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CLARÊNCIO GOMES BARACHO NETO

HABITAT SUITABILITY, MOVEMENTS, AND DIVING BEHAVIOR OF THE SEI WHALE (*Balaenoptera borealis*) OFF THE COAST OF BRAZIL

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Orientador: Dr. Alexandre Novaes Zerbini

Coorientador: Dra. Marta Jussara Cremer

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“O mar, uma vez lançado seu feitiço, mantém-nos para sempre em sua rede de maravilha.” (Jacques-Yves Cousteau).

RESUMO

A baleia-sei (*Balaenoptera borealis*) é uma espécie de grande cetáceo ainda pouco conhecida, especialmente em regiões tropicais do Hemisfério Sul, apesar de ter sido amplamente explorada pela indústria baleeira no século XX. Classificada como "Em Perigo" pela União Internacional para Conservação da Natureza (IUCN), sua recuperação populacional e conservação dependem do conhecimento sobre sua ecologia espacial, comportamento e uso do habitat para que as interações com atividades antropogênicas sejam minimizadas. Esta tese de doutorado busca suprir lacunas críticas nesse conhecimento, reunindo dados inéditos obtidos na Bacia de Santos, sudeste do Brasil, região de elevada biodiversidade, mas também marcada por intensa atividade humana. Utilizou-se modelagem de distribuição de espécies (SDMs) para estimar a adequabilidade de habitat da baleia-sei na região da Bacia de Santos a partir de dados de presença e ausência verdadeira, e com o uso de algoritmos de aprendizado de máquina integrados em um modelo de consenso, foi possível gerar mapas preditivos para a espécie na área de estudo. Os modelos apresentaram desempenho excelente, com a profundidade média sendo o preditor mais relevante, seguida por temperatura da superfície do mar, velocidade superficial da corrente e concentração de clorofila. As áreas de maior adequabilidade coincidiram com a quebra da plataforma continental e talude continental e próximos aos cânions submarinos, destacando a importância dos gradientes ambientais estáticos e dinâmicos na distribuição da espécie. O padrão de ocorrência, movimentos e a ocupação na área de estudo foi avaliado por meio de 26 baleias monitoradas por telemetria satelital utilizando modelos ocultos de Markov (Hidden Markov Models) e revelou que as baleias alternam entre dois estados comportamentais. Movimentos direcionais relacionados com o deslocamento (“Transit”) e movimentos menos direcionais e relacionados a comportamentos de reprodução, alimentação e descanso (Area-Restricted Search – ARS). ARS foi frequentemente registrado em regiões topograficamente complexas, como os cânions submarinos de Cananéia e São Sebastião, além da Cadeia Vitória-Trindade. O comportamento de mergulho foi registrado por transmissores satelitais e sensores de alta resolução (DTAG e CATS) e demonstraram que 93% dos mergulhos ocorreram em profundidades iguais ou inferiores a 20 metros, faixa de influência de grandes embarcações indicando um risco elevado de colisões. Modelos aditivos mistos revelaram que variáveis ambientais (temperatura da superfície do mar, profundidade local, concentração de clorofila, período do dia e fase lunar) e comportamentais (estado comportamental e forma do mergulho) modulam a profundidade e a duração dos mergulhos. Episódios pontuais de provável alimentação próximo à superfície sugerem forrageamento oportunista, mesmo em áreas tradicionalmente consideradas como reprodutivas. De forma integrada, os resultados desta tese contribuem significativamente para a compreensão da ecologia da baleia-sei em regiões tropicais, reforçam a importância da Bacia de Santos como área de uso recorrente e alertam para os riscos advindos do intenso tráfego marítimo e das atividades offshore. As evidências de alimentação oportunista em áreas reprodutivas desafiam paradigmas clássicos sobre a segregação funcional dos habitats e indicam a necessidade de abordagens conservacionistas mais abrangentes. Esta tese fornece uma base científica robusta para o planejamento espacial marinho, mitigação de impactos antropogênicos e definição de áreas prioritárias para a conservação desta espécie ameaçada no Atlântico Sul Ocidental.

Palavras-chave: Baleia-sei; adequabilidade de habitat; movimentos; comportamento de mergulho.

ABSTRACT

The sei whale (*Balaenoptera borealis*) is a large cetacean species that remains poorly understood, especially in tropical regions of the Southern Hemisphere, despite having been heavily exploited by the whaling industry during the 20th century. Listed as "Endangered" by the International Union for Conservation of Nature (IUCN), its population recovery and conservation depend on advancing knowledge about its spatial ecology, behavior, and habitat use. This doctoral thesis aims to address critical gaps in such knowledge by compiling novel data collected in the Santos Basin, southeastern Brazil, an area of high biodiversity but also subject to intense human activity. Species distribution models (SDMs) were applied to estimate habitat suitability for sei whales using true presence-absence data, and predictive maps were generated through ensemble models integrating machine learning algorithms. The models showed excellent performance, with mean depth emerging as the most important predictor, followed by sea surface temperature, surface current velocity, and chlorophyll concentration. Areas of highest suitability coincided with the continental shelf break, upper slope, and submarine canyon regions, emphasizing the role of static and dynamic environmental gradients in the species' distribution. Patterns of occurrence, movement, and habitat use were investigated using satellite telemetry data from 26 tracked whales and analyzed through Hidden Markov Models, revealing that individuals alternate between two behavioral states: directional movements associated with transit and less directed movements linked to reproductive, feeding, or resting behaviors (Area-Restricted Search – ARS). ARS behavior was frequently recorded in topographically complex regions such as the Cananéia and São Sebastião submarine canyons and the Vitória-Trindade seamounts Chain. Dive behavior, recorded through satellite transmitters and high-resolution non-invasive sensors (DTAG and CATS), showed that 93% of dives occurred at depths ≤20 meters, within the draft range of large vessels, indicating a high risk of ship strikes. Generalized additive mixed models (GAMMs) revealed that dive depth and duration are modulated by both environmental variables (sea surface temperature, local bathymetry, chlorophyll concentration, diel period, and lunar phase) and behavioral factors (behavioral state and dive shape). Occasional events of likely feeding near the surface suggest opportunistic foraging, even within areas traditionally regarded as breeding habitats. Altogether, the results of this thesis significantly advance the understanding of sei whale ecology in tropical regions, reinforce the importance of the Santos Basin as a recurrently used area, and raise concerns about the threats posed by intense maritime traffic and offshore industrial activities. Evidence of opportunistic feeding in breeding grounds challenges classical paradigms of functional habitat segregation and calls for more integrative conservation approaches. This thesis provides a robust scientific basis for marine spatial planning, mitigation of anthropogenic impacts, and identification of priority areas for the conservation of this endangered species in the Southwestern Atlantic.

Keywords: sei whale; habitat suitability; movements; dive behavior.

SUMÁRIO

GENERAL INTRODUCTION

The study of the relationships between species and their environments has always been a central theme in ecology, forming the foundation for understanding distribution and abundance patterns (Bühler et al., 2023). The importance of climatic conditions and their relationship with the distribution of plants and animals was recognized early, as noted by Humboldt and Bonpland (1807). Climate, in conjunction with other environmental factors, has long been recognized as a major determinant of plant species distribution globally (e.g., Box, 1981; Walker, 1981). Moreover, responses to demographic, evolutionary, and ecological factors, both historical and contemporary, related to habitat characteristics and anthropogenic disturbances also influence species distribution, particularly in marine ecosystems (Genner & Hawkins, 2016). Among the factors that most explain habitat selection, prey availability stands out (Bühler et al., 2023).

Habitats are areas that provide the resources and conditions necessary for an organism's survival and reproduction (Nandy et al., 2019). These include food, shelter, and other biotic and abiotic factors (Nandy et al., 2019; Gillespies, 2024). For migratory species, habitats also encompass corridors and seasonal areas used for feeding and breeding (Krausman, 1999). Habitat use describes how a species exploits these resources, whether foraging, mating, birthing, or avoiding predators. These activities define distinct habitat functions, though overlap can occur in space and time. The distribution of cetaceans (and their prey) can respond to both static variables (e.g., bathymetry and coastal slope) and dynamic variables that fluctuate across different temporal and spatial scales (e.g., temperature, chlorophyll) (Redfern et al., 2006). The factors influencing cetacean distribution can be categorized into environmental, oceanographic, biotic, and anthropogenic variables (Cañadas & Hammond, 2008). Habitat modeling, in turn, is a powerful analytical tool for understanding these patterns, investigating where animals are found, why they occur in specific locations, and where they are expected to occur (Redfern et al., 2006; Garaffo et al., 2011). Habitat models can be either explanatory, aiming to identify which variables are important in habitat selection, or predictive, forecasting where animals are most likely to occur given certain habitat conditions (Guisan et al., 2000). Understanding how environmental variables determine distribution and habitat use is crucial for assessing potential anthropogenic and climate change impacts on threatened species (Elith et al., 2009). This knowledge, in turn, informs the development of management plans and conservation actions and the designation of protected areas for these species (Margules & Pressey, 2000).

Animal movement is a complex and multifaceted phenomenon that plays a crucial role in various ecological processes, and it is driven by a combination of intrinsic factors, such as behavioral strategies, and extrinsic factors, including environmental conditions and temporal dynamics (Linssen et al., 2024). Understanding animal movement is essential for addressing ecological questions, informing conservation efforts, and assessing broader ecosystem functions (Abrahms, 2016). This influences the structure and dynamics of populations and ecosystems (Hoover et al., 2020). Animals can move horizontally, like most terrestrial animals, in search of mates, shelter, and food. In aquatic vertebrates, these movements also occur in a vertical direction, forming a three-dimensional strategy of space use (Riaz et al., 2021). In this sense, dive behavior is a crucial component of the ecology and survival of many marine species, including air-breathing mammals, birds, fish, and reptiles (Roncon et al., 2018). Dive behavior is primarily driven by the need to access food. Many marine predators, such as seals, whales, and seabirds, dive to depths where prey is concentrated. This behavior is influenced by a combination of physiological adaptations, environmental conditions, and ecological pressures (Roncon et al., 2018).

