Title

Where the Whales Go:The Migration Routes of Humpbacks in the South West Atlantic

Author
Thouless, Clare

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Clare Thouless
Masters of Advanced Studies Candidate – Marine Biodiversity and Conservation
Scripps Institution of Oceanography

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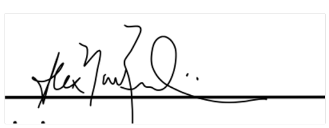
Signature: 
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Heidi Batchelor

Abstract

The migration patterns of humpback whales in the southwestern Atlantic have not been studied in detail. Humpback whales that winter off the coast of Brazil migrate south to offshore waters around South Georgia and the South Sandwich Islands. This project uses data collected from satellite tags attached to humpback whales off the coast of Brazil between 2003 and 2019 to establish what paths they take and whether they use oceanic features, in particular seamounts, during their migrations. The results show that this population of humpbacks leave the Brazilian coast using two different paths, cross over multiple seamounts, including the Rio Grande Rise, and most of them use a direct path to their feeding grounds. The results indicate that humpback whales may use seamounts during their migration, although further research is required to understand their potential use of seamounts during their migration.

Key words: Humpback whales, Seamounts, Migration Routes, Satellite Tracking

Introduction

Humpback whales (*Megaptera novaeangliae*)

Humpback whales are a pan-global species of baleen whales. They are found in all major oceans (IWC, 2021a). Due to their behavior near the surface, which includes breaching and tail slapping, and their preference for continental shelfs, they are the focus for many whale watching operations and one of the most commonly observed whales (IWC, 2021b). Humpbacks produce complex vocalisations, which may be the most widely heard and recognised noise from a marine animal. They are the sixth largest whale species.

The population of humpback whales in this study winter off the coast of Brazil and migrate to Antarctic waters during the summer months to feed. There is limited interchange with other populations and for management purposes they are considered a distinct population.

Feeding

Humpbacks feed on krill and small fish by straining huge quantities of water through their baleen plates. In the Southern Hemisphere they feed primarily on krill (*Euphausia superba*) (Kawamura 1994) and can consume up to 2,000 pounds of food a day during the summer months (NOAA, 2021). They generally engage in very limited feeding during their migrating and breeding seasons, and therefore must build up fat reserves during the summer months.

Humpbacks sometimes engage in coordinated feeding when the fish that they feed on are found in high abundances (Valsecchi et al. 2002). Coordinated feeding includes the use of bubble nets (Wiley et al. 2011) and vertical lunge feeding (D'Vincent et al. 1985). Bubble netting is an elaborate and complex behavior, whereby multiple animals work together to release a stream of bubbles around a shoal of fish, trapping them in an area for feeding (Wiley et al. 2011). This behavior appears to be performed by an opportunistic grouping of individuals, rather than through kin groups (Valasecchi et al. 2002). Humpbacks are largely solitary, although mothers remain with their calves for the first year of their life (Valasecchi et al. 2002). Beyond the first year, humpbacks do not seem to remain with related individuals, even when engaging in cooperative feeding (Valasecchi et al. 2002). This behavior is therefore likely a form of reciprocal altruism (Valasecchi et al. 2002).

Breeding and migrations

Humpbacks undertake long annual migrations. They breed in tropical and sub-tropical waters during the winter months, before migrating to higher latitudes to feed during the summer.

Female humpbacks produce one calf during the breeding season. Their gestation period is typically 12 months and calves are about 14 ft when they are born (Chittleborough 1958). The mother lactates for over 11 months (Chittleborough 1958), during which time the calf remains with her. They tend to produce one calf every two or more years, but some individuals produce two calves in two years (Chittleborough 1958). Humpbacks in the Southern Hemisphere reach sexual maturity between ages 10 to 12 (Best 2020).

Male humpbacks produce long complex songs during the breeding season. Their songs may last for half an hour and are made up of repeated, complicated phrases (Payne & McVay 1971). These songs are believed to be for the purpose of attracting a mate and perhaps to intimidate other males in the area (Tyack 1981). All humpbacks within the same population sing the same song and different populations exhibit different dialects (Winn et al. 2008). A population's song may change over time and can evolve to incorporate the songs of immigrant whales (Noad et al. 2009). Mothers and calves also produce non-song vocalisations to remain in contact with one another and possibly modify these vocalisations in response to a perceived threat (Zoidis et al. 2008).

In the Southern Hemisphere, humpbacks tend not to feed during their breeding season in the austral winter/spring (Chittleborough 1965). After breeding, mating and calving in warmer waters during the winter, humpbacks undertake long migrations to richer feeding grounds at higher latitudes, where their prey species are found in high abundance. Humpback whales have the one of the longest migrations of any mammal (Robbins et al. 2011). Every population migrates annually between their low-latitude breeding grounds in tropical or semi-tropical waters, to rich, high-latitude feeding grounds in higher latitudes during the summer months (IWC, 2021a), except for the Arabian Sea population, which remains in the same area year round (Minton et al. 2008) and may migrate longitudinally within their range (e.g., Wilson et al. 2018).

Threats and conservation status

Humpback whales are globally classified as Least Concern and their populations are increasing (Cooke 2018). They have been listed in Appendix I by CITES since 1975 (Cooke 2018).

Commercial take and subsistence hunting

Humpback whales were heavily overexploited by the whaling industry until the moratorium on commercial whaling in 1985. An estimated 20,000 humpbacks were caught by whaling operations during the 20th century in the Southern Hemisphere (Allison 2017). About 2,000 were taken off the coast of Brazil, but far more were taken in Antarctic and sub-Antarctic waters (Cooke 2018), where humpbacks from Brazil migrate in the summer. Several thousand were also taken off the coast of Brazil in the 19th century (de Morais et al. 2017), but this population is estimated to be near their pre-exploitation size currently (Zerbini et al. 2019). The population of humpback whales that winter off the coast of Brazil has increased to 25,000 individuals in 2019 (Zerbini et al. 2019).

The estimated population size of humpbacks in the Southern Hemisphere was 97,000 individuals in 2015 (Cooke 2018). While this is an increase from 60,000 in 1942, and the particular population considered in this study are thought to have fully recovered, it is still below the pre-whaling estimated population of 138,000 (Cooke 2018).

The commercial take of all large whales, including humpbacks, was banned by the International Whaling Commission in 1982 for all signatories (IWC, para 10(e)). Iceland, Norway and Japan still engage in commercial whaling, although only within their territorial waters (IWC, 2021) and some countries engage in 'scientific whaling'. Subsistence hunting of some whale species is allowed under the Convention for Regulation of Whaling of the IWC, but does not occur in Brazil (IWC, 2021 (b)).

Fishing

Humpbacks are known to become entangled in fishing gear (Ryan et al. 2016, Johnson et al. 2005). Scar-based studies have been conducted to assess humpback whale entanglement in fishing gear and have found evidence of entanglement in all populations studied (Fleming & Jackson 2011). Humpbacks are most frequently caught in pots lines and gillnets (Johnson et al. 2005). Entanglements may only result in minor injuries, but may also have more serious consequences. In Scotland, three of twelve reported entanglements of humpbacks resulted in a fatality (Ryan et al. 2016). On the eastern seaboard of the USA humpbacks are the most common species observed in fishing gear entanglements (Glass et al. 2009). Entanglement may also have long term reproductive effects; one study found that females with entanglement injuries had fewer calves than those without injuries from fishing gear (Robbins & Mattila 2001).

Ship Strikes

Humpbacks are also vulnerable to ship strikes, particularly as they spend a significant amount of time in coastal waters (Cooke 2018). They are the second most commonly reported species involved in ship strikes (Fleming & Jackson 2011). Member states are encouraged to report ship strikes to the IWC, but very few of them do so and therefore the total numbers of injuries and fatalities are unknown (Cooke 2018). Ship strikes may cause blunt trauma and deep wounds due to propellors and can either cause injuries, death or strandings (Fleming & Jackson 2011). Mitigation measures include speed reductions and shifting of major shipping routes in areas of high whale densities (IMO 2007).

Anthropogenic Noise

Although the exact effects of anthropogenic noise on humpback whales is unknown, it is likely to be causing some physical or behavioral impact (Fleming & Jackson 2011). There is evidence that anthropogenic noise is associated with a change in feeding calls in humpback whales in Alaska

(Doyle et al. 2008). Additionally, increased noise from ships directly impacts feeding activity; bottom feeding humpbacks had a lower descent rate and fewer side-roll feeding events in the presence of ship engines (Blair et al. 2016). There is also evidence that male humpback whales lengthened their songs while low-frequency active (LFA) sonar was ongoing (Miller et al. 2000) and the length remained altered for up to two hours after the LSA sonar ceased (Fristrup et al. 2003). Whales may avoid or move out of areas with high levels of noise (Weilgart 2007). The long-term impacts of increased anthropogenic noise on humpbacks are not fully understood (Fleming & Jackson 2011), but may include damage during early development (Weilgart 2007) and unknown negative cumulative effects (Fleming & Jackson 2011).

