0158	<.0001
dawn shallow - dawn deep	-1.32964	0.0274	<.0001
dawn shallow - day deep	-1.35936	0.0195	<.0001
dawn shallow - dusk deep	-1.57355	0.0461	<.0001
dawn shallow - night deep	-1.41263	0.0242	<.0001
day shallow - dusk shallow	0.13407	0.0165	<.0001
day shallow - night shallow	0.11031	0.0118	<.0001
day shallow - dawn deep	-1.32157	0.0274	<.0001
day shallow - day deep	-1.35130	0.0134	<.0001
day shallow - dusk deep	-1;56549	0.0442	<.0001
day shallow - night deep	-1.40456	0.0217	<.0001
dusk shallow - night shallow	-0.02376	0.0169	0.8563
dusk shallow - dawn deep	-1.45564	0.0309	<.0001
dusk shallow - day deep	-1.48537	0.0206	<.0001
dusk shallow - dusk deep	-1.69956	0.0445	<.0001
dusk shallow - night deep	-1.53864	0.0250	<.0001
night shallow - dawn deep	-1.43189	0.0277	<.0001
night shallow - day deep	-1.46161	0.0170	<.0001
night shallow - dusk deep	-1.67580	0.0444	<.0001
night shallow - night deep	-1.51488	0.0202	<.0001
dawn deep - day deep	-0.02972	0.0267	0.9538
dawn deep - dusk deep	-0.24392	0.0496	<.0001
dawn deep - night deep	-0.08299	0.0300	0.1041
day deep - dusk deep	-0.21419	0.0441	<.0001
day deep - night deep	-0.05327	0.0213	0.1928
dusk deep - night deep	0.16092	0.0461	0.0113

Pairwise differences of diel phase and depth range at Feeding area			
contrast	**estimate**	**SE**	***p*.value**
dawn shallow - day shallow	-0.0992	0.0238	0.0008
dawn shallow - dusk shallow	-0.2176	0.0293	<.0001
dawn shallow - night shallow	-0.0421	0.0237	0.6367
dawn shallow - dawn deep	-1.0815	0.0383	<.0001
dawn shallow - day deep	-1.2469	0.0270	<.0001
dawn shallow - dusk deep	-1.1077	0.0443	<.0001
dawn shallow - night deep	-0.9523	0.0284	<.0001

day shallow - dusk shallow	-0.1185	0.0215	<.0001
day shallow - night shallow	0.0571	0.0172	0.0199
day shallow - dawn deep	-0.9824	0.0390	<.0001
day shallow - day deep	-1.1477	0.0152	<.0001
day shallow - dusk deep	-1.0085	0.0394	<.0001
day shallow - night deep	-0.8532	0.0235	<.0001
dusk shallow - night shallow	0.1755	0.0213	<.0001
dusk shallow - dawn deep	-0.8639	0.0424	<.0001
dusk shallow - day deep	-1.0293	0.0248	<.0001
dusk shallow - dusk deep	-0.8901	0.0379	<.0001
dusk shallow - night deep	-0.7347	0.0269	<.0001
night shallow - dawn deep	-1.0394	0.0388	<.0001
night shallow - day deep	-1.2048	0.0212	<.0001
night shallow - dusk deep	-1.0656	0.0397	<.0001
night shallow - night deep	-0.9102	0.0178	<.0001
dawn deep - day deep	-0.1654	0.0399	0.0009
dawn deep - dusk deep	-0.0262	0.0533	0.9997
dawn deep - night deep	0.1292	0.0408	0.0335
day deep - dusk deep	0.1392	0.0402	0.0125
day deep - night deep	0.2946	0.0256	<.0001
dusk deep - night deep	0.1554	0.0421	0.0055

Pairwise differences of depth range by diel phase in each habitat. The statistical differences were estimated from a linear mixed effects model accounting for the random effect of whale.

Table S12 - Pairwise differences dive depth by moon phase in each habitat.

Pairwise differences dive depth of moon phase at Breeding area			
	estimate	**SE**	***p*.value**
firstquarter - fullmoon	0.1577	0.0431	0.0015
firstquarter - lastquarter	0.0139	0.0418	0.9872
firstquarter - newmoon	-0.0223	0.0399	0.9442
fullmoon - lastquarter	-0.1437	0.0398	0.0017
fullmoon - newmoon	-0.1800	0.0392	<.0001
lastquarter - newmoon	-0.0362	0.0347	0.7239

Pairwise differences dive depth of moon phase at Migration			
	estimate	**SE**	***p*.value**
firstquarter - fullmoon	-0.0722	0.0509	0.4877
firstquarter - lastquarter	-0.0532	0.0505	0.7179
firstquarter - newmoon	-0.0161	0.0501	0.9886
fullmoon - lastquarter	0.0191	0.0486	0.9795
fullmoon - newmoon	0.0562	0.0495	0.6683
lastquarter - newmoon	0.0371	0.0473	0.8611

Pairwise differences dive depth of moon phase at Feeding area			
	estimate	**SE**	***p*.value**
firstquarter - fullmoon	0.01766	0.0497	0.9846
firstquarter - lastquarter	0.00482	0.0489	0.9997
firstquarter - newmoon	0.03103	0.0512	0.9303
fullmoon - lastquarter	-0.01285	0.0515	0.9946
fullmoon - newmoon	0.01337	0.0552	0.9950
lastquarter - newmoon	0.02621	0.0527	0.9597

Pairwise differences dive depth by moon phase in each habitat. The statistical differences were estimated from a linear mixed effects model accounting for the random effect of whale.