Whales (suborder Mysticeti) are highly mobile animals, and their distribution, abundance, and behavior are influenced by the marine environment at various temporal and spatial scales (Fernandez et al., 2018). They are known for undertaking large seasonal migrations between breeding and feeding areas (Zerbini et al., 2011; Riekkola et al., 2020) and, on a smaller spatial scale, they perform vertical movements (diving) that can reach great depths, often in response to prey distribution (Panigada et al., 1999).

The sei whale (*Balaenoptera borealis*; Lesson, 1838) is one of the whale species in the family Balaenopteridae and one of the least studied (Horwood, 2009; Mizroch et al. 2016; Horwood, 2017). It is a cosmopolitan species, occurring from tropical to polar regions across all oceans (Horwood, 2017). However, its global distribution remains poorly understood due to its unpredictable occurrence patterns. Sei whales may be observed in each area for several years and then suddenly disappear (Jefferson et al., 2008; Lodi & Borobia, 2013). According to Mizroch et al. (2016), although feeding areas are relatively well defined, the location of their breeding grounds remains a mystery, as this species migrates through oceanic waters, where they are difficult to observe. However, the use of metal cylinders known as *discovery marks*, which were introduced into live whales by whalers and later recovered upon their capture, suggests a connection between sei whales off the coast of Brazil and Area II of the Antarctic region (IWC, 1977). A connection between sei whales from Brazil and the Falkland Islands was recently established (Weir et al., 2020).

Sei whales, like other large cetaceans, experienced significant pressure from commercial whaling on a global scale. In the Western South Atlantic Ocean, catches occurred in the South Georgia Islands (Horwood, 2009) and Brazil, at whaling stations in Cabo Frio (RJ) and Costinha (PB) (Paiva & Grangeiro, 1970). In northeastern Brazil, approximately 5,000 sei whales were hunted between 1947 and 1974 (Paiva & Grangeiro, 1970; Zerbini et al., 1997). Due to intense whaling during the 19th and 20th centuries and the resulting population decline, the species is currently classified as "Endangered" by the IUCN (Cooke 2018). Surveys conducted in the former whaling grounds of northeastern Brazil between 1998 and 2001 recorded only two individuals of this species (Andriolo et al., 2010).

Most of the available information on sei whales in Brazil is scattered and comes from stranded individuals or opportunistic sightings (Barros, 1991; Simões-Lopes & Ximenez, 1993; Ramos et al., 2010; Santos et al., 2010). Their occurrence is considered occasional (Lodi & Borobia, 2013), and virtually nothing is known about their genetic structure, behavior, migration patterns, or the factors influencing their distribution along the Brazilian coast. This knowledge gap is likely due to the logistical challenges of studying them in remote and difficult-to-access regions.

To effectively manage migratory species and marine ecosystems, it is imperative to understand the causes, patterns, mechanisms, and consequences of individual movement (Kot et al., 2023) and habitat use (Lin, 2017). A comprehensive understanding of how sei whales utilize space is fundamental for their conservation and management (Prieto et al., 2014).

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CHAPTER I: Habitat suitability of the Endangered sei whale in the Santos Basin, Southwest Atlantic Ocean

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Abstract

Understanding the environmental drivers of cetacean distribution is critical for the conservation of poorly known and endangered species. We used ensemble species distribution modeling to assess habitat suitability for the sei whale (*Balaenoptera borealis*) in the Santos Basin, a biologically rich and industrially active region off southeastern Brazil. Presence-absence data were obtained from systematic ship-based surveys conducted between 2016 and 2024. Environmental predictors included bathymetric, oceanographic, and productivity-related variables. After evaluating four algorithms (GLM, GAM, RF, GBM), only RF and GBM were used to construct an ensemble model using three combination strategies. The ensemble showed excellent performance (AUC = 0.990, TSS = 0.920, Kappa = 0.668). Mean depth was the most important predictor, followed by sea surface temperature, current velocity, and chlorophyll-a concentration. Suitable habitats were concentrated along the shelf break and upper slope, particularly near the Cananéia and São Sebastião submarine canyons. Residual analysis indicated low bias and good calibration, with remaining errors likely linked to unmeasured environmental heterogeneity. These findings highlight the relevance of static and dynamic environmental gradients in shaping sei whale distribution and provide a robust spatial baseline for conservation planning and impact assessment in a key region for oil exploration and maritime traffic.

Key words: Habitat suitability, ensemble modeling, sei whale.

Introduction

Species distribution models (SDMs) have become fundamental tools in ecology, biogeography, and conservation biology, offering a structured approach to understand how environmental variables shape the distribution of organisms across space and time (Elith and Leathwick, 2009).

Linking species occurrence data to environmental predictors, SDMs enable researchers not only to describe current habitat preferences but also to generate predictive maps that can be used for conservation planning, resource management, and biodiversity assessments (Franklin 2010). Furthermore, SDMs allow projections of future species distributions under different climate change scenarios, aiding in the identification of potential range shifts and emerging conservation priorities (Guisan and Thuiller 2005). The SDM are particularly valuable in marine ecosystems, where direct and continuous sampling is often logistically challenging, and environmental gradients are complex and dynamic (Redfern et al. 2006).

Whilen SDMs provide a broad framework for relating species occurrences to environmental variables (Elith and Leathwick 2009), habitat suitability modeling (HSM) represents a specific application focused on identifying and characterizing areas that offer favourable conditions for the persistence of species (Franklin 2010). Given the accelerating pace of anthropogenic environmental changes, habitat suitability modeling represents a critical methodology for anticipating threats, guiding mitigation strategies, and supporting evidence-based policy decisions (Elith and Leathwick 2009; Franklin 2010; Guisan and Thuiller 2005, Maricato et al. 2025).

The sei whales (*Balaenoptera borealis*) are recognized as endangered species and experienced intense exploitation across its global range, particularly in the North Pacific and Southern Ocean (Horwood 1987), resulting in a severe decline in population numbers (Reilly et al. 2008, Cooke 2018). In South Hemisphere, sei whale it is estimated that 205,000 sei whales were caught during the 1900s, particularly between the 1950s and 1970s (Rocha et al. 2014).

Along the south–southeast coast of Brazil, sei whale occurrence and movements are primarily associated with the continental slope region, particularly near submarine canyons and upwelling systems (Baracho-Neto et al. 2025), however, there remains a significant knowledge gap regarding suitable habitats and the environmental variables that influence the presence of sei whales in this region.

In this study, we apply habitat suitability modeling to predict the habitat suitability of sei whales (*Balaenoptera borealis*) in the Santos Basin, Southeastern Brazil, to delineate high-suitability areas, evaluate the influence of key environmental variables, and provide baseline information to support conservation planning and risk mitigation in an area of intensifying human activity.

We hypothesise that suitable habitats for sei whales are determined by both static variables, such as mean depth and slope, and dynamic variables, including chlorophyll concentration, sea surface temperature, and ocean current velocity.

Materials and Methods

Information about sei whales was obtained during the Cetacean Monitoring Project in Santos Basin (PMC-BS), south and southeastern Brazil, executed by PETROBRAS as demanded by IBAMA (Brazilian Institute of Environment and Renewable Natural Resources) in the federal environmental licensing of oil and gas production and transportation at the Santos Basin.

Study area

The Santos Basin (SB) has a maximum width of 200 km and is located between Cabo Frio, State of Rio de Janeiro (~23ºS) and the island of Santa Catarina, State of Santa Catarina (~28ºS), covering the coastal region of four Brazilian states and occupies approximately 150,000 km^2 (Figure 1) (Castro et al. 2006, Brandini et al. 2018).

In the northern sector of the basin, the continental shelf and slope are primarily affected by the Brazil Current, which carries tropical, warm, and nutrient-poor waters southward (Brandini et al. 2018) and in the vicinity of Cabo Frio, persistent northeast winds promote seasonal upwelling of South Atlantic Central Water (SACW) into surface layers, generating a frontal system that advances southward along the shelf. This process boosts productivity and alters both the composition and density of phytoplankton communities (Brandini et al. 2018, Palma and Matano 2009).

At the southern boundary, the continental shelf and slope are influenced by the convergence of the Brazil Current with cold subantarctic waters transported northward by the

Malvinas/Falkland Current, as well as by the influx of continental waters from the La Plata River and Patos Lagoon plumes (Moller et al. 2008, Matano et al. 2010).

Positioned along the central slope of the Santos Basin, the Cananéia Canyon is a prominent submarine structure shaped by successive retrogressive slump events. Its head is notably broad and stepped, spanning about 23 km across and reaching an elevation of 370 meters (Hercos et al. 2023). Approximately 150 km to the north, the São Sebastião Canyon emerges as a similarly narrow and linear feature, originating on the continental shelf at depths between 150 and 200 meters and descending to depths greater than 1,500 meters. These two canyons play key roles in the sedimentary processes of the Santos Basin shelf, serving as pathways for nutrient-rich deep waters and contributing to the region's geological and ecological diversity (Figueiredo Jr et al. 2023).