Pollution

Humpback whales can accumulate pollutants in their fatty blubber, such as lipophilic compounds and pesticides through inhaling polluted air or through bioaccumulation (Fleming & Jackson 2011). Pollutant contamination may be a factor in lower reproductive rates for female humpback whales in southern California (Krahn et al. 2004), where large amounts of DDT were dumped in the last century (Kivenson et al. 2019). However, the impacts of contamination on humpback whales, including that from petroleum and wastewater, are not understood yet (Fleming & Jackson 2011).

<u>South Western Atlantic Humpbacks Whales</u>

The southwestern Atlantic humpback whale population (also known as breeding stock "A" by the IWC (IWC, 2011) winters off the coast of Brazil. The population was estimated to be made up of 6,406 individuals in 2005 and the population was increasing in 2010 (Andriolo et al. 2010) and is believed to be nearly their pre-exploitation numbers (Zerbini et al., 2019). Humpbacks occur along much of the Brazilian coast and their main breeding habitat ranges from as far north as Natal (5° South) (Zerbini et al. 2004) (Fig. 1) and as far south as Arraial do Cabo area (23° South) (Andriolo et al. 2010) (Fig. 1). This population breeds mainly around the Abrolhos Bank (Fig. 1), but they may also breed further north (Zerbini et al. 2004). The abundance of humpbacks around the Abrolhos Banks begins to increase in

Figure 1: Map of humpback whale wintering ground.

early July and peaks in September (Morete et al. 2003). It is during this time that calves are born and mating occurs. By late November most of the whales have started their migration south (Morete et al. 2003).

Throughout the 20th century it was unclear where the exact feeding grounds for the humpback whales that wintered in Brazil were located (Stevick et al. 2004). IWC defined six different management areas for baleen whales in Antarctic waters (IWC 1998). It was suggested that humpbacks from Brazil migrated to Area II, near South Georgia or the Antarctic Peninsula area (Stevick et al. 2004). However, a study of individually identified humpbacks in the Antarctic Peninsular did not support the latter theory (Stevick et al. 2004). Satellite telemetry studies demonstrated that these humpbacks migrated to offshore feeding areas around South Georgia and the South Sandwich Islands (Zerbini et al. 2006; 2011, Horton et al. 2020).

Although the feeding grounds for the population of humpbacks that winters in Brazil have been identified, little is known about the paths they take and features they use during their migrations.

Seamounts

Seamounts are submarine mountains rising over 1000m from the seafloor, although the term is used interchangeably to describe any undersea feature rising over 100m from the seabed (Yesson et al. 2011). Seamounts create upwellings bring an increase in local productivity to seamounts, making them important areas for both primary and secondary productivity in open ocean. The upwelling transport nutrients to surface waters as currents are forced upwards by the bathymetry of the seamounts (Pitcher et al. 2007). This nutrient rich water leads to an increase in plankton and smaller fish that feed on plankton (Boehlert & Genin 1987)

Seamounts are important foraging areas and migration stops for larger pelagic marine species. The abundance of prey around seamounts draws in many larger predatory species, such as tuna (Holland & Grubbs 2007) and beaked whales (Johnstone et al. 2008).

In the early 2000s, there was little evidence that large marine mammals, such as humpback whales, visited seamounts for foraging or during their migrations (Pitcher et al. 2007). However, in recent years numerous studies have found that humpbacks do spend time at seamounts (Garrigue et al. 2015, Derville et al. 2020, Derville et al. 2018, Dulau 2017).

Although it has been shown that other populations of humpback whales deviate towards and use areas around seamounts for some period, this has not been studied for the population of humpback whales that breeds in Brazil. It is currently unknown what features they use during their migrations and whether seamounts are important navigation markers or stop off points.

This project will begin to look at the routes that this population of humpback whales take during their migration into Antarctic waters and whether they deviate towards seamounts or spend more time around them during their migrations.

Understanding the movement patterns of animals allows for effective management and conservation strategies to be implemented. If humpbacks are using seamounts during their migration then shifting shipping routes to avoid them will reduce anthropogenic noise and potentially minimize the risk of ship strikes. Creating no fishing zones will reduce the number of humpbacks that become entangled in fishing gear. The Brazilian government is currently attempting to expand their continental waters to allow them to carry out mining on the Rio Grande Rise. Assessing whether the Rise is an important feature for these humpbacks will help to develop an understanding of how mining this area may impact them. Mining will not only increase noise pollution, driving whales away from this area, but may also increase sediment suspension, leading to difficultly in navigation and an accumulation of suspended particles and pollutants.

Methods

The data for this study were collected using satellite telemetry PPT tags implanted into the whales. All whales were tagged off the coast of Brazil from a ridged hull inflatable boat (Zerbini et al. 2006, Horton et al. 2020). From 2003 until 2008 tags were implanted into the whale using an extended fibreglass pole. After 2008 they were implanted using a modified pneumatic line-thrower. Tags were implanted close to the dorsal fin. Biopsies were carried out to determine the sex of the whale. The size was an indication of age classes and the presence of a calf was also included in the data.

Telemetry data was downloaded from Argos and Wildlife Computers portals. A total of 168 whales were tagged throughout the whole study. Data from 2003 to 2012 was collected using PTT SPOT tags with location classes of error of 3, 2, 1, 0, A, B, Z, with 3 being the highest accuracy and Z the lowest. The second data set used the Argos SPLASH10 tags and had the same error classification, as well as error radius, semi-major and minor error axis and ellipse orientation error. The tags use the Doppler shift and put out VHS signals. To combine the two data sets, the average of these four types of errors was calculated for each classification (3, 2, 1, 0, A, B, Z) for the SPLASH data and the averages for each classification were assigned to the SPOT data. The individual whales were identified using the tag number and the year that the whale was tagged (e.g. 87765.09). The datasets were then combined in R, along with the metadata, which included information about the tagging location and sex of the whale.

Plots were created in the open-source software R using the package *ggplot2* to assess whether error radius, error axis and ellipse orientation error increased with increasing latitude. The graphs showed that error did not increase with latitude and therefore only locations classified as "Z" were removed.

The data were filtered in R so that only the locations above 19.5° south were included in the dataset, as this study focused on the migratory behavior of humpback whales. This was the latitude at which the whales left the breeding grounds and began to migrate south. Whales with fewer than 50 locations recorded north of 19.5° south were removed from further analysis as their tags stopped transmitting before the individual initiated their migration towards higher latitudes. Once the date format was changed to UTC, the data was then filtered by speed. Speeds above 18km/h (Derville et al. 2019) were filtered out on R using the package *ArgosFilter,* because these speeds were biologically implausible and therefore likely to be a position error.

The completed data set was then inputted into Arc GIS. Locations on land, while the tag was being tested before deployment, were identified and then removed on Arc GIS. All the data were projected in Robinson's world projection, which gives a fairly accurate representation of the poles, but looks less distorted than more accurate representations of the poles. After all the whale tracks were imported in Arc and displayed, 14 tracks were found to be from whales that had not left the Brazilian coastline by the time the tags stopped transmitting, so these tracks were removed from the study. A total of 47 whales were included in the final analysis.

A grid of 2,500 squares was created over the study area, with a length and height of around 48km each. The count of points for each whale in each grid cell was calculated in Arc and displayed along a colour gradient. The count of points for all the whales combined was also calculated using the same fishnet grid. A straight line was drawn from the furthest northern point or the point at which the whale left the coastline and the furthest southern point or the point at which it reached its feeding grounds. This was determined to be the point at which the whale stopped heading in mostly one direction and began a more meandering track.

A shapefile of world seamounts was downloaded from the data publishing website Pangea (Yesson et al. 2020). The authors of the file used algorithms to predict the locations of global seamounts based on global bathymetry SRTM v.11. A chi-squared test was carried to test whether sex influenced the route whales took.

Results

Tagging

After the data were filtered for high errors, latitude, speed and number of locations, a total of 61 tracks were added to Arc. Of these whales, fourteen did not have migration data and so 47 whales were left in the final analysis, 25 female, 15 males and the sex of 7 individuals was not identified (Fig. 2). Only one female whale was not accompanied by a calf, while none of the unidentified whales were accompanied by a calf. The number of locations per whale was between 55 and 2,438. The majority of locations had an accuracy of "B" (59.0%), followed by "A" (17.9%). All the whales included in the analysis were tagged between 2003 and 2019. The tagging occurred between early September and late November. The whales in the study were tracked for between 1 and 9 months.

	Female	Male	Unidentified
Accompanied by a calf	24	0	0
Not accompanied by a calf	1	15	7

Figure 2: Sex of the whales and presence of calves.

<u>Starting Routes</u>

The whales left the coastline using two different routes, one coastal and the other offshore Thirty three of the whales used the offshore route (Fig.3). They followed the Besnard Bank opposite a town called Linhares and then turned south. A total of 81.8% of whales that used this route travelled directly over the Vitória-Trindade range. Fourteen whales travelled along the coast until they reached a point east of Rio de Janeiro, at which point they headed southeast, which is the coastal route (Fig. 3). The Vitória seamount is further north than where whales using this route start their migration and none using this route travel over it. The sex of the whale did not significantly impact which route the whale took ($X^2 = 0.98$, df = 2, $p<0.05$).