Table S13 - Pairwise differences dive duration by moon phase in each habitat.

Pairwise differences dive duration of moon phases at Breeding area			
	estimate	**SE**	***p*.value**
firstquarter - fullmoon	0.1427	0.0588	0.0718
firstquarter - lastquarter	0.0971	0.0570	0.3215
firstquarter - newmoon	0.0622	0.0545	0.6635
fullmoon - lastquarter	-0.0456	0.0544	0.8363
fullmoon - newmoon	-0.0805	0.0537	0.4384
lastquarter - newmoon	-0.0349	0.0472	0.8816

Pairwise differences dive duration of moon phases at Migration			
	estimate	**SE**	***p*.value**
firstquarter - fullmoon	-0.1015	0.0654	0.4065
firstquarter - lastquarter	-0.0346	0.0651	0.9514
firstquarter - newmoon	-0.0173	0.0648	0.9933
fullmoon - lastquarter	0.0669	0.0624	0.7067
fullmoon - newmoon	0.0842	0.0640	0.5528
lastquarter - newmoon	0.0173	0.0610	0.9921

Pairwise differences dive duration of moon phases at Feeding area			
	estimate	**SE**	***p*.value**
firstquarter - fullmoon	0.1696	0.0591	0.0214
firstquarter - lastquarter	0.0718	0.0585	0.6092
firstquarter - newmoon	0.1354	0.0607	0.1145
fullmoon - lastquarter	-0.0979	0.0611	0.3780
fullmoon - newmoon	-0.0342	0.0656	0.9539
lastquarter - newmoon	0.0637	0.0623	0.7363

Pairwise differences dive duration by moon phase in each habitat. The statistical differences were estimated from a linear mixed effects model accounting for the random effect of whale.

Table S14 - Pairwise differences of depth range by moon phase in each habitat.

Pairwise differences of moon phase and depth range at Breeding area

contrast	estimate	SE	*p*.value
firstquarter shallow - fullmoon shallow	0.1641	0.0407	0.0014
firstquarter shallow - lastquarter shallow	0.0324	0.0391	0.9915
firstquarter shallow - newmoon shallow	-0.0215	0.0373	0.9991
firstquarter shallow - firstquarter deep	-1.2922	0.0598	<.0001
firstquarter shallow - fullmoon deep	-1.2091	0.0994	<.0001
firstquarter shallow - lastquarter deep	-1.0853	0.0852	<.0001
firstquarter shallow - newmoon deep	-1.2248	0.1164	<.0001
fullmoon shallow - lastquarter shallow	-0.1317	0.0370	0.0090
fullmoon shallow - newmoon shallow	-0.1857	0.0383	<.0001
fullmoon shallow - firstquarter deep	-1.4563	0.0711	<.0001
fullmoon shallow - fullmoon deep	-1.3733	0.0919	<.0001
fullmoon shallow - lastquarter deep	-1.2495	0.0841	<.0001
fullmoon shallow - newmoon deep	-1.3889	0.1167	<.0001
lastquarter shallow - newmoon shallow	-0.0540	0.0328	0.7215
lastquarter shallow - first quarter deep	-1.3247	0.0700	<.0001
lastquarter shallow - fullmoon deep	-1.2416	0.0981	<.0001
lastquarter shallow - lastquarter deep	-1.1178	0.0771	<.0001
lastquarter shallow - newmoon deep	-1.2573	0.1150	<.0001
newmoon shallow - firstquarter deep	-1.2707	0.0689	<.0001
newmoon shallow - fullmoon deep	-1.1876	0.0985	<.0001
newmoon shallow - lastquarter deep	-1.0638	0.0826	<.0001
newmoon shallow - newmoon deep	-1.2033	0.1106	<.0001
firstquarter deep - fullmoon deep	0.0831	0.1152	0.9964
firstquarter deep - lastquarter deep	0.2069	0.1031	0.4772
firstquarter deep - newmoon deep	0.0674	0.1300	0.9996
fullmoon deep - lastquarter deep	0.1238	0.1238	0.9745
fullmoon deep - newmoon deep	-0.0157	0.1478	1.0000
lastquarter deep - newmoon deep	-0.1395	0.1377	0.9727