The Santos Basin is actually the major area for oil and gas exploration in Brazil, particularly known for its sub-salt oil fields accounting for a substantial hydrocarbon production of Brazil (Souza and Sgarb 2019). The region is also contiguous to the largest urban areas of Brazil, with many ports, intense fishing activities and tourism. Due to the intense traffic of large vessels, it is considered a ship-strike risk hotspot for large whales (Nisi et al. 2024).

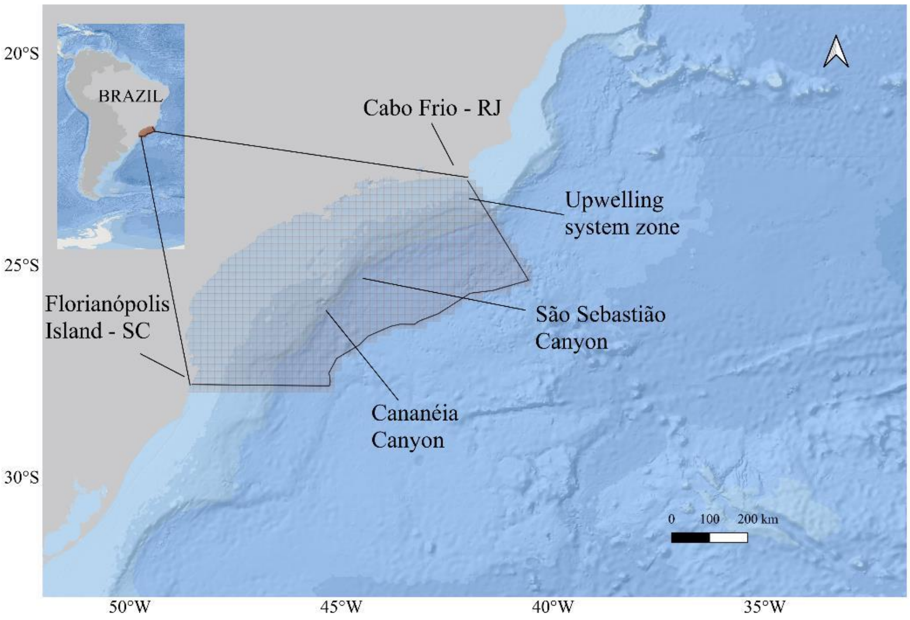

Figure 1. Study area showing the boundaries of the Santos Basin, the 16 km² grid cells corresponding to the sampling units, as well as the main submarine canyons and the approximate area of the Cabo Frio upwelling system in the Southwestern Atlantic Ocean.

Sampling design

The research involved ship-based line transect surveys with distance sampling to estimate cetacean density and characterize the cetacean community hereafter referred to as sighting surveys, as well as additional ship-based surveys aimed at locating individuals suitable for satellite tagging hereafter referred to telemetry surveys. Both coastal and oceanic waters were surveyed using a 23.7-meter motorized vessel, covering a grid of analytical blocks approximately 16 km² in area (~0.16° resolution). These blocks served as the fundamental spatial units for both whale detection and the extraction of environmental data (Figure 1).

The surveys were conducted throughout all seasons of the year; however, only sei whale detections and associated environmental predictors from campaigns conducted between June and December were used, due to the seasonal occurrence pattern of sei whales in the study area (Baracho-Neto et al. 2025)

Data analysis

We modelled the habitat suitability of the sei whale (*Balaenoptera borealis*) within the SB using a species distribution modeling (SDM) approach. Our methodological framework follows the ODMAP protocol (Zurell et al. 2020) (Table S2), incorporating data preprocessing, model calibration, validation, ensemble modeling, and prediction mapping.

Environmental predictors were assigned to the centroids of each analysis block and included depth, slope, sea surface temperature (SST), salinity, chlorophyll-a concentration, and surface current velocity (Table S1). To reduce collinearity, we applied the variance inflation factor (VIF < 3) using the `usdm` package (Naimi et al. 2014) and visually examined Pearson correlation matrices (|r| < 0.7) (Zuur et al. 2009, Elith et al. 2010, Dormann et al. 2013).

We used the R package `biomod2` (Thuiller et al. 2009) to implement four algorithms: Generalized Linear Models (GLM), Generalized Additive Models (GAM), Random Forest (RF), and Gradient Boosted Machines (GBM). Each model was trained using 70% of the data and validated with 30% through five-fold cross-validation. Model performance was assessed through sensitivity, specificity, calibration, and validation (AUC), following standard practices for model evaluation (Swets 1988, Allouche et al. 2006) (Table 1).

Based on the evaluation of individual model performance, only the Random Forest (RF) and Gradient Boosted Machines (GBM) algorithms were selected for ensemble modeling. The ensemble was constructed using the 'BIOMOD_EnsembleModeling' function, applying the simple mean (EMmean) based on AUC scores. Model performance was assessed using three evaluation metrics: the Area Under the ROC Curve (ROC; Swets 1988), the True Skill Statistic (TSS; Allouche et al. 2006), and Cohen's Kappa coefficient (Kappa; Cohen 1960). Performance metrics were independently calculated for the ensemble model, based on the combined predictions from RF and GBM, rather than by averaging individual model performances.

Model residuals, calculated as the difference between observed presence and predicted suitability, were further analyzed through a histogram and summarized using descriptive statistics, including mean residual, mean absolute error (MAE), and standard deviation (SD).

Habitat suitability values, ranging from 0 (low suitability) to 1 (high suitability), were assigned to each analysis block and exported as continuous spatial layers. Residuals were calculated as the difference between observed presence and predicted suitability values and mapped to evaluate spatial patterns of model error.

Variable importance was assessed through permutation-based analysis, which quantifies the contribution of each predictor by measuring the decrease in model performance when its values are randomly permuted.

Table 1. Model evaluation metrics for the four algorithms (GLM, GAM, RF, and GBM) based on cross-validation testing data. Sensitivity and specificity represent the proportion of correctly predicted presences and absences, respectively. Calibration indicates the agreement between predicted and observed probabilities. Validation corresponds to the area under the ROC curve (AUC), assessing the overall model discrimination capacity.

Algorithm	Sensitivity (%)	Specificity (%)	Calibration	Validation (AUC)
RF	100	99.8	1.00	0.85
GBM	100	94.7	0.985	0.87
GLM	91.4	68.8	0.86	0.85
GAM	95.0	85.6	0.946	0.82

Results

Between 2016 and 2024, 119 sei whale groups were recorded (26 groups during sighting surveys and 93 during telemetry surveys), with group size spanning from one to 32 individuals, including three calves (mean = 3.4 ± 4.1; median = 2).

For more details on the sei whale occurrence data described in this study, see Baracho-Neto et al. (2025).

Model performance

The ensemble model combining Random Forest (RF) and Generalized Boosted Regression Models (GBM) exhibited excellent predictive performance. The ensemble achieved an AUC of 0.990, a TSS of 0.920, and a Kappa coefficient of 0.668 (Figure 2).

Residual analysis revealed a low mean residual value (-0.049), indicating minimal bias in model predictions. The mean absolute error (MAE) was 0.083, and the standard deviation of residuals was 0.145, suggesting that prediction errors were symmetrically distributed and relatively small (Table 2).

The histogram of residuals, overlaid with a normal density curve, revealed a symmetric distribution centred near zero, indicating well-calibrated predictions and minimal systematic bias in the ensemble model (Figure 3).

Table 2. Summary statistics of model residuals (Observed – Predicted) for the ensemble habitat suitability model.

Statistic	Value
Mean Residual	-0.049
Mean Absolute Error (MAE)	0.083
Standard Deviation (SD)	0.145

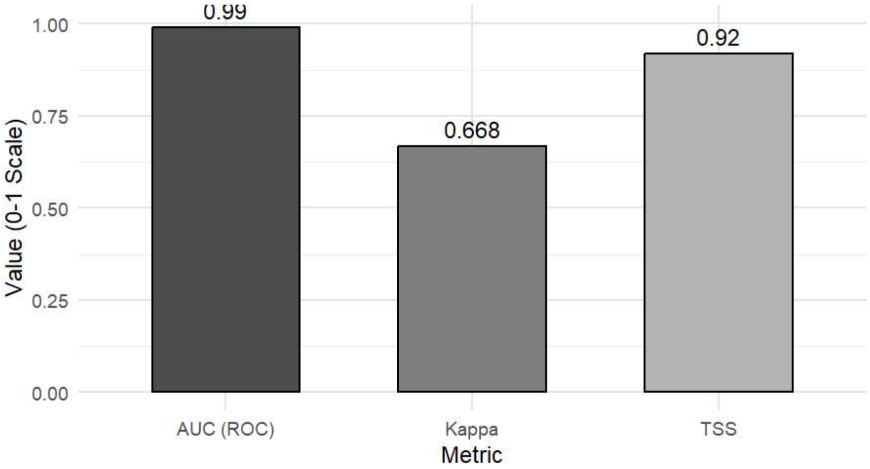

Figure 2. Evaluation metrics for the ensemble habitat suitability model combining Random Forest (RF) and Generalized Boosted Regression Models (GBM). Values are shown for the Area Under the ROC Curve (AUC), the True Skill Statistic (TSS), and Cohen's Kappa coefficient (Kappa), indicating high model accuracy, strong discriminatory capacity, and moderate agreement beyond chance, respectively.