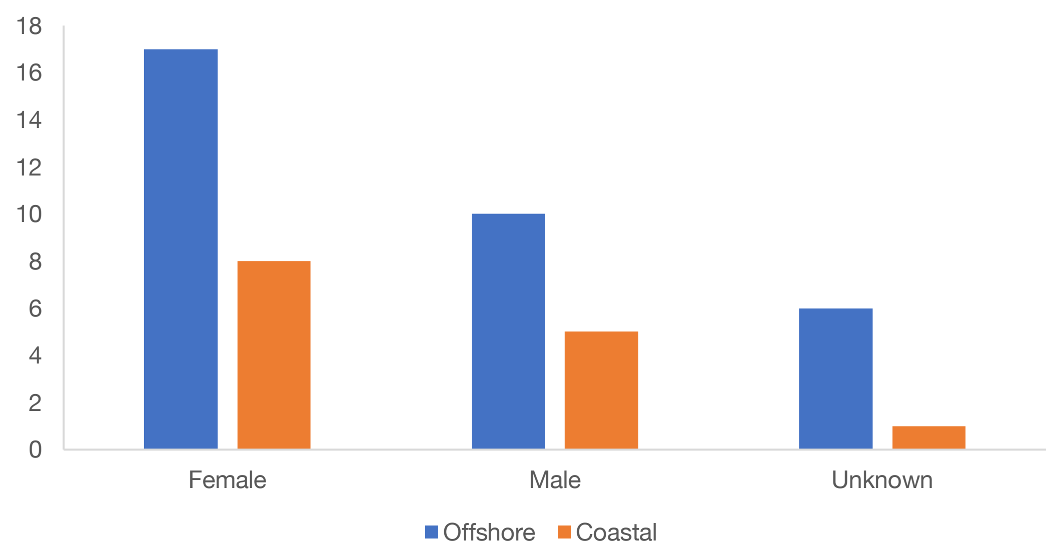

Figure 3: Number of whales migrating along different routes based

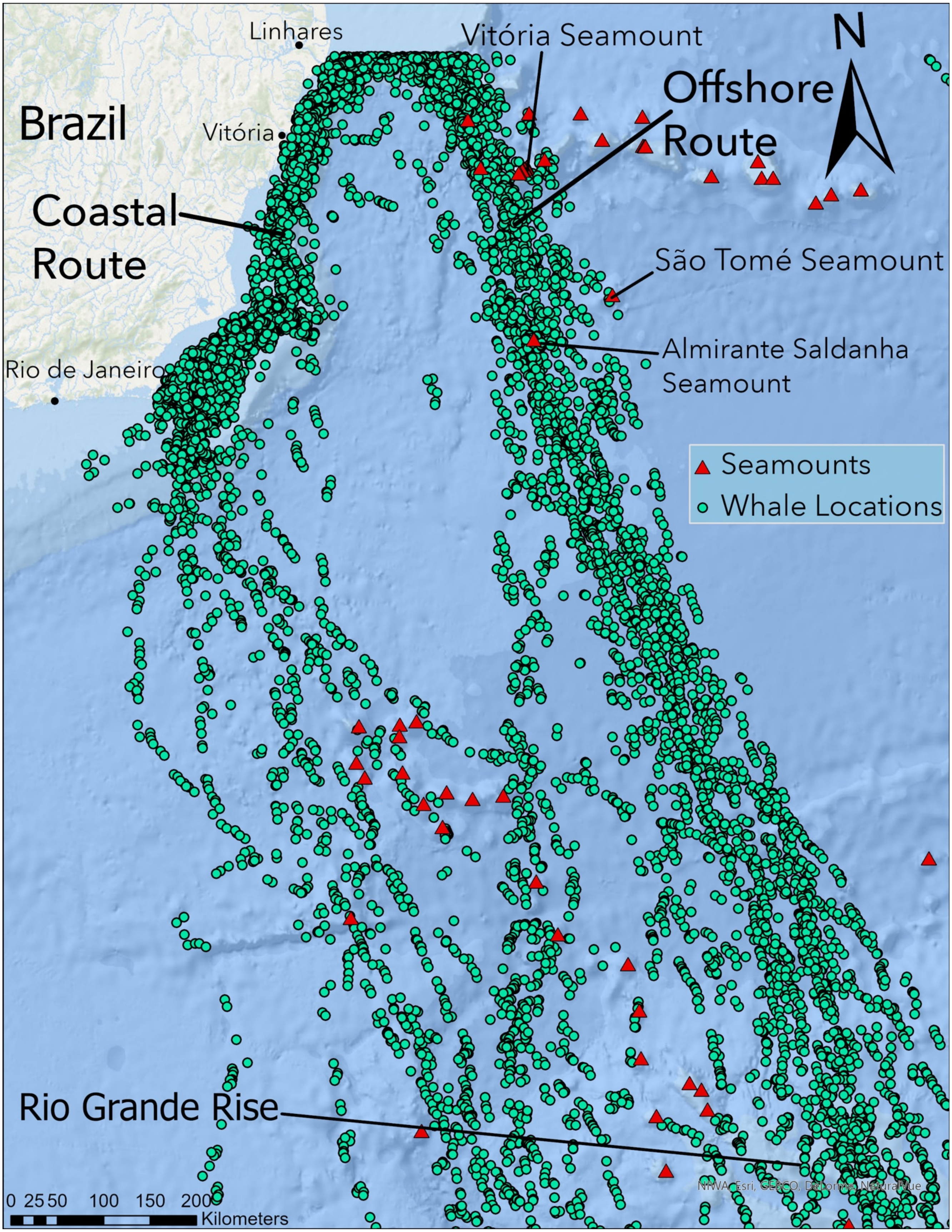

Figure 4: Satellite locations for all whales included in the study showing the initial part of their migration. Map shows the offshore and coastal routes.

The Rio Grande Rise

Twenty three of the whales (48.9%) travel directly over the Rio Grande Rise. A total of 41 whales (80.9%) travel within 150km of the rise. There was a slightly higher number of location points per grid cell around the Rio Grande Rise (Fig. 5). Many whales using the coastal route cross over the seamount ridge north of the Rio Grande Rise.

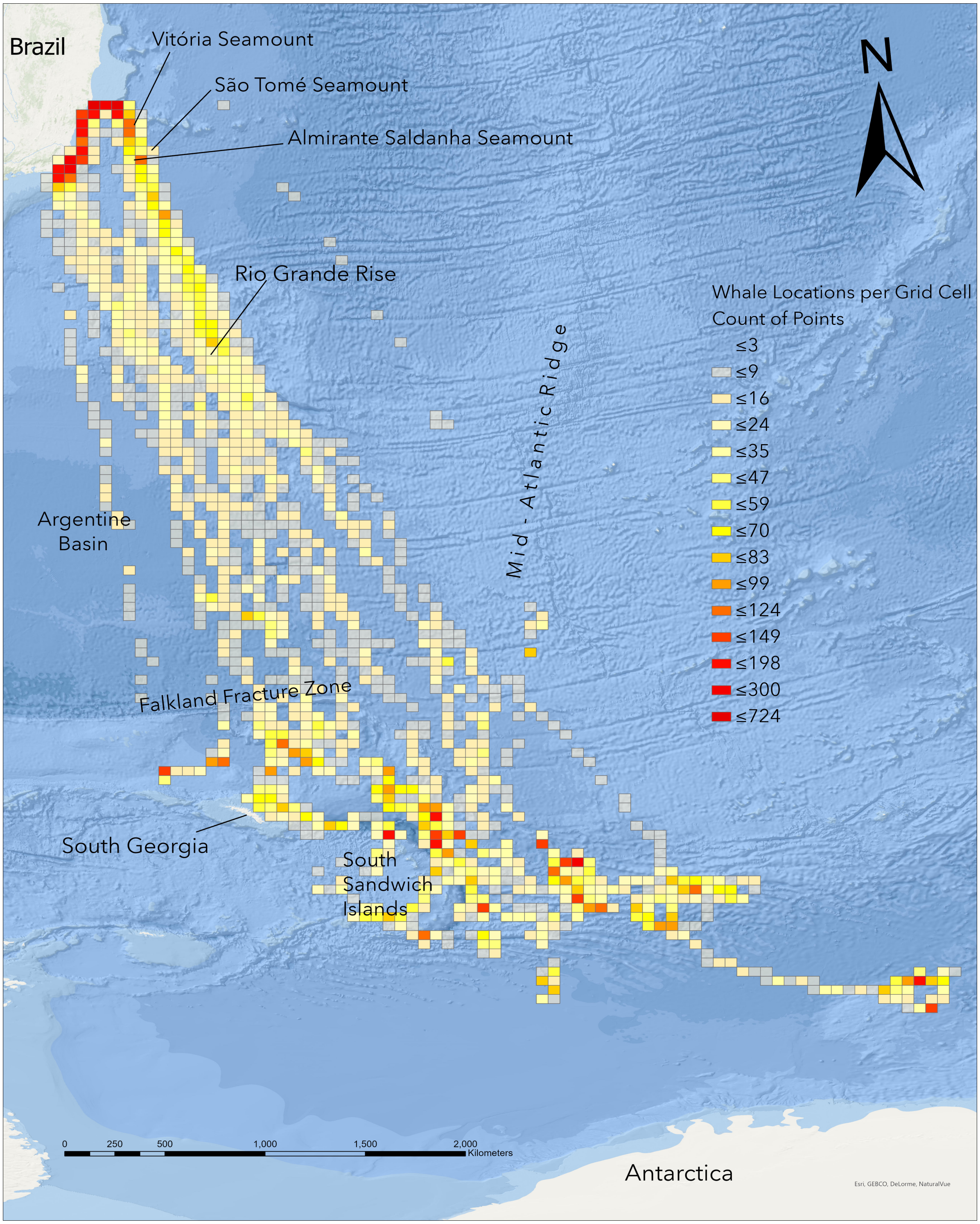

Figure 5: Count of location points per grid cell.