Pairwise differences of moon phase and depth range at Migration			
contrast	**estimate**	**SE**	***p*.value**
firstquarter shallow - fullmoon shallow	0.0313	0.0332	0.9818
firstquarter shallow - lastquarter shallow	-0.0230	0.0327	0.9970
firstquarter shallow - newmoon shallow	-0.0442	0.0320	0.8654
firstquarter shallow - firstquarter deep	-1.5032	0.0294	<.0001
firstquarter shallow - fullmoon deep	-1.5801	0.0420	<.0001
firstquarter shallow - lastquarter deep	-1.6140	0.0389	<.0001
firstquarter shallow - newmoon deep	-1.4973	0.0421	<.0001
fullmoon shallow - lastquarter shallow	-0.0543	0.0318	0.6832
fullmoon shallow - newmoon shallow	-0.0755	0.0320	0.2597
fullmoon shallow - firstquarter deep	-1.5345	0.0422	<.0001

fullmoon shallow - fullmoon deep	-1.6114	0.0293	<.0001
fullmoon shallow - lastquarter deep	-1.6453	0.0381	<.0001
fullmoon shallow - newmoon deep	-1.5286	0.0420	<.0001
lastquarter shallow - newmoon shallow	-0.0212	0.0303	0.9970
lastquarter shallow - first quarter deep	-1.4802	0.0417	<.0001
lastquarter shallow - fullmoon deep	-1.5571	0.0408	<.0001
lastquarter shallow - lastquarter deep	-1.5910	0.0245	<.0001
lastquarter shallow - newmoon deep	-1.4743	0.0407	<.0001
newmoon shallow - firstquarter deep	-1.4590	0.0412	<.0001
newmoon shallow - fullmoon deep	-1.5359	0.0410	<.0001
newmoon shallow - lastquarter deep	-1.5698	0.0369	<.0001
newmoon shallow - newmoon deep	-1.4531	0.0300	<.0001
firstquarter deep - fullmoon deep	-0.0769	0.0494	0.7768
firstquarter deep - lastquarter deep	-0.1108	0.0467	0.2546
firstquarter deep - newmoon deep	0.0059	0.0494	1.0000
fullmoon deep - lastquarter deep	-0.0339	0.0459	0.9958
fullmoon deep - newmoon deep	0.0828	0.0493	0.7003
lastquarter deep - newmoon deep	0.1167	0.0458	0.1754

Pairwise differences of moon phase and depth range at Feeding area			
contrast	**estimate**	**SE**	***p*.value**
firstquarter shallow - fullmoon shallow	-0.044601	0.0376	0.9365
firstquarter shallow - lastquarter shallow	-0.020732	0.0372	0.9993
firstquarter shallow - newmoon shallow	0.000693	0.0386	1.0000
firstquarter shallow - firstquarter deep	-0.971463	0.0276	<.0001
firstquarter shallow - fullmoon deep	-0.982415	0.0461	<.0001
firstquarter shallow - lastquarter deep	-0.972147	0.0437	<.0001
firstquarter shallow - newmoon deep	-1.024272	0.0471	<.0001
fullmoon shallow - lastquarter shallow	0.023868	0.0380	0.9985
fullmoon shallow - newmoon shallow	0.045293	0.0410	0.9559
fullmoon shallow - firstquarter deep	-0.926862	0.0451	<.0001
fullmoon shallow - fullmoon deep	-0.937814	0.0292	<.0001
fullmoon shallow - lastquarter deep	-0.927546	0.0443	<.0001
fullmoon shallow - newmoon deep	-0.979671	0.0491	<.0001
lastquarter shallow - newmoon shallow	0.021425	0.0387	0.9993
lastquarter shallow - first quarter deep	-0.950730	0.0448	<.0001
lastquarter shallow - fullmoon deep	-0.961683	0.0464	<.0001
lastquarter shallow - lastquarter deep	-0.951414	0.0256	<.0001
lastquarter shallow - newmoon deep	-1.003540	0.0469	<.0001
newmoon shallow - firstquarter deep	-0.972155	0.0459	<.0001
newmoon shallow - fullmoon deep	-0.983108	0.0489	<.0001
newmoon shallow - lastquarter deep	-0.972840	0.0448	<.0001

newmoon shallow - newmoon deep	-1.024965	0.0303	<.0001
firstquarter deep - fullmoon deep	-0.010953	0.0524	1.0000
firstquarter deep - lastquarter deep	-0.000684	0.0503	1.0000
firstquarter deep - newmoon deep	-0.052809	0.0533	0.9758
fullmoon deep - lastquarter deep	0.010268	0.0517	1.0000
fullmoon deep - newmoon deep	-0.041857	0.0558	0.9954
lastquarter deep - newmoon deep	-0.052125	0.0521	0.9744

Pairwise differences of depth range by moon phase in each habitat. The statistical differences were estimated from a linear mixed effects model accounting for the random effect of whale.

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