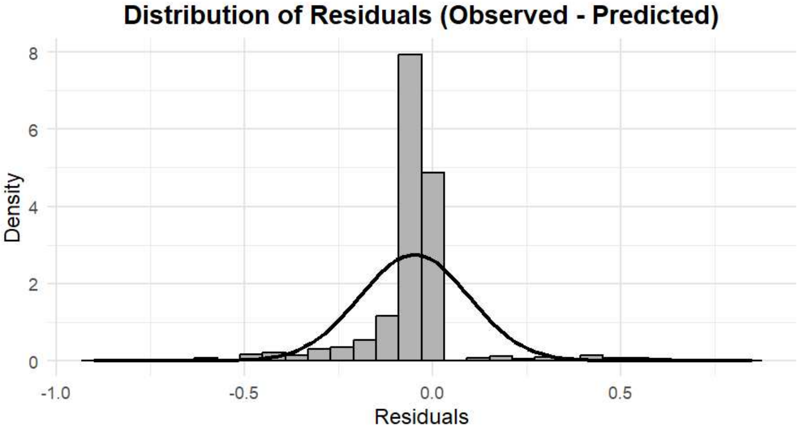

Figure 3. Histogram of residuals (observed presence – predicted suitability) for the ensemble model. The distribution is approximately centred on zero, indicating minimal bias in predictions.

Environmental predictors importance

Permutation-based analysis revealed that mean depth was the most influential environmental predictor in the ensemble model (44%). Other variables, including sea surface temperature (18%), current velocity, and chlorophyll concentration (14%), also contributed to model performance, while slope range had comparatively lower importance (10%) (Figure 4).

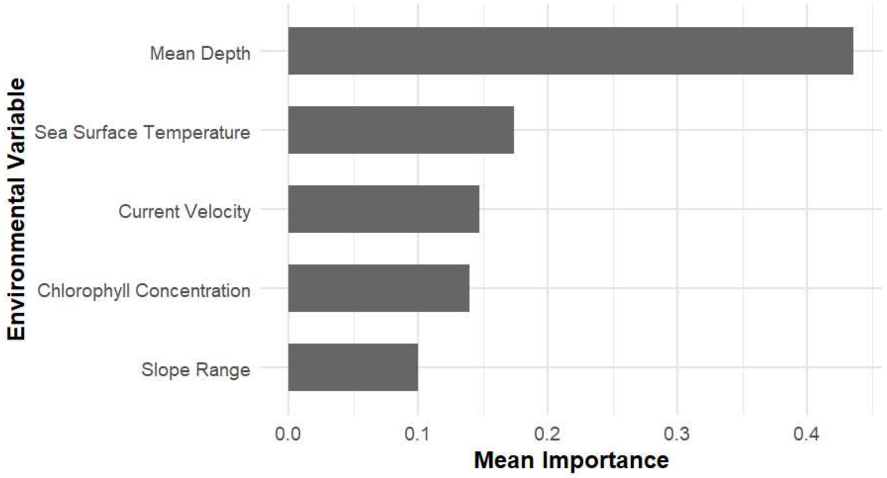

Figure 4**.** Mean importance of environmental predictors used in the ensemble habitat suitability model (Random Forest and Gradient Boosting Machine).

Habitat suitability patterns

Habitat suitability predictions indicated that suitable areas for sei whales were predominantly concentrated along the shelf break and the upper continental slope between 24°S and 27°S (Figure 5).

The spatial distribution of residuals revealed a predominantly neutral pattern, with most analysis blocks displaying values close to zero, indicating good model calibration (Figure 6). Positive residuals (in red), where observed presence exceeded predicted suitability, were sparsely distributed and generally isolated. Negative residuals (in blue), indicating overprediction by the model, were also scattered and did not form large contiguous areas (Figure 6).

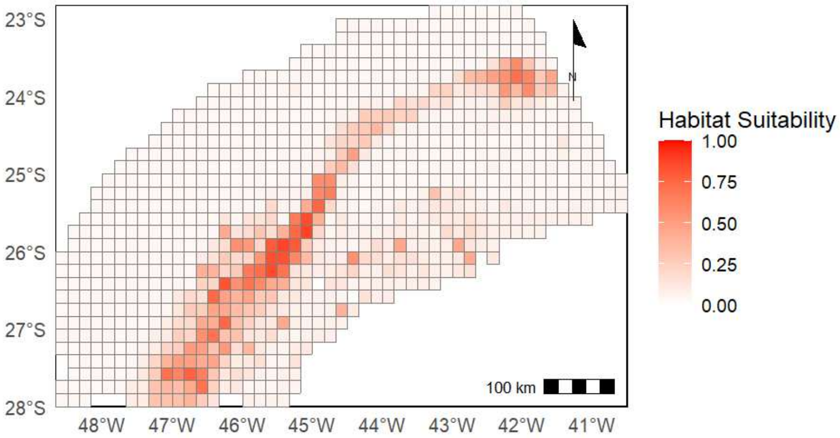

Figure 5. Predicted habitat suitability for *Balaenoptera borealis* based on the ensemble model combining Random Forest and GBM. Suitability values range from 0 (low suitability) to 1 (high suitability).

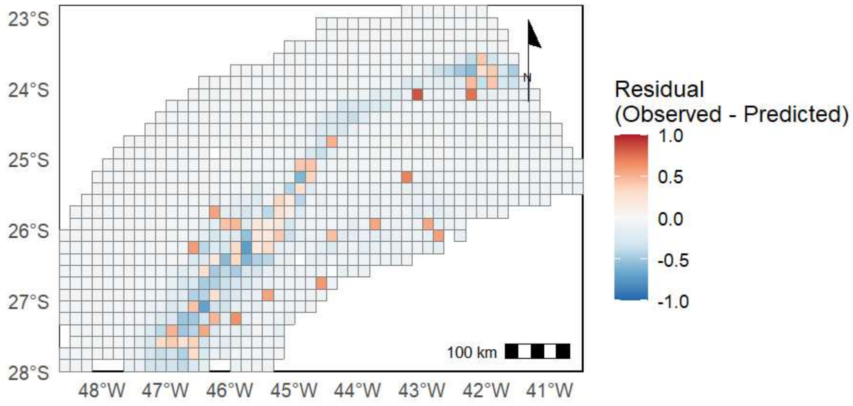

Figure 6. Spatial distribution of residuals between observed presence data and predicted habitat suitability for *Balaenoptera borealis*. Positive residuals (in red) indicate areas where the species was observed but suitability was underestimated by the model. Negative residuals (in blue) correspond to overpredicted suitability in the absence of observed presences. Neutral values (white) indicate accurate model predictions.

Discussion

Model performance

The ensemble model, combining Random Forest (RF) and Generalized Boosted Regression Model (GBM) algorithms, exhibited outstanding predictive performance in modeling habitat suitability for *Balaenoptera borealis*. The high evaluation metrics, AUC (0.990), TSS (0.920), and Kappa (0.668), indicate a robust capacity to distinguish suitable from unsuitable habitat areas (Swets 1988, Allouche et al. 2006, Freeman & Moisen 2008).

The Area Under the ROC Curve (AUC) is a widely accepted metric for assessing model discrimination ability, being insensitive to prevalence and decision thresholds (Swets 1988). AUC values close to 1, as observed in this study, reflect an excellent balance between true positive and false positive rates. The True Skill Statistic (TSS) provides additional validation by accounting for both sensitivity and specificity and remains independent of species prevalence (Allouche et al. 2006). The TSS value of 0.920 indicates high predictive power, minimizing both omission and commission errors. Furthermore, Cohen's Kappa coefficient, which adjusts for random agreement between observed and predicted occurrences (Cohen 1960), yielded a value of 0.668, representing substantial agreement according to established interpretative scales.

The ensemble approach improved predictive reliability by leveraging the complementary strengths of RF and GBM. Ensemble methods are known to enhance model robustness by reducing the variance and bias associated with individual algorithms (Dietterich 2000, Araújo and New 2007). The results thus confirm the suitability of ensemble modeling for habitat suitability studies of highly mobile marine species such as sei whales.

Environmental predictors importance

The dominant influence of depth aligns with others study. Depth was the most important predictor in both simple and full models of sei whale distribution in the North Atlantic where whales were more frequently observed in deep waters (Houghton et al. 2020). Indeed, the occurrence pattern in deep waters is well documented for this species in the SB (Baracho-Neto et al. 2025) and throughout its global range (Horwood 2009, Iñíguez et al. 2010, Prieto et al. 2014, Mizroch et al. 2016, Acevedo et al. 2017, Español-Jiménez et al. 2019, Cisterna-Concha et al. 2023). Depth was an important predictor in their GAM and MaxEnt models for sei whales around the Falkland Islands. However, sei whales in that region were frequently encountered over shallower, inner shelf habitats characterized by relatively flat bathymetry (Baines and Weir 2020). This finding suggests ecological sei whale plasticity in habitat use.

Sea surface temperature (SST) emerged as an important environmental predictor for sei whale distribution in several studies. In the Falkland Islands, SST was the most influential variable in the MaxEnt model, contributing 68% to the final predictions (Baines and Weir 2020). Sei whale density increased continuously with rising SST values, suggesting a seasonal preference for warmer surface waters during summer, likely linked to prey aggregation dynamics. Similarly, in the North Atlantic, SST is a relevant, albeit secondary, predictor after bathymetry and sea surface height anomalies (Houghton et al. 2020). In contrast, SST did not emerge as a significant predictor for Bryde's whales in southeastern Brazil, where other factors such as distance to coast and depth were more influential (Tardin et al. 2017). Nevertheless, SST has been widely associated with productivity patterns and prey distribution for cetacean species across various biogeographic regions (Croll et al. 2005, Tynan and Polovina 2004, Derville et al. 2018, Houghton et al. 2020, Ramírez-León et al. 2021), reinforcing its ecological relevance for mobile marine predators.