Other Seamounts

Most of the whales that leave the Brazilian coast using the offshore route travel directly over the Vitória-Trindade seamount range (27 whales or 81.8%). Twelve whales travel directly over the Almirante Saldanha seamount and 3 over the Sao Tome seamount (Fig. 6).

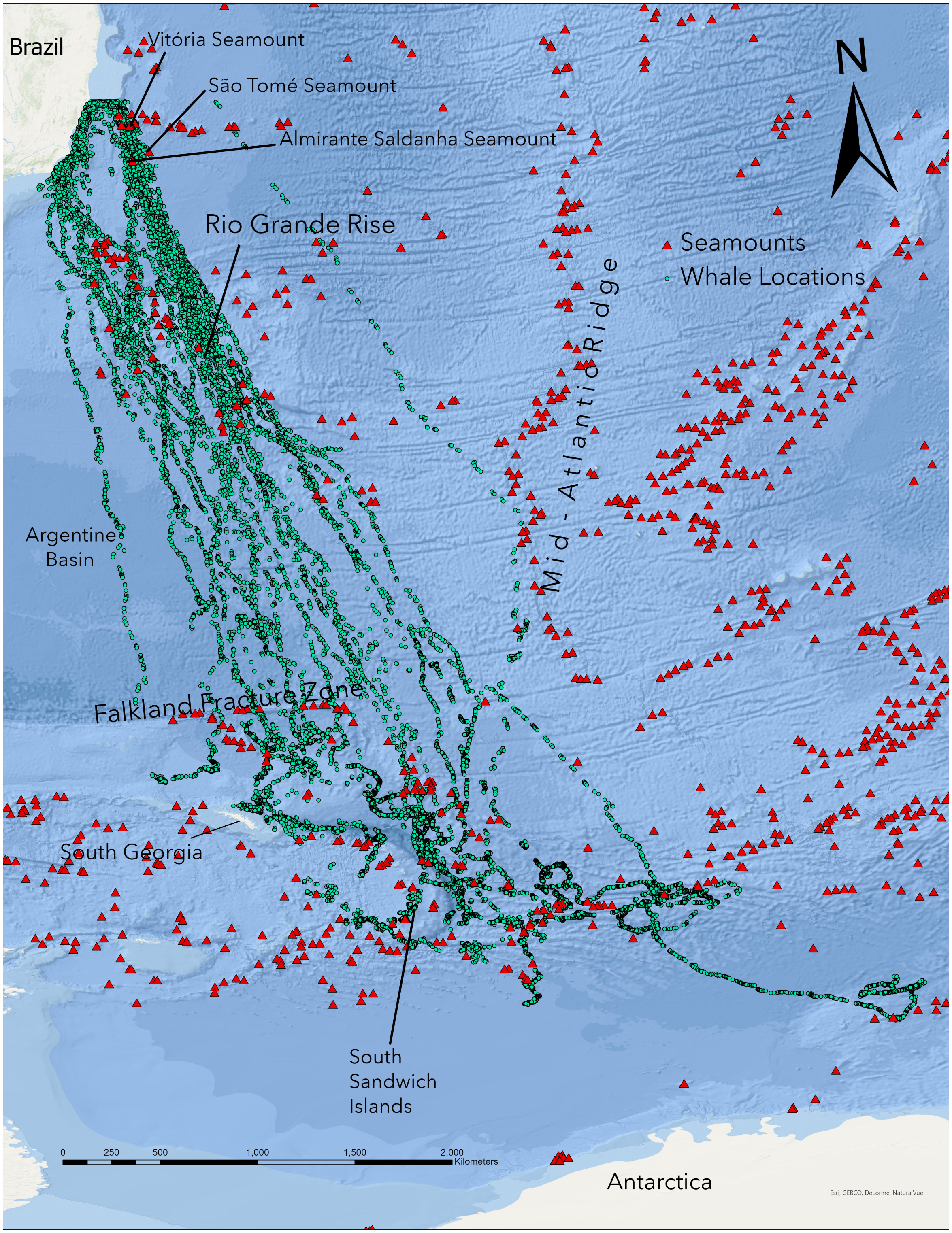

Figure 6: Map of all whale locations and seamounts in the study area.

Individual Variation

Three of the whales used a very different migration route (Fig. 7); one travelled further east until the Mid-Atlantic Ridge and then followed the ridge directly south (87765.09, purple line). Another travelled in a more southerly direction over the Argentine Basin (171995.18, pink line). The final whale with a very different migration path travelled directly to the Rio Grande Rise before turning around and travelling back to the Almirante Saldanha seamount, close to the point at which it started its migration (120942.17, green line). All three whales were females with calves.

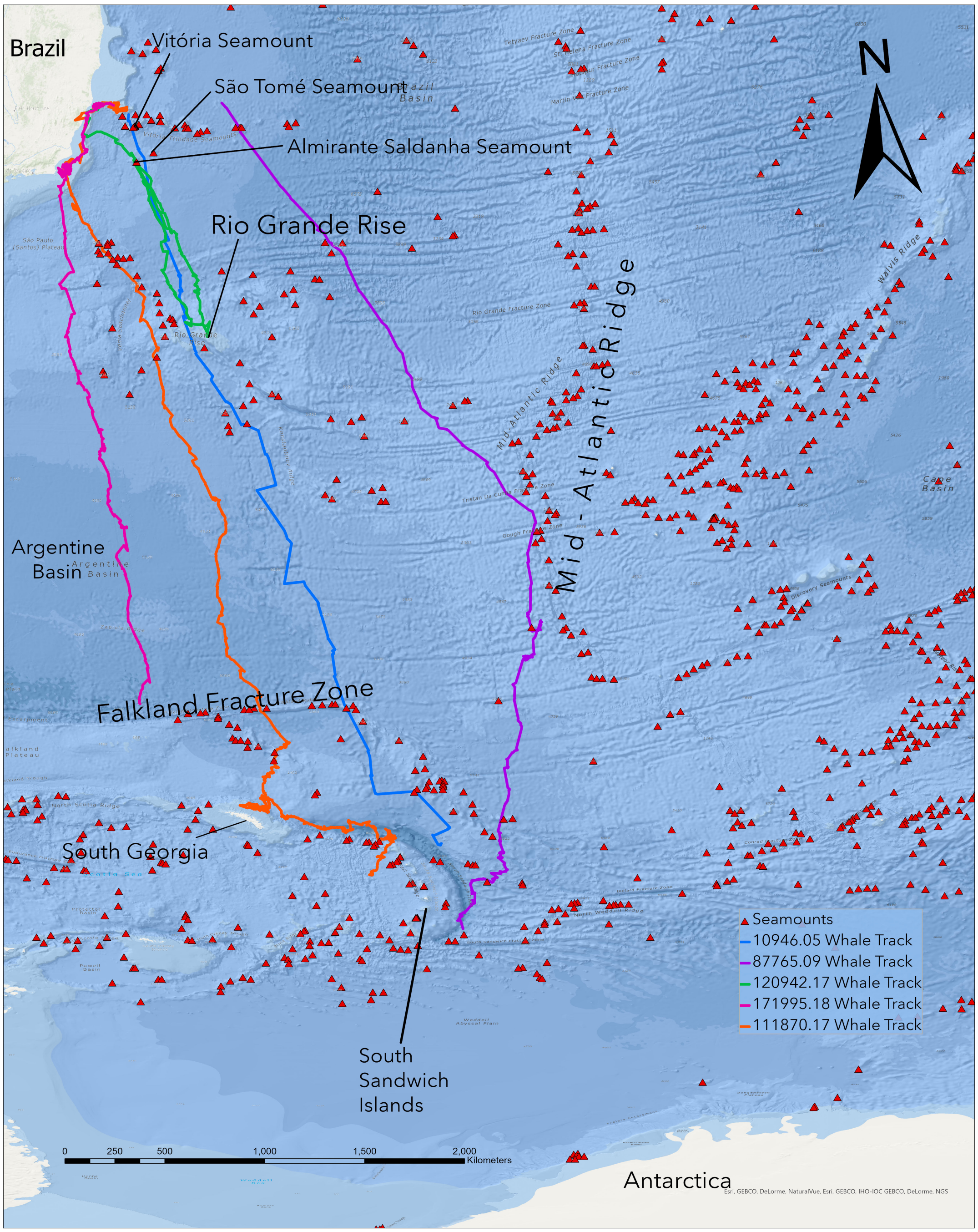

Figure 7: Tracks of five whales. 10946.05 shows typical route 1 migration over Rio Grande Rise. 111870.17 shows typical route 2 migration over ridge north of the Rio Grande Rise. 87765.09, 120942.17 & 171995.18 show different migration routes.