The chlorophyll-a concentration is a well-established indicator of phytoplankton abundance and productivity gradients, as shown in cetacean habitat studies (Ramírez-León et al. 2021). In breeding areas, where baleen whales engage in minimal or no foraging activity, environmental variables associated with primary productivity, such as chlorophyll-a concentration, may exert limited influence on habitat selection, as observed for humpback whales in New Caledonia by Derville et al. (2018). Although chlorophyll-a concentration is often used as a proxy for primary productivity in cetacean habitat models, its predictive power can vary depending on regional trophic dynamics. In the Cabo Frio upwelling system off southeastern Brazil, high chlorophyll-a levels did not correspond to higher Bryde's whale occurrence, likely due to trophic decoupling between primary production and zooplankton aggregation (Tardin et al. 2017). In contrast, chlorophyll-a was an important predictor of Bryde's whale distribution in a broader region of southeastern Brazil, where upwelling-driven productivity more directly supported higher trophic levels (Maricato et al. 2024). These contrasting results suggest that while chlorophyll-a can serve as a useful indicator of suitable habitats, its reliability is contingent upon local ecological processes that regulate prey availability. In the present study, the association between chlorophyll-a concentration and habitat suitability may suggest that sei whales engage in opportunistic foraging during the breeding season, exploiting locally available prey in productive shelf and slope environments (Baracho-Neto et al. 2025).

Current velocity, though less commonly emphasized in traditional habitat models, emerged as an ecologically plausible predictor in this study. Ocean currents are known to influence fine-scale prey dynamics, modulate nutrient transport, and shape aggregation zones for zooplankton and forage fish, which are key to mysticete foraging success (Mercker et al. 2024).

In this study, slope range was used as a measure of seabed heterogeneity and showed the lowest contribution to the ensemble model. However, areas of higher habitat suitability were predominantly associated with the shelf break, upper slope, and regions near submarine canyons, where the seabed exhibited greater slope range due to abrupt topographic transitions between shallow and deep waters. A positive association between slope and Bryde's whale occurrence in the same region has also been reported, highlighting the role of bathymetric complexity in enhancing prey availability (Dalpaz et al. 2023).

Collectively, these results underscore the importance of combining both static (e.g., depth) and dynamic (e.g., SST, chlorophyll, currents) environmental variables to accurately capture the ecological drivers of sei whale distribution.

Habitat suitability patterns

The habitat suitability map revealed that the most suitable areas for sei whales in the study region are concentrated along the shelf break and upper continental slope, particularly between 24°S and 27°S. These zones are characterized by abrupt depth transitions and increased bathymetric complexity, which are often associated with elevated biological productivity and prey aggregation (Hooker and Baird 2001, Tynan and Polovina 2004, Croll et al. 2005). These high-suitability zones geographically coincided with the locations of the Cananéia and São Sebastião submarine canyons. Submarine canyons can attract cetaceans due to a combination of physical, oceanographic, and biological processes that enhance productivity and prey availability. The habitat heterogeneity generated by steep and varied bathymetry contributes to increased foraging opportunities in these areas (Moors-Murphy, 2014).

The habitat suitability data presented here are consistent with movement patterns of sei whales tracked via satellite telemetry, which revealed ARS behavior and high occupancy in the shelf break and upper continental slope region, particularly near the Cananéia and São Sebastião canyons (Baracho-Neto et al. 2025).

Residuals exhibited a geographically structured pattern, with the largest mismatches between observed presence and predicted suitability occurring near the outer margins of high-suitability areas, particularly in offshore and northeastern portions of the study region. These localized residual patterns likely reflect the influence of unmeasured environmental gradients or fine-scale oceanographic dynamics not captured by the predictor variables included in the model (Elith and Leathwick 2009). Although these areas did receive survey effort, telemetry-based sampling was spatially concentrated in specific regions, potentially contributing to residual clustering. Therefore, the observed residuals are not merely a result of sampling gaps, but may also indicate ecological complexity, transient habitat features, or limited spatial representativeness in the input data. The spatial distribution of residuals provides valuable diagnostic insight, highlighting regions where predictive uncertainty remains high and where future modeling efforts could benefit from incorporating additional dynamic or mesoscale variables (Elith and Leathwick 2009).

Conclusion

This study provides novel insights into the habitat preferences of the endangered sei whale (*Balaenoptera borealis*) during the breeding season in the Southwestern Atlantic. In this region, ecological knowledge of the species remains limited. By applying ensemble modeling techniques to true presence-absence data, we identified key environmental predictors and mapped areas of high habitat suitability, particularly along the shelf break, upper slope, and submarine canyon regions. These findings contribute to closing critical knowledge gaps for this globally vulnerable species, emphasizing the importance of dynamic and topographically complex habitats even in putative reproductive grounds.

From a conservation perspective, identifying and characterizing suitable habitats is essential for informing spatial planning and mitigating potential threats, such as ship strikes and habitat degradation. Future efforts should focus on integrating dynamic oceanographic variables, expanding survey coverage across transitional offshore zones, and considering the cumulative impacts of maritime activities. Strengthening research and monitoring initiatives in these key areas will be vital for advancing sei whale conservation in Brazilian waters and contributing to broader management frameworks for sei whale in the South Atlantic.

Acknowledgments

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Supplementary Material

Table S1. Description of environmental and behavioral variables used as candidate predictors in the GAMM models to evaluate the diving behavior of sei whales (*Balaenoptera borealis*).

Candidate predictor variables	Source
Mean Depth (m)	General Bathymetric Chart of the Oceans (GEBCO)
Maximum Depth (m)	General Bathymetric Chart of the Oceans (GEBCO)
Minimum Depth (m)	General Bathymetric Chart of the Oceans (GEBCO)
Depth Range (m)	General Bathymetric Chart of the Oceans (GEBCO)
Mean Slope (°)	General Bathymetric Chart of the Oceans (GEBCO)
Slope Range (°)	General Bathymetric Chart of the Oceans (GEBCO)
Mean Current Velocity (m/s)	NOAA OSCAR – Ocean Surface Current Analysis - Real Time
Mean Sea Surface Temperature (°C)	Danish Meteorological Institute (DMI)

Maximum Sea Surface Temperature (°C)	Danish Meteorological Institute (DMI)
Minimum Sea Surface Temperature (°C)	Danish Meteorological Institute (DMI)
Temperature Range (°C)	Danish Meteorological Institute (DMI)
Mean Salinity (PSU)	U.S. Naval Oceanographic Office (NAVOCEANO)
Mean Chlorophyll-a (mg/m³)	NASA Ocean Color Group
Maximum Chlorophyll-a (mg/m³)	NASA Ocean Color Group

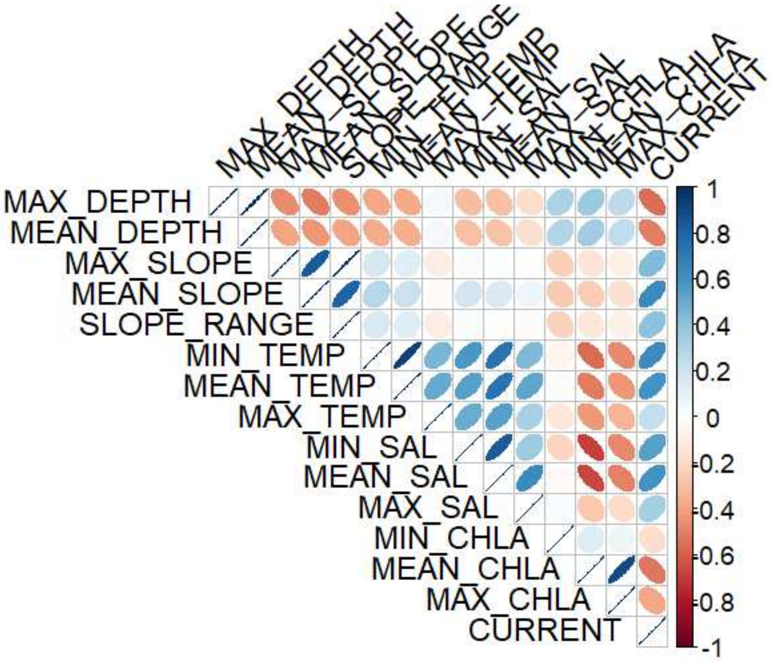

Figure S1. Pairwise Pearson correlation matrix among environmental predictor variables used in the habitat suitability models for *Balaenoptera borealis*. The ellipses indicate the strength and direction of correlations: blue tones represent positive correlations, red tones indicate negative correlations, and the color intensity corresponds to the correlation coefficient (r), as shown in the scale bar. Before model selection, highly correlated variable pairs (|r| > 0.7) were evaluated for multicollinearity.

Table S2. Summary adapted from the ODMAP protocol describing habitat suitability modeling steps and metadata for sei whales (*Balaenoptera borealis*), following Zurell et al. (2020).