Discussion

This project aimed to establish what routes humpback whales took during their migrations from the Brazilian coast to Antarctic waters and what features they may be using for socialising, opportunistic feeding and navigation. Understanding which areas are important habitats for these whales can help to inform future conservation actions, as well as guiding future research. Overall, most of the whales use similar routes to each other, travelling in a south easterly direction over an area around the Rio Grande Rise Seamount chain. All the whales use two routes at the beginning of their migration; either leaving the coastline along the Besnard Bank or following the coastline until the point north of Rio de Janeiro. Regardless of the route they take to leave the coast, many of the whales (48.9%) travelled directly over the Rio Grande Rise. A total of 87.2% of the whales followed a course that took them near the Rio Grande Rise.

Use of Seamounts

This study suggests that certain seamounts may be important for humpback whales migrating between Brazil and their feeding grounds in Antarctic and sub-Antarctic waters. The Rio Grande Rise and the seamount ridge to the north of the Rio Grande Rise in particular appear to be significant locations for most of the whales during their migration. Many whales modify their course to head towards the Rio Grande Rise and some further modify their course while travelling over the Rio Grande Rise or soon after they have moved south of it. The grid counts (Fig. 5) show that there is a higher density of satellite transmissions over the Rio Grande Rise than over other areas they migrate through.

Most of the whales using the offshore route at the beginning of their migration followed the shallow water Besnard Bank before turning south and travelled over the Vitória seamount. Almost half of the whales that used the offshore route also travelled over the Almirante Saldanha seamount. These two seamounts appear to be important locations for humpback whales using the offshore routes at the beginning of their migrations.

Although this study demonstrates that this population humpback whales predominantly choose a migration path that takes them over or near the Rio Grande Rise, further research is required to ascertain whether they spend time over the Rise or modify their speed.

Although the importance of seamounts as offshore feeding grounds for many species such as billfish and sharks (Kimley 1993) has been known for many years, the advent of satellite tracking for large marine mammals has allowed scientists to more recently begin studying whether the same is true for humpback whales. These studies have shown that humpback whales do spend time around seamounts in many parts of the world. For example, humpback whales in both New Caledonia and near Madagascar/Reunion Islands travel over and spend time near seamounts (Garrigue et al. 2015, Derville et al. 2020, Dulau et al. 2017). Whales use the La Perouse Seamount, near Madagascar, possibly as a breeding ground (Dualu et al. 2017). Humpback whales in New Caledonia were commonly associated with seamounts during their migrations (Garrigue et al. 2015). The whales often remained in areas in close proximity to seamounts for periods of time and change their behaviour near seamounts (Garrigue et al. 2015). Two seamounts were used extensively by whales in this area; La Torche and Antigonia (Garrigue et al. 2015). Residency time of humpback whale also increases in proximity to seamounts, as well as their dive depth (Derville et al. 2020). Although the reasons for their increased residency time and deeper dives is currently unknown, several hypotheses have been suggested (Derville et al. 2020).

Humpback whales' increased dive depths around seamount may be for navigational purposes if they may use seamounts to orientate themselves (Derville et al. 2020). Seamounts create eddies and influence currents (Boehlert & Genin 1987), as well as having geomagnetic effects, which the whales may use to navigate (Garrigue et al. 2015). Humpback whales carried out higher rates of deep, U shaped dives in proximity to seamounts than in open ocean (Derville et al. 2020). This may be for navigational purposes or for opportunistic feeding, as these dives are characteristic of feeding dives (Derville et al. 2020). They may also be socialising around seamounts during their migrations, and the dives are used to listen to or communicate with conspecifics (Derville et al. 2020).

Many of the whales in this study altered their direction of travel as they neared the Rio Grande Rise. Whales that started their migration using the second route often followed the seamount chain north of the Rio Grande Rise and then navigated either over the Rise or to the west of it. Other whales changed direction over the Rise and then remained travelling in that direction until they reached Antarctic waters. This suggests that these whales may be using the Rio Grande Rise for navigational purposes.

<u>Two different paths</u>

The humpback whales observed in this study left the wintering grounds off Brazil using two different routes. The group using the offshore routes started heading in a south westerly direction further north, off the coast from Linhares (Fig. 4). They appeared to follow a shallow water contour east along the Besnard Bank. Most whales using this migration pattern then turned south across the Vitória-Tridade ridge and followed the same course to the Rio Grande Rise.

The majority of the whales (70.2%) use this offshore migration path, leaving coastal waters further north than the other route. In total 17 female whales, 10 males and 6 whales of unidentified sex followed this route. One individual, 87760.08, started further south than Linhares and traveled north first before following the Besnard Bank and turning southeast.

The group of whales using the coastal route closely followed the coastline until it bends to the west at a point close to Rio de Janeiro (Fig. 4). At this point they left the coast in a south easterly direction. They tended to head towards along a seamount ridge to the north west of the Rio Grande Rise before following a more southerly route. Eight females, five males and one individual of unidentified sex followed this route. The sex of the whale or presence of a calf did not appear to influence which route each whale took at the beginning of their migration.

Individual Variation
The humpback whales followed two paths at the beginning of their migration south and many followed a similar route to their feeding grounds in Antarctic waters. Many passed over Vitória-Trindade seamounts if they used the offshore route (Fig. 4) and most of the whales passed over the Rio Grande Rise or migrated within 150km of it. However, there was substantial individual variation between the routes taken by some of the whales.

While most whales headed in a south easterly direction over the Rio Grande Rise, one whale travelled in a more easterly direction (Fig. 7). Whale 87783.09, which was tagged in 2009 and tracked for five and a half months, travelled directly over the Colombia Seamount and then followed the same course until it reached the Mid-Atlantic Rise. She then followed the Mid-Atlantic Ridge directly south until it reached the South Sandwich Islands. When she reached the Mid-Atlantic Ridge, she turned at an approximate 90° angle and followed it for over 600km. It is possible that she used the ridge for opportunistic feeding or that oceanographic features around the ridge were used as navigation cues towards the South Sandwich Islands as she followed, nearly parallel to the ridge until she reached the feeding grounds. This whale was tagged further north that the other whales. It is possible that there is a separate sub-population of humpback whales that breeds further north and even has a different migration pattern from the rest of the population given the species known site fidelity for certain habitats.

Another whale, 171995.18, followed a more southerly route across the Argentine Basin and arrived at the feeding grounds further west than the other whales (Fig. 7). She avoided all seamounts in the area during her migration.

A female with a calf (120942.17) traveled to the Rio Grande Rise before she turned around and traced her original route back to the Almirante Saldanha seamount, where her tagged stopped transmitting after one month (Fig. 7). As whales do not generally feed during their migration and this female had a nursing calf with her, this behavior is believed to be unusual as it could have substantially extended the time it took her to reach the feeding grounds. This behaviour has been recorded for females and it has been hypothesised that this occurred because the whale suffered a miscarriage (if pregnant) or a calf (if lactating). Returning towards the breeding grounds could provide an opportunity to reproduce again if in fact the loss of the fetus or the calf occurred. Although humpbacks generally fast while breeding and migrating, feeding has been observed in the breeding grounds off the coast of Brazil (Pinto de Sá Alves et al. 2009) and in other areas outside their feeding grounds (Derville et al. 2019). She may therefore have fed while over the Rio Grande Rise and when she returned to Almirante Saldanha seamount.

The whales 87783.09, 171995.18 and 120942.17 were females with calves. However, as the majority of whales in this study were females with calves, it is not clear whether this was the reason they used a different migration route. Humpbacks' calves are vulnerable to killer whale (*Orcinus orca*) attacks (Pitman et al. 2015). Humpbacks are known to display defensive and aggressive behaviors when threatened by killer whales, and group together (Ford et al. 2008). If the female whales with calves are travelling alone, they may choose different routes to avoid killer whales. In New Caledonia maternal whales appear to avoid other whales in shallow water, leading to social segregation (Derville et al. 2018). This segregation did not occur over the Southern Seamounts (Derville et al. 2018). Because the majority of whales in this study were females and they mainly followed typical migration paths, without showing signs of social segregation. Therefore, the different routes chosen by these whales may be due to individual personality or memory from previous migrations (Dall et al. 2004, Hertel et al. 2020).

Previous research has found that routes taken by humpbacks vary between individuals during their migration (Garrigue et al. 2015) and feeding (Kennedy et al. 2014). Whales in these studies used multiple migratory paths. However, from looking at the data in this study, it appears that humpback whales in the southwest Atlantic used less variable routes. Although there were two that migrated along a somewhat different path, most of the whales followed generally the same route until they reached Sub-antarctic waters. Most of them traveled near the Rio Grande Rise and in a south easterly direction. As they approached the feeding grounds, their tracks diverged as they neared South Georgia, the South Sandwich Islands or the Falkland Fracture Zone.

Policy Implications

Climate change

Climate change may have several impacts on the migrations of humpback whales. The main impact is that Antarctic krill (*Euphausia superba*) populations, the main source of food for humpback whales in Antarctic waters, are likely to decrease (Flores et al. 2012). This may result in longer migrations for humpback whales, increasing the cost of movement and decreasing the length of the feeding season (Learmonth et al. 2006). The reduction in krill numbers is likely to lead to increased competition over food and a potential decline in the numbers of humpback whales (Tulloch et al. 2019). Therefore, ongoing protection is needed to reduce these losses in the future (Tulloch et al. 2019), such as the formation of new Marine Mammal Protection Areas in areas that are important habitats for them. Whale species with adaptable migration patterns may be more resilient to the impacts of climate change (Tulloch et al. 2019), but as most of the whales in this population have a fairly direct route to their feeding routes, it seems unlikely that their route will be changed.

Fishing and Shipping

Due to the fish-aggregating effects of seamounts, they often experience higher densities of fishing than surrounding waters (O'Driscoll & Clark 2015). As Humpbacks are vulnerable to entanglement in fishing gear (Ryan et al. 2016, Johnson et al. 2005), this increases their exposure to risk over seamounts. Due to the fragility of habitats and species found on seamounts (Alder & Wood 2004), as well as their potentially high levels of endemism (de Forges et al. 2000), there have been calls to protect seamounts from destructive fishing practices, including from the United Nations General Assembly (Resolution 61/105 in 2006). Seamounts are classified as vulnerable marine ecosystems and should therefore be protected from fishing activity (Watling & Auster 2017). Creating marine protected areas (MPAs) can have a beneficial impact on marine mammals (Gromley et al. 2012) and therefore protecting seamounts that humpbacks whales migrate over may help prevent future population declines, as well as protecting other unique and valuable habitats and fauna.

A shipping route from Rio de Janeiro to Southern Africa crosses the path of these migrating whales (Rodrigue 2016). Global shipping is expected to increase by 240–1,209% by 2050 (Sardain et al. 2019). As shipping increases, so too does the likelihood of ship strikes on whales, as well as increasing marine anthropogenic noise. Policies such as reducing speed limits and/or creating novel routes to avoid areas with high densities of whales during certain times of year will help to reduce this threat. This study indicates that these policies may be useful in the areas surrounding the Rio Grande Rise and the Vitória-Trindade ridge while this population of humpbacks in migrating past these areas.

Mining

The Rio Grande Rise was formed from volcanic activity at a continental fracture zone (Camboa & Rabinowitz 1984). The rise has a ferromanganese crust, which is made up of iron and manganese and also includes high levels of nickel and lithium (Benites et al. 2020). Currently, a Brazilian company, International Seabed Authority, has a 15-year exploration contract, but the Brazilian government is attempting to withdraw this (da Silva 2021). The Commission on the Limits of the Continental Shelf is negotiating with Brazil over a significant change to the limit of their continental shelf (DSM Observer, 2019). The Brazilian government is negotiating to include the rise into its outer continental shelf (da Silva 2021) so that it can start mining the Rio Grande Rise.

Deep sea mining may affect humpback whales in several way. Firstly, deep sea mining will increase anthropogenic noise (Drazen et al. 2020). This may limit humpback whales' ability to communicate and may increase the risk of calves becoming separated from their mothers (Indeck et al. 2020). Secondly, deep sea mining creates sediment plumes from collectors and discharge (Drazen et al. 2020). This sediment may cause distress by blocking sensory organs (Drazen et al. 2020), as well as reducing visual communication ability and visual cues for navigation. If humpback whales use the Rio Grande Rise as a feeding ground, sediment may also alter prey dynamics and potentially influence the behavior of the whales. Thirdly, metal released into the water column may cause toxic build up (Hauton et al. 2017).

Limitations and Further Research

There are several limitations of this study, which the use of analysis and modelling techniques on the data would help to resolve. As tags on marine mammals only transmit when the animal surfaces, the rate of transmission is not uniform. Therefore, unless models are created, which estimate where a whale will be at regular time intervals, it is not possible to calculate the density of the whale locations. Instead, a proxy measurement of number of locations inside each grid square was used. Although this does not give a measure of density, it may help to show where the whales are spending time during their migrations.

Further research is required to establish whether there is a higher density of humpbacks whales over seamounts during their migrations. Models can assess whether the whales are changing direction more over seamounts and whether they change the speed at which they are travelling, which are important measurements to assess whether seamounts are important habitats for them. The telemetry data used in this study also included information about diving behaviors even though that was not analysed here. The analysis of this data may show whether humpback whales migrating over or near seamounts in this area modify their diving behavior, which may be a useful indicator of whether they may be using seamounts for supplementary feeding, communication or navigational purposes.

Conclusions

Although mostly descriptive, this study indicates that humpback whales in the southwest Atlantic do migrate over seamounts, such as the Rio Grande Rise, the seamount ridge to the north of it, Vitória-Trindade seamounts and Almirante Saldanha seamount. As their routes appear to be consistent between individuals across different years, it may be beneficial to create Marine Mammal Protection Areas over these habitats, to protect against threats during their migrations. Further research is needed to establish whether these seamounts are essential habitats for them and whether their behavior changes in proximity to seamounts.

References

1. International Whaling Commission (2021 (a)). *Commercial Whaling* [Online]. Available at: <https://iwc.int/commercial> [Accessed 15 April 2021].

2. International Whaling Commission (2021 (b)). *Aboriginal Subsistence Whaling in the Arctic* [Online]. Available at: <https://iwc.int/aboriginal> [Accessed 20 April 2021].

3. NOAA (2021). *Humpback Whale* [Online] Available at: <https://www.fisheries.noaa.gov/species/humpback-whale> [Accessed 21 March 2021].

4. Kawamura, A. (1994). A review of baleen whale feeding in the Southern Ocean. *Rep. Int. Whal. Commn*, **44**, pp.261-271.

5. Valsecchi, E., Hale, P., Corkeron, P. and Amos, W. (2002). Social structure in migrating humpback whales (Megaptera novaeangliae). *Molecular Ecology*, **11**(3), pp.507-518.

6. Wiley, D., Ware, C., Bocconcelli, A., Cholewiak, D., Friedlaender, A., Thompson, M. and Weinrich, M. (2011). Underwater components of humpback whale bubble-net feeding behaviour. *Behaviour*, **148**, pp.575-602.

7. D'Vincent, C.G., Nilson, R.M. and Hanna, R.E. (1985). Vocalization and coordinated feeding behavior of the humpback whale in southeastern Alaska. *The Scientific Reports the Whales Research Institute*, **36**, pp.41-47.

8. Chittleborough, R.G. (1958). The breeding cycle of the female humpback whale, Megaptera nodosa (Bonnaterre). *Marine and Freshwater Research*, **9**(1), pp.1-18.

9. Best, P.B. (2020). A note on the age at sexual maturity of humpback whales. *The Journal of Cetacean Research and Management*, **3**, pp.71-73.

10. Payne, R.S. and McVay, S. (1971). Songs of humpback whales. *Science*, **173**(3997), pp.585-597.

11. Tyack, P. (1981). Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behavioral Ecology and Sociobiology*, **8**(2), pp.105-116.

12. Winn, H.E., Thompson, T.J., Cummings, W.C., Hain, J., Hudnall, J., Hays, H. and Steiner, W.W. (1981). Song of the humpback whale—population comparisons. *Behavioral Ecology and Sociobiology*, **8**(1), pp.41-46.

13. Noad, M.J., Cato, D.H., Bryden, M.M., Jenner, M.N. and Jenner, K.C.S. (2000). Cultural revolution in whale songs. *Nature*, **408**(6812), pp.537-537.

14. Zoidis, A.M., Smultea, M.A., Frankel, A.S., Hopkins, J.L., Day, A., McFarland, A.S., Whitt, A.D. and Fertl, D. (2008). Vocalizations produced by humpback whale (Megaptera novaeangliae) calves recorded in Hawaii. *The Journal of the Acoustical Society of America*, **123**(3), pp.1737-1746.

15. Chittleborough R.G. (1965) Dynamics of two populations of the humpback whale, Megaptera novaeangliae (Borowski). *Australian Journal of Marine and Freshwater Research*, **16**, 33-128.

16. Robbins, J., Dalla Rosa, L., Allen, J.M., Mattila, D.K., Secchi, E.R., Friedlaender, A.S., Stevick, P.T., Nowacek, D.P. and Steele, D. (2011). Return movement of a humpback whale between the Antarctic Peninsula and American Samoa: a seasonal migration record. *Endangered Species Research*, **13**, pp.117-21.