ODMAP Element	Description
1. Objective	Predict habitat suitability for sei whales (Balaenoptera borealis) in the Santos Basin, SE

	Brazil.
2. Taxon	Balaenoptera borealis (Sei whale)
3. Study area	Santos Basin, Southwestern Atlantic (~23°S–28°S)
4. Time period	2016–2024 (occurrence data from June to December only)
5. Data type	Presence/absence (true absences from unsampled grid cells)
6. Sampling strategy	Ship-based sighting and telemetry surveys across 16 km^2 blocks
7. Spatial resolution	0.16° (~16 km^2 grid blocks)
8. Environmental predictors	Mean depth, slope range, SST (mean, max, min), SST range, salinity, current velocity, chlorophyll-a (mean, max)
9. Data sources (predictors)	GEBCO, DMI, NAVOCEANO, NOAA OSCAR, NASA Ocean Color
10. Collinearity check	VIF < 0.7; Pearson's correlation ($\|r\| < 0.7$)
11. Modeling algorithm(s)	GLM, GAM, RF, GBM (using biomod2 R package)
12. Software and packages	R 4.x, biomod2, usdm, raster, ggplot2, sp, sf
13. Data partitioning	5-fold cross-validation (70% training / 30% testing)
14. Ensemble strategy	Simple mean (EMmean), committee averaging (EMca), weighted mean by AUC (EMwmean)
15. Evaluation metrics	ROC, TSS, Kappa, sensitivity, specificity, calibration
16. Model selection criteria	Only RF and GBM selected for ensemble modeling based on performance
17. Final output	Continuous habitat suitability maps (0–1), residual maps, predictor importance barplots
18. Residual analysis	Mean residual, MAE, SD; residual maps and histogram with normal curve overlay
19. Interpretation	High suitability linked to slope break, canyons, and thermal/chlorophyll fronts
20. Supplementary files	predictor table, ODMAP summary

CHAPTER II Movements of the endangered sei whale (*Balaenoptera borealis*) in the southwestern Atlantic Ocean

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Key words: Movements, satellite transmitters, digital tags, sei whale

ABSTRACT

The sei whale (*Balaenoptera borealis*) was once abundant n the Southwestern Atlantic Ocean. Following intensive whaling, the species was severely depleted and is now considered endangered due to its low numbers and prolonged history of exploitation. While some occurrence data exists for sei whales in the Southwestern Atlantic Ocean, the understanding on this species' population ecology remains limited. In this study, we used information from visual surveys and from satellite telemetry to investigate sei whales' occurrence and movements in Santos Basin, off southeastern Brazil, in tropical waters of the Atlantic coast of South America. Between 2016 and 2024, 119 sei whale groups were sighted in the study area, with group sizes varying from 1 to 32 individuals (mean = 3.4 ± 4.1). Although the Brazilian coast is a presumed breeding ground, only three calves were recorded. A total of 26 sei whales were tagged during the study period, with track duration ranging from 3 to 53 days (mean = 22.5 ± 16.9). Total distance travelled ranged from 112.6 to 4,313.7 km (mean = 1,522.1 ± 1,179.5). A

Hidden Markov Model (HMM) was fitted to telemetry data to predict behavioral states from location data. Models showed that sei whales predominantly engaged in Area Restricted Search (ARS) (53.6%) during the monitoring period, while transiting behavior was classified in 46.4% of the locations. Most of the locations estimated as ARS were in areas with marked topographic features such as submarine canyons along the continental slope of southeastern Brazil and close to seamounts. The occupancy time indicates frequent and yearly use of these areas, but movement patterns were not predictable and provide important information on use of breeding grounds. Since ARS occurred in areas considered productive, it may be related to opportunistic feeding, but more research is needed to describe this species behavior in tropical breeding grounds. This work brings an unprecedented and robust data set on this species, showing its regular occurrence and movements in the pelagic waters of the southeastern Brazilian coast during winter and spring

INTRODUCTION

The sei whale (*Balaenoptera borealis*) is the third largest member of the Balaenopteridae family and can be found in all oceans, predominantly in deep waters or near the continental slopes of temperate to subpolar waters (Mizroch et al. 2016, Horwood 2009). It is one of the least known whales, and the species has a reputation for its unpredictable occurrence, appearing in an area followed by their disappearance and subsequent absence for many years (Tonnesen & Johnsen 1982, Mizroch et al. 2016, Horwood, 2017). Furthermore, the scarce information about the species is limited to observations in polar and temperate regions (Cisterna-Concha et al. 2023, Weir et al. 2021, Huijser et al. 2018, Acevedo et al. 2017, Prieto et al. 2014, Iñínguez et al. 2010). Sei whale is currently listed on the IUCN Red List as a globally endangered species mainly because of the whaling industry exploitation (Cooke 2018). In the Southern Hemisphere it is estimated that 205,000 sei whales were caught during the 1900s, particularly between the 1950s and 1970s (Rocha et al. 2014). The IWC divides the sei whale globally into three main populations, North Atlantic, North Pacific and Southern Hemisphere and their respective 'stocks' for management purposes (Donovan 1991). Tagucho et al. (2021) showed a hierarchical genetic structuring of sei whales globally, with high genetic diversity in the Southern Hemisphere and North Pacific. Additionally, whales in the Southern Hemisphere were genetically closer to North Pacific whales than to North Atlantic whales.

On the coast of northeastern Brazil, sei whales were abundant in the whaling period, but after the intense whaling activity, their presence became rare (Zerbini et al. 1997, Andriolo et al. 2010). However, recent records evidence the occurrence of this species in other parts of the Southwestern Atlantic Ocean (SWA), including different regions of the Brazilian coast, but mostly in the southeastern region, where more searching effort was made (Belgrano et al. 2007, Iñíguez et al. 2010, DiTullio et al. 2016, Weir et al. 2021). Heissler et al. (2016) suggest that waters around Vitoria-Trindade Seamounts Chain and Trindade and Martin Vaz Archipelago could be a calving ground based on 13 sightings, including two calves. Further photo-identification comparisons revealed a migratory connection between Santos Basin, southeastern Brazil and the Falkland Islands, off Argentina (Weir et al. 2020). While these studies brought relevant information on this poorly known and endangered species, the understanding of its movements and ecology remains limited, especially in their tropical breeding grounds.

Animal movement plays an essential role in numerous ecological processes and is vital for our comprehension of animal behavior, population dynamics and structure, and the consequences of climate change (McClintock & Michelot 2018). Particularly for wide-ranging, migratory and endangered species, movements and occupation time are tools that help to establish conservation plans like Important Marine Mammals Areas (IMMA) (Tetlei et al. 2022) and blue corridors, important migratory corridors that link critical habitats for whales and other marine organisms (Palacios et al. 2023). In this study, we used a large-scale and long-term dataset collected in a systematic cetacean monitoring project to investigate sei whales' distribution and satellite tags to get information about the movements and occupation time in the Santos basin, in the Southwestern Atlantic Ocean.

MATERIALS AND METHODS

Information about sei whales was obtained during the Cetacean Monitoring Project in Santos Basin (PMC-BS), south and southeastern Brazil, executed by PETROBRAS as demanded by IBAMA (Brazilian Institute of Environment and Renewable Natural Resources) in the federal environmental licensing of oil and gas production and transportation at the Santos Basin. The project included ship-based line transect with distance sampling surveys to estimate density and identify the cetacean community, referred to here as sighting surveys; and ship-based surveys to locate species that could potentially be tagged with satellite transmitters, referred to here as telemetry surveys.

Study área

The Santos Basin (SB) has a maximum width of 200 km and is located between Cabo Frio, State of Rio de Janeiro (~23ºS) and the island of Santa Catarina, State of Santa Catarina (~28ºS), covering the coastal region of four Brazilian states and occupies approximately 150,000 km^2 (Castro & Miranda 1998, Brandini et al. 2018) (Figure 1). Most of the shelf of Santos Basin is commonly referred to in the literature as the South Brazil Bight. Different hydrographic dynamics characterize SB. In the north portion of the basin, the continental shelf and the slope are influenced mainly by the tropical warm waters of the Brazil Current, which transports southwards tropical, warm, and oligotrophic waters (Brandini et al. 2018). In the northern limit of SB, near Cabo Frio, seasonal persistent northeast winds in the summer trigger upwellings of the South Atlantic Central Water (SACW) to superficial layers, creating a front that moves southwards on the shelf, enhancing productivity and changing the composition and density of phytoplankton communities (Brandini et al. 2018, Palma & Matano 2009). In the southern limit, the continental shelf and the slope are under the influence of the confluence of the Brazil Current and the subantarctic cold waters carried by the Malvinas/Falkland’s Current northwards, along with input of continental waters from La Plata River and Patos Lagoon plumes (Moller et al. 2008, Matano et al. 2010). In the SB's central slope is the Cananéia Canyon, which is a mature conduit resulting from successive retrogressive collapses (slumps) and has a large, stepped head 23 km wide and 370 m high (Hercos et al. 2023). Approximately 150 km to the north is the São Sebastião Canyon, another linear and elongated structure, starting at shallower depths on the continental shelf (~150-200 m) and reaching depths greater than 1,500 meters. The Cananéia and São Sebastião Canyons play a significant role in shaping the sedimentary characteristics of the Santos Basin shelf area, channeling nutrient-rich waters from the bottom, and contributing to the overall geological and biological diversity of the region (Figueiredo Jr et al. 2023*)*.

The Santos Basin is actually the major area for oil and gas exploration in Brazil, particularly known for its sub-salt oil fields accounting for a substantial hydrocarbon production of Brazil (Souza & Sgarb 2019). The region is also contiguous to the largest urban areas of Brazil, with many ports, intense fishing activities and tourism. Due to the intense traffic of large vessels, it is considered a ship-strike risk hotspot for large whales (Nisi et al. 2024).

Sighting surveys

The sampling design of these surveys was systematic, covering hot and cold seasons of the year. The surveys were conducted aboard a 23.7 meter-long supply ship adapted to research from November 2016 to September 2024. Each survey covered the entire Santos Basin and employed pre-defined line transects at regular spacing. Each survey spanned from 36 to 46 days. The survey lines were arranged in a zigzag pattern, shifting between 60 and 90 km from one campaign to another to minimize spatial sampling bias. These lines were oriented perpendicular to the coastline, traversing the depth gradient of the study area (from coastal to oceanic waters and vice-versa). All transect lines can be seen in Supplementary Material Figure S1. Detailed information about field procedures of the sighting surveys is available in Correa et al. (2023).