17. Minton, G., Collins, T., Pomilla, C., Findlay, K.P., Rosenbaum, H., Baldwin, R. & Brownell Jr., R.L.,Clapham, P.J., Baker, C.S. & Taylor, B.L. (2008) Megaptera novaeangliae, Arabian Sea subpopulation. *IUCN Red List of Threatened Species* [Online]. Available at: <https://arabianseawhalenetworkdotorg.files.wordpress.com/2015/10/minton-et-al-2008_iucn-redlist-assessment-arabian-seamegaptera-novaeangliae.pdf> [Accessed 12 April 2021].

18. Willson, A., Baldwin, R., Cerchio, S., Childerhouse, S., Collins, T., Findlay, K., Genov, T., Godley, B., Al Harthi, S., Leslie, M., MacDonald, D., Minton, G., Zerbini, A. and Witt, M. (2018). Update on satellite telemetry studies and first unmanned aerial vehicle assisted health assessment studies of Arabian Sea humpback whales off the coast of Oman. Paper SC/67B/CMP/13 Rev 1 presented to the IWC Scientific Committee, Bled, Slovenia, 23 April-6 May 2018. pp.15.

19. Cooke, J.G. 2018. *Megaptera novaeangliae*. The IUCN Red List of Threatened Species 2018 [Online]. e.T13006A50362794. Available at: <https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T13006A50362794.en>. [Accessed 13 April 2021]

20. Allison, C. (2006). Documentation of the creation of the Southern Hemisphere humpback catch series, February 2006, Cambridge, UK. Paper SC/A06/HW47 presented to the IWC Workshop on Comprehensive Assessment of Southern Hemisphere Humpback Whales, Hobart, Tasmania, 3–7 April 2006.

21. de Morais, I.O.B., Danilewicz, D., Zerbini, A.N., Edmundson, W., Hart, I.B. and Bortolotto, G.A. (2017). From the southern right whale hunting decline to the humpback whaling expansion: a review of whale catch records in the tropical western South Atlantic Ocean. *Mammal Review*, **47**(1), pp.11-23.

22. Zerbini, A.N., Adams, G., Best, J., Clapham, P.J., Jackson, J.A. and Punt A.E. (2019). Assessing the Recovery of an Antarctic Predator from Historical Exploitation. Royal Society Open Science, 6(10): 190368 DOI: 10.1098/rsos.190368.

23. Ryan, C., Leaper, R., Evans, P.G., Dyke, K., Robinson, K.P., Haskins, G.N., Calderan, S., van Geel, N., Harries, O., Froud, K. and Brownlow, A. (2016). Entanglement: an emerging threat to humpback whales in Scottish waters. Paper SC/66b/HIM/01 submitted to the International Whaling Commission Scientific Committee.

24. Johnson, A., Salvador, G., Kenney, J., Robbins, J., Kraus, S., Landry, S. and Clapham, P. (2005). Fishing gear involved in entanglements of right and humpback whales. *Marine Mammal Science*, **21**(4), pp.635-645.

25. Fleming, A. and Jackson, J. (2011). Global review of humpback whales (Megaptera novaeangliae). *NOAA* [Online]. Available at:<https://repository.library.noaa.gov/view/noaa/4489>. [Accessed 2 April 2021].

26. IWC (2011). Report of the Workshop on the Comprehensive Assessment of Southern Hemisphere humpback whales. *Journal of Cetacean Research and Management special issue*, **3**, pp.5-50

27. Glass A.H., Cole T.V.N., Garron M. (2009). Mortality and serious injury determinations for baleen whale stocks along the United States eastern seaboard and adjacent Canadian Maritimes, 2003-2007. Northeast Fisheries Science Center Reference Document 11-18. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center., Woods Hole, MA.

28. Robbins, J. & Mattila, D.K. (2001) Monitoring entanglements of humpback whales (*Megaptera novaeangliae*) in the Gulf of Maine on the basis of caudal peduncle scarring. Report to the 53rd Scientific Committee Meeting of the International Whaling Commission, Hammersmith, UK. Document No. SC/53/NAH25.

29. International Maritime Organisation (2007). Measures for minimizing the risks of collisions with cetaceans. Agenda item 18. Marine Environment Protection Committee, 57th Session, pp.5.

30. Doyle, L.R., McCowan, B., Hanser, S.F., Chyba, C., Bucci, T. and Blue, J.E. (2008). Applicability of information theory to the quantification of responses to anthropogenic noise by southeast Alaskan humpback whales. *Entropy*, **10**(2), pp.33-46.

31. Blair, H.B., Merchant, N.D., Friedlaender, A.S., Wiley, D.N. and Parks, S.E. (2016). Evidence for ship noise impacts on humpback whale foraging behaviour. *Biology Letters*, **12**(8), pp.20160005.

32. Miller, P.J., Biassoni, N., Samuels, A. and Tyack, P.L. (2000). Whale songs lengthen in response to sonar. *Nature*, **405**(6789), pp.903-903.

33. Fristrup K.M., Hatch L.T. and Clark C.W. (2003). Variation in humpback whale (Megaptera novaeangliae) song length in relation to low-frequency sound broadcasts. *Journal of the Acoustical Society of America,* **113**(6), pp.3411-3424.

34. Weilgart, L.S. (2007). The impacts of anthropogenic ocean noise on cetaceans and implications for management. *Canadian Journal of Zoology*, **85**(11), pp.1091-1116.

35. Krahn, M.M., Herman, D.P., Ylitalo, G.M., Sloan, C.A., Burrows, D.G., Hobbs, R.C., Mahoney, B.A., Yanagida, G.K., Calambokidis, J. and Moore, S.E. (2004). Stratification of lipids, fatty acids and organochlorine contaminants in blubber of white whales and killer whales. *Journal of Cetacean Research and Management*, **6**(2), pp.175-189.

36. Kivenson, V., Lemkau, K.L., Pizarro, O., Yoerger, D.R., Kaiser, C., Nelson, R.K., Carmichael, C., Paul, B.G., Reddy, C.M. and Valentine, D.L. (2019). Ocean dumping of containerized DDT waste was a sloppy process. *Environmental science & Technology*, **53**(6), pp.2971-2980.

37. Rosenbaum, H.C., Pomilla, C., Mendez, M., Leslie, M.S., Best, P.B., Findlay, K.P., Minton, G., Ersts, P.J., Collins, T., Engel, M.H. and Bonatto, S.L. (2009). Population structure of humpback whales from their breeding grounds in the South Atlantic and Indian Oceans. *PLoS One*, **4**(10), 7318. DOI: p.e7318.

38. Andriolo, A., Kinas, P.G., Engel, M.H., Martins, C.C.A. and Rufino, A.M. (2010). Humpback whales within the Brazilian breeding ground: distribution and population size estimate. *Endangered Species Research*, **11**(3), pp.233-243.

39. Zerbini, A.N., Andriolo, A.., Da Rocha, J.M., Simões-Lopes, P.C., Siciliano, S., Pizzorno, J.L., Waite, J.M., Demaster, D.P. and Vanblaricom, G.R. (2004). Winter distribution and abundance of humpback whales (*Megaptera novaeangliae*) off Northeastern Brazil. *Journal of Cetacean Research and Management*, **6**(1), pp.101-107.

40. Morete, M.E., Pace Iii, R.M., Martins, C.C.A., Freitas, A.C. and Engel, M.H. (2003). Indexing seasonal abundance of humpback whales around Abrolhos Archipelago, Bahia, Brazil. *Latin American Journal of Aquatic Mammals*, **2**(1), pp.21-28.

41. Stevick, P., Aguayo-Lobo, A., Allen, J., Ávila, I.C., Capella, J., Castro, C., Chater, K., Rosa, L.D., Engel, M.H., Félix, F. and Flórez-González, L. (2004). Migrations of individually identified humpback whales between the Antarctic Peninsula and South America. *Journal of Cetacean Research and Management*, **6**(2), pp.109-113.

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

43. Zerbini, A.N., Andriolo, A., Heide-Jorgensen, M.P., Moreira, S.C., Pizzorno, J.L., Miai, Y.G., Vanblaricom, G.R. and DeMaster, D.P. (2011). Migration and summer destinations of humpback whales (Megaptera novaeangliae) in the western South Atlantic Ocean. Journal of Cetacean Research and Management Special Issue, **31**, pp.13-18.

44. Horton, T.W., Zerbini, A.N., Andriolo, A., Danilewicz, D. and Sucunza, F. (2020). Multi-Decadal Humpback Whale Migratory Route Fidelity Despite Oceanographic and Geomagnetic Change. Frontiers in Marine Science **7**(414), pp.1-19.

45. Yesson, C., Clark, M.R., Taylor, M.L. and Rogers, A.D. (2011). The global distribution of seamounts based on 30 arc seconds bathymetry data. *Deep Sea Research Part I: Oceanographic Research Papers*, **58**(4), pp.442-453.

46. Wessel, P. (2007). Introduction and characterisation of seamounts: Seamount characteristics, in Pitcher, T. J., Morato, T., Hart, J. B. P., Malcolm R. Clark, M. R., Haggan N. and Santos, R., S. eds. (2007). *Seamounts: Ecology, Fisheries and Conservation.* Oxford, Blackwell Scientific, pp.3-26..

47. Boehlert, G.W. and Genin, A. (1987). A review of the effects of seamounts on biological processes. *Seamounts, Islands and Atolls*, **43**, pp.319-334.

48. Holland, K.N. and Grubbs, R.D. (2007). Fish visitors to seamounts: tunas and billfish at seamounts, in Pitcher, T. J., Morato, T., Hart, J. B. P., Malcolm R. Clark, M. R., Haggan N. and Santos, R., S. eds. (2007). *Seamounts: Ecology, Fisheries and Conservation.* Oxford, Blackwell Scientific, pp.189-201.

49. Johnston, D.W., McDonald, M., Polovina, J., Domokos, R., Wiggins, S. and Hildebrand, J. (2008). Temporal patterns in the acoustic signals of beaked whales at Cross Seamount. *Biology Letters*, **4**(2), pp.208-211.

50. Kaschner, K. (2007). Air-breathing visitors to seamounts: Marine Mammals, in Pitcher, T. J., Morato, T., Hart, J. B. P., Malcolm R. Clark, M. R., Haggan N. and Santos, R., S. eds. (2007). *Seamounts: Ecology, Fisheries and Conservation.* Oxford, Blackwell Scientific, pp.230-238.

51. Garrigue, C., Clapham, P.J., Geyer, Y., Kennedy, A.S. and Zerbini, A.N. (2015). Satellite tracking reveals novel migratory patterns and the importance of seamounts for endangered South Pacific humpback whales. *Royal Society Open Science*, **2**(11), p.150489

52. Derville, S., Torres, L.G., Zerbini, A.N., Oremus, M. and Garrigue, C. (2020). Horizontal and vertical movements of humpback whales inform the use of critical pelagic habitats in the western South Pacific. *Scientific Reports*, **10**(1), pp.1-13.

53. Derville, S., Torres, L.G. and Garrigue, C. (2018). Social segregation of humpback whales in contrasted coastal and oceanic breeding habitats. *Journal of Mammalogy*, **99**(1), pp.41-54.

54. Dulau, V., Pinet, P., Geyer, Y., Fayan, J., Mongin, P., Cottarel, G., Zerbini, A. and Cerchio, S. (2017). Continuous movement behavior of humpback whales during the breeding season in the southwest Indian Ocean: on the road again! *Movement Ecology*, **5**(1), pp.1-17.

55. Derville, S., Torres, L.G., Dodémont, R., Perard, V. and Garrigue, C. (2019). From land and sea, long-term data reveal persistent humpback whale (Megaptera novaeangliae) breeding habitat in New Caledonia. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **29**(10), pp.1697-1711.

56. Yesson, C., Letessier, T., B., Nimmo-Smith, A., Hosegood, P., Brierley, A. S., Hardouin, M., Proud, R., (2020). List of seamounts in the world oceans - An update. PANGAEA [Onine]. Available at: <https://doi.org/10.1594/PANGAEA.921688>. [Accessed 10 March 2021].

57. Klimley, A.P. (1993). Highly directional swimming by scalloped hammerhead sharks, Sphyrna lewini, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. *Marine Biology*, **117**(1), pp.1-22.

58. Pinto de sa Alves, L.C., Andriolo, A., Zerbini, A., Altmayer Pizzorno, J.L. and Clapham, P. (2009). Record of feeding by humpback whales (Megaptera novaeangliae) in tropical waters off Brazil. *Publications, Agencies and Staff of the US Department of Commerce*, **45**, pp.416-418.

59. Pitman, R.L., Totterdell, J.A., Fearnbach, H., Ballance, L.T., Durban, J.W. and Kemps, H., (2015). Whale killers: prevalence and ecological implications of killer whale predation on humpback whale calves off Western Australia. *Marine Mammal Science*, **31**(2), pp.629-657.

60. Ford, J.K. and Reeves, R.R. (2008). Fight or flight: antipredator strategies of baleen whales. *Mammal Review*, **38**(1), pp.50-86.

61. Dall, S.R., Houston, A.I. and McNamara, J.M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, **7**(8), pp.734-739.

62. Hertel, A.G., Niemelä, P.T., Dingemanse, N.J. and Mueller, T. (2020). A guide for studying among-individual behavioral variation from movement data in the wild. *Movement Ecology*, **8**(1), pp.1-18.

63. Kennedy, A.S., Zerbini, A.N., Rone, B.K. and Clapham, P.J. (2014). Individual variation in movements of satellite-tracked humpback whales *Megaptera novaeangliae* in the eastern Aleutian Islands and Bering Sea. *Endangered Species Research*, **23**(2), pp.187-195.

64. Flores, H., Atkinson, A., Kawaguchi, S., Krafft, B.A., Milinevsky, G., Nicol, S., Reiss, C., Tarling, G.A., Werner, R., Rebolledo, E.B. and Cirelli, V. (2012). Impact of climate change on Antarctic krill. *Marine Ecology Progress Series*, **458**, pp.1-19.

65. Learmonth, J.A., MacLeod, C.D., Santos, M.B., Pierce, G.J., Crick, H.Q.P. and Robinson, R.A. (2006). Potential effects of climate change on marine mammals. *Oceanography and Marine Biology*, **44**, pp.431-464.

66. Tulloch, V.J., Plagányi, É.E., Brown, C., Richardson, A.J. and Matear, R. (2019). Future recovery of baleen whales is imperiled by climate change. *Global Change Biology*, **25**(4), pp.1263-1281.

67. O'Driscoll, R.L. and Clark, M.R. (2005). Quantifying the relative intensity of fishing on New Zealand seamounts. *New Zealand Journal of Marine and Freshwater Research*, **39**(4), pp.839-850.

68. Alder, J. and Wood, L. (2004). Managing and protecting seamounts ecosystems, in Morato, T. and Pauly D. eds. (2004). *Seamounts: Biodiversity and Fisheries. Fisheries Center Research Reports*, **12**(5), pp.67-74.

69. de Forges, B.R., Koslow, J.A. and Poore, G.C.B. (2000). Diversity and endemism of the benthic seamount fauna in the southwest Pacific. *Nature*, **405**(6789), pp.944-947.

70. Watling, L. and Auster, P.J. (2017). Seamounts on the high seas should be managed as vulnerable marine ecosystems. *Frontiers in Marine Science*, **4**(14), pp.1-4.

71. Gormley, A.M., Slooten, E., Dawson, S., Barker, R.J., Rayment, W., du Fresne, S. and Bräger, S. (2012). First evidence that marine protected areas can work for marine mammals. *Journal of Applied Ecology*, **49**(2), pp.474-480.

72. Rodrigue, J.P. (2016). Maritime transport. International Encyclopedia of Geography: People, the Earth, Environment and Technology: People, the Earth, Environment and Technology, pp.1-7.

73. Sardain, A., Sardain, E. and Leung, B. (2019). Global forecasts of shipping traffic and biological invasions to 2050. *Nature Sustainability*, **2**(4), pp.274-282.

74. Camboa, L.A.P. and Rabinowitz, P.D. (1984). The evolution of the Rio Grande Rise in the southwest Atlantic Ocean. *Marine Geology*, **58**(1-2), pp.35-58.

75. Benites, M., Hein, J.R., Mizell, K., Blackburn, T. and Jovane, L. (2020). Genesis and evolution of ferromanganese crusts from the summit of Rio Grande Rise, Southwest Atlantic Ocean. *Minerals*, **10**(4), p.349-385.

76. da Silva, A.P. (2021). Brazil advances over the Area: The inclusion of the Rio Grande Rise within the Brazilian outer continental shelf and its consequences for other states and for the common heritage of mankind. *Marine Policy*, **125**,104399. DOI: p.104399.

77. DSM Observer (2019). One of the most significant deep-sea mining negotiations is underway at the Commission on the Limits of the Continental Shelf [Online]. Available at: <https://dsmobserver.com/2019/10/one-of-the-most-significant-deep-sea-mining-negotiations-is-underway-at-the-commission-on-the-limits-of-the-continental-shelf/> [Accessed 11 February 2021].

78. Drazen, J.C., Smith, C.R., Gjerde, K.M., Haddock, S.H., Carter, G.S., Choy, C.A., Clark, M.R., Dutrieux, P., Goetze, E., Hauton, C. and Hatta, M. (2020). Opinion: Midwater ecosystems must be considered when evaluating environmental risks of deep-sea mining. *Proceedings of the National Academy of Sciences*, **117**(30), pp.17455-17460.

79. Indeck, K.L., Girola, E., Torterotot, M., Noad, M.J. and Dunlop, R.A. (2020). Adult female-calf acoustic communication signals in migrating east Australian humpback whales. *Bioacoustics*, **0**(0)pp.1-24.

80. Hauton, C., Brown, A., Thatje, S., Mestre, N.C., Bebianno, M.J., Martins, I., Bettencourt, R., Canals, M., Sanchez-Vidal, A., Shillito, B. and Ravaux, J. (2017). Identifying toxic impacts of metals potentially released during deep-sea mining—a synthesis of the challenges to quantifying risk. *Frontiers in Marine Science*, **4**, p.368-381.