Three observers were positioned at an approximate height of seven meters above sea level, using binoculars to assist in detecting and identifying species. The geographical position was recorded for each encounter, along with group size and presence of calves. The sampling effort was carried out following the ‘passing mode’ during daylight hours, varying from eight to 11 hours each day, depending on the season.

Telemetry surveys

The telemetry surveys covered mainly cetacean high-density habitats, such as the coastal and slope regions, lasting from 22 to 40 days of effort. These surveys were conducted mainly in the winter (whale’s breeding season). Searching method was the same used in Sighting surveys but followed the ‘closing mode’. When conditions permitted, two rigid-hulled inflatable boats were released from the main boat for tag deployment attempts.

Satellite transmitters were remotely deployed on sei whales using a 180 lb crossbow (Excalibur Vixen II). We utilized Wildlife Computers, model SPLASH10, in the Low Impact Minimally Percutaneous External-electronics Transmitter (LIMPET) configuration (Andrews et al. 2008). These tags were anchored in the central region of the dorsal fin by two stainless steel 6-petals barbed darts (6.7 cm), which had been previously sterilized in an autoclave. For this study, we focused only on the analysis of location data.

The tags transmitted data via the Argos satellite system and were activated with a salt-water switch. They were programmed to transmit daily during periods of high overpass coverage of the Argos satellites in this region, totaling around 10 or 11 hours per day. The transmission rate was limited to 450 transmissions per day.

Twenty six sei whales were tagged. The average transmission interval between successive points of 2.15 (± 0.70) hours. Locations where errors that could not be estimated and within land were removed.

To standardize and minimize possible biases when estimating behavioral states, tracks with transmission intervals greater than 24 hours were segmented, thus preventing state models from generating pseudo linearity space during the standardization of intervals by continuous-time correlated-random-walk (CTCRW) models. Tracks and/or track segments with less than 10 location points have been removed.

The ‘crawlWrap’ function from the ‘momentuHMM’ package (McClintock & Michelot 2018) of R software (R Core Team 2024) was used to fit a CRCRW model. As model parameters, the time interval was set to 4 hours, a value that comprises 90% of the transmission intervals recorded in the raw data (Prieto et al. 2014) (Figure S 2), using the "Nelder-Mead" convergence method and with the parameter retryFits = 200 (which defines the number of attempts for the model to converge).

Modeling behavioral states

With the tracks regularized by CTCRW, a Hidden Markov Model (HMM) was fitted to model the behavioral states using the ‘prepData’ function from the ‘mommentuHMM’ package. This function calculates step length (modeled with a gamma distribution) and turning angle (modeled with a ‘*wrpcauchy’* distribution) intervals which are the variables used as predictors of two behavioral modes of whales: ‘Area Restricted Search’ (ARS) was characterized by short step length and low turn angle concentration; and ‘Transit’ was characterized by a long step length and high turning angle.

The visual evaluation of the distribution of steps and angles allows the identification of the initial parameter estimates of the behavioral states. To obtain an adjusted and validated model, the first step of model selection consisted of building a first model with more comprehensive parameters using the function retryFits = 1000, and then the estimated parameters for this model were used applying the ‘getPar0’ function to optimize a second model. The best model was chosen by the lowest log-likelihood value.

Occupancy time

The sei whales locations predicted by CTCRW were plotted in a grid of 50 x 50 km cells to identify high-use areas by whales. The occupancy time (in hours) spent by whales in each grid square was computed by multiplying the total number of positions in each grid square by 4 (h) and dividing the result by the number of different individuals who visited each grid. This approach provides relevant information on space use by whales (Garrigue et al. 2015, Sepúlveda et al. 2018).

Biopsy sampling and genetic sex determination

Biopsy samples for sex determination were collected during telemetry cruises using a 150 lb crossbow with darts containing adapted stainless-steel tips (Lambertsen 1987, Sinclair et al. 2015). Skin samples were preserved in 70% ethanol and stored at 20°C (Amos 1991). DNA was extracted using a DNeasy Blood and Tissue kit (Qiagen) according to the manufacturer's protocol. Molecular sex identification was carried out using a multiplexed PCR protocol to amplify fragments of the male-specific genes Sry with regions of the ZFX genes as positive controls (Gilson et al. 1998).

RESULTS

Distribution of sightings

Between 2016 and 2024, 119 sei whale groups were recorded (26 groups during sighting surveys and 93 during telemetry surveys), with group size spanning from one to 32 individuals (mean = 3.4 ± 4.1; median = 2). Most groups (n = 66; 71%) were between one and three individuals. The larger aggregation observed, of 32 whales, was estimated with the aid of an UAV (Fig.1), with 7.5% of groups larger than 10 individuals (n = 7). A calf was present in three groups (2.5%). Sei whales were observed in depths ranging from 100 to 2,349 m (mean = 692 ± 554 m) (Fig.2). A summary of the records, group size, coordinates, and depth of sightings can be seen in Supplementary Material Table S1. Sei whales were seen in the study area from June to November, but mainly in the Winter months: June (0.8%), July (48.7%), August (31%), September (14.2%), October (4.2%) and November (0.8%).

Telemetry data and biopsy samples

A total of 26 sei whales were tagged and biopsy samples were obtained from nine individuals, seven males and two females (Table 1). Transmission duration ranged from three to 53 days (mean = 22.5 ± 16.9). Total track length ranged from 112.6 to 4,313.7 km (mean = 1,522.1 ± 1,179.5).

The tracking data revealed that although there have been some inner shelf movements, offshore habitats were more important for sei whales during the breeding season, mainly on the continental slope. The tagged whales moved in a wide range of directions reaching latitudes between 18º and 39º S (Fig. 3A).

The northernmost movements were carried out by two individuals (PTT58007 and PTT197762). These movements began in July and ended in August 2019 and 2020, respectively, reaching the Vitória-Trindade Seamounts Chain (18ºS). The PTT58007 was tagged near the northern boundary of the study area (~23º S). After being tagged, the whale moved away from the slope and headed north, while the PTT197762 was tagged in the Cananéia Canyon and moved along the slope until reaching the Vitória-Trindade Seamounts Chain.

The southernmost movement was carried out by three individuals (PTT197766, PTT197767 and PTT244914) that exhibited similar movement patterns. The first two were tagged near Cananéia Canyon in August 2020 and initially moved along the continental slope between Cananéia and São Sebastião Canyons. They then began a more directed southward migration towards the oceanic region off the La Plata River mouth (~39ºS). The third whale was tagged in July 2024 near São Sebastião Canyon, moved briefly around that area, then proceeded to Cananéia Canyon before also heading south towards the La Plata River mouth. The whales eventually moved away from the continental slope as they approached the La Plata River plume.

The movements of other individuals were monitored only while they stayed within Santos Basin over the slope, moving between the canyons, going back and forth without a defined direction (Fig. 2A).

CTRW and HMM Model Results

CTRW estimated a total of 3,230 locations for 26 tagged whales resulting in 29 track segments. Of these track segments, four represent the movement of a single whale (Fig. 2). The whale PTT244911, even after data processing, presented a large transmission interval, for this reason, it was necessary to segment it once more into 12-hour intervals, transforming it into five new track segments (PTT244911, PTT244911_a, PTT244911_b, PTT244911_c and PTT244911_d). This approach allowed the CTCRW random run model to converge. The track segment PTT244911_a presented less than ten locations and was excluded from the analysis.

The HMM showed that sei whales were mostly engaged in the ARS behavioral mode (53.6% of the locations) (Fig. 3B). Most of the locations estimated as ARS were situated near specific bathymetric features, more notably the Cananéia Canyon (~26º S), the São Sebastião Canyon (~25º S), the continental slope off Cabo Frio (~23º S) and close to the Vitória-Trindade Seamount Chain (18º S). A total of 46.4% of the locations were classified as “Transit”, which were commonly observed along the southeastern and southern oceanic regions of Brazil, mostly along the slope or adjacent to it.

Occupancy Times

The areas with greater occupancy time were consistent with those where ARS behavioral mode was more predominant. Higher occupancy was documented close to Cananéia Canyon, São Sebastião Canyon, along the continental slope of Cabo Frio and close to Vitória-Trindade Seamounts Chain (Fig. 3C).

DISCUSSION

Sei whale distribution

This work presented the most complete record of sei whales in lower latitudes in the South Atlantic, including information about movements, group size and distribution. All the records occurred primarily near the continental shelf break during the austral winter and spring, the breeding season for baleen whales in the South Hemisphere (Corkeron & Connor 2006). The peak of sei whale sightings (July to September) in the present study coincides with the austral Winter, which was the period of greatest abundance of sightings and catches in the former whaling station in Costinha, Northeast of Brazil in the 60s (Paiva & Grangeiro 1965, 1970). However, it is important to highlight that the telemetry surveys were conducted during the months of known peak abundance for large whales in the Southern Hemisphere to maximize encounters with them, but eventually some cruises were carried out later in the season, during austral Spring, and invariably fewer groups of the species were detected.

Sei whales used to be common on the eastern coast of South America as they were targeted by whaling operations off Brazil's northeast (Costinha) and southeast (Cabo Frio) in the 1960s; since then they became rare probably driven to slow numbers due to whaling pressure (Paiva & Grangeiro 1965, 1970). Limited information suggested that sei whales continued to be rare in the 1990s-early 2000s from surveys that were done in the SB (Zerbini et al. 2004, Andriolo et al. 2010, Di Tullio et al. 2016). The surveys of the present study showed that sei whales have become more common in recent years, at least in southeastern and southern Brazil. Simultaneously, sei whales are also becoming more common in other areas in the western South Atlantic and the South Hemisphere (Iñíguez et al. 2010, Heissler et al. 2016, Acevedo et al. 2017, Español-Jiménez et al. 2019, Cisterna-Concha et al. 2023). Probably as a reflection of population recovery (Cooke 2018, Weir et al. 2020), but also greater searching effort.

Sei whale group size and calves’ records

Only three calves were observed during the entire study period, in July, August and October. Heissler et al. (2016) recorded three calves around the Vitória-Trindade seamount chain (~18ºS) and Paiva & Grangeiro (1965, 1970) recorded pregnant females in Northeast of Brazil (~ 6º S) indicating a large calving ground for sei whales in the South Atlantic. A small number of calves may reflect a small population that is still recovering after whaling. Another possible explanation is that the sei whales use the south-southeast coast of Brazil for other purposes besides calving and breeding. Through information collected from a land station, Paiva & Grangeiro (1965, 1970) highlighted that the region of Costinha in the state of Paraiba (~7º S) was an important breeding ground for the sei whale on the coast of Brazil. Costinha is 2,500 km north from SB and sei whales can feed opportunistically in SB while migrating to Costinha where they give birth.

Groups observed in Santos Basin were generally small, with a mean close to three individuals and a median of two whales per group, and a large proportion of solitary individuals (28%). Larger groups containing up to 32 individuals have been observed in SB, with the larger aggregations occurring mainly around the Cananéia and São Sebastião Canyons.

In the former whaling ground in the Northeast of Brazil, also a breeding ground but in lower latitudes than our study area, the sei whales' groups contained five to six individuals (Paiva & Grangeiro 1965, 1970), but these observations were made decades ago. In a recent study near the Falkland Islands (~51º S), known as a feeding area, sei whales were mostly observed alone, but groups reached up to five individuals (Weir et al. 2021). In Golfo de San Jorge (46º S), in the Argentinian Patagonia, the maximum recorded groups of sei whales were of five individuals (Iñinguez et al. 2010), while on the east coast of South America between latitudes of 10º to 30ºS small separate groups of three to five sei whales were recorded (Budylenko 1977). Thus, group organization may have changed recently due to the depletion of the population. In November in latitudes of 42º to 45º on the east coast of South America sei whales form groups of up to 20 to 40 individuals (Budylenko 1977). Large groups of baleen whales have been reported for feeding purposes in high latitudes (Landino et al. 1992, Baine et al. 2017, Herr et al. 2022). These aggregations are often associated with the availability of abundant prey, such as krill, indicating the importance of specific feeding grounds (Nowacek et al. 2011). However, large "super-groups" of humpback whales were observed in lower latitudes, in the Benguela Upwelling System (Findlay et al. 2017) and in Australia (Pirota et al. 2020), feeding aggregations not previously observed in breeding grounds. These observations suggest that the Benguela Upwelling System and other productive regions may be important seasonal feeding grounds for humpback whales during the breeding season in lower latitudes, and this may be a common strategy to cope with the lower energetic intake in breeding grounds or may be the result of a changing environment. In our study, larger groups of sei whales were observed near shelf-break canyons where productivity is usually high and could also be involved in opportunistic feeding behavior. The observation of seabirds preying on schools of small fish near the whales support this interpretation. Moreover, the largest group recorded in our study, that included 32 individuals, was accompanied by killer whales near the Cananéia Canyon (Hille et al. unpubl. data) (Figure S 6). The presence of killer whales may also explain the formation of large groups in breeding grounds for predator defense or dilution of predatory risk (Weller 2002). Nonetheless, no direct predation behavior was observed by killer whales in our study and little is known about the breeding behavior of the Sei whale, that may involve the formation of larger aggregations.

Sei whale movement patterns

The sei whale’s groups and movements were concentrated on the continental slope, but some inshore movements over the continental shelf were also observed. These movements are likely exploratory and correspond to the transit behavioral state

(46.4%) estimated for the shelf region, but occupation time in this shelf region was low. Nonetheless, it draws attention to the fact that species with oceanic habits can approach the coast occasionally. Pivari et al. (2024) recorded sounds known as downsweep calls attributed to sei whales in Ilhabela (~23º S), São Paulo, Brazil, an island very close to the continent and with shallow water around. In the North Atlantic Ocean, depth associated with the shelf break/slope was consistently one of the strongest explanatory variables affecting sei whale density, indicating a preference for deeper waters of the slope (Houghton et al. 2020).

Although no complete migration movement was recorded in this study, three whales started moving steadily southwards early in July and August along the continental slope which may be related to the onset of migration to their feedings areas in the southern higher latitudes, such as the Falkland Islands. Although the tags have stopped transmitting, the direction in which the animals were moving would have taken them close to the Falkland (Malvinas) Islands, a known migratory connection of sei whales sighted in Brazil (Weir et al. 2020). During the whaling period in the Northeast of Brazil, the sei whales started migrating toward the south in October (Paiva & Grangeiro 1965, 1960). These differences in time suggest a sex segregation during migration. Paiva & Grangeiro (1965, 1960) studied in detail the size and sex composition of sei whales caught in Costinha; they reported the predominance of large males up to 60 to 70% in the catches. At least one of these three tagged individuals who moved early to the south was determined to be male.

The regular yearly occurrence, formation of large aggregations and ARS behavior in the SB suggest that this region is an important tropical breeding and possible feeding ground for the species. However, telemetry data show that whales are transiting in a wide latitudinal range off the Brazilian oceanic waters, to the south and to the north of SB. The northernmost movement of a tagged individual reached the Vitoria-Trindade Seamounts Chain before transmission stopped. In this area, the presence of sei whales has already been documented (Heissler et al. 2016). So, filling the gaps of visual sampling effort along offshore regions of Brazil and additional telemetry efforts are necessary to describe if there are specific regions preferred for mating, calving or opportunistic feeding behaviors.

Sei whales use of upwelling systems, submarine canyons and seamounts in a tropical breeding ground

Our study found that the continental slope off south-southeast of Brazil, especially near upwelling systems in front of Cabo Frio, around Cananéia and São Sebastião Canyons and around to Vitoria-Trindade Seamounts Chain, is the region where sei whales spent more time, and the highest concentration of locations where they were engaged in ARS behavior (53.3%). Sei whales' distribution is known to respond to oceanographic conditions such as oceanic fronts, that create dynamic and productive habitats that attract the whales for feeding purposes (Murase et al. 2014) and this may be the case even for tropical breeding grounds. The waters off the south-southeast coast of Brazil, particularly around the Cabo Frio area (~23ºS) and along the shelf-break are well known for their relatively high biological productivity due to upwelling of the South Atlantic Central Water to the surface layers (Brandini et al. 2018), increasing density of potential prey for baleen whales, such as copepods and other zooplankton (Prieto et al. 2012). Therefore, a plausible explanation for ARS and high occupancy near the upwelling systems off Cabo Frio and along specific areas along the shelf-break is opportunistic feeding behavior. Opportunistic feeding is likely an essential component of energy replacement after long migration and during high energetic demand activities such as mating and calving, especially for streamlined balaenopterids such as the sei whale, that are faster and have a thinner blubber. Indeed, the Mauritanian upwelling zone, particularly near canyons, is regarded as a crucial winter habitat for balaenopteridae whales like sei and blue whales (*Balaenoptera musculus*) due to optimal prey conditions, even in the breeding season (Baines & Reichelt, 2024). Records of feeding behavior of humpback whales in tropical/subtropical breeding areas are increasingly common (e.g., Zurita & Castillejos-Moguel 2013, Frisch-Jordán et al. 2019; Alves et al. 2009, Danilewicz et al. 2009, Bortolotto et al. 2016, Siciliano et al. 2019). Burton et al. (2023) provide evidence of likely foraging behavior by pygmy blue whales (*B. m. brevicauda*) in the chlorophyll-rich waters of Timor Trough (~10º S) during late austral winter and early austral spring, challenging the traditional view of uninterrupted migration without feeding. Certain areas in the Southeast Pacific, such as the year-round upwelling systems off the coast of Peru, can support significant prey populations, making them viable feeding grounds for humpback whales even during their breeding season (Pirota et al. 2021).

Numerous cetacean species concentrate in deep submarine canyons, where complex seafloor topography and ocean currents interact to promote suitable foraging conditions (Rennie et al. 2009, Moors-Murphy 2014, Santora et al. 2014). Submarine canyons can attract cetaceans due to various physical, oceanographic, and biological mechanisms that enhance abundance in these areas, such as the habitat heterogeneity created by varied depths (Moors-Murphy 2014). The unique topography of submarine canyons can create upwelling and downwelling currents, which can concentrate nutrients and attract prey (Kent et al. 2020). Canyons can influence water flow, creating dynamic oceanographic conditions that promote prey aggregation and facilitate feeding opportunities for cetaceans (De Leo et al. 2010). It was recently described that features such as canyons and incised valleys in the shelf-break may create flows of deeper nutrient-rich waters such as the South Atlantic Central Waters (SACW) to the slope and shelf, which influences the marine communities (Castro et al. 2023). The SB is expected to be a breeding area or part of this, but opportunistic feeding should be an essential component of energy replacement after long migration.

In our work, at least two tagged whales arrived in the Vitória-Trindade Seamounts Chain, where they spent more time and the ARS behavior was recorded. Several studies reported significant associations of cetaceans to seamounts (Wong & Whitehead 2014, Tobeña et al. 2016, Romagosa et al. 2020). Garrigue et al. (2015) suggested that seamounts of the South Pacific are crucial offshore habitats resulting in high occupancy rates for humpback whales and speculated that these areas, may play various roles in the migratory cycle of the whales, including breeding, habitats, resting areas during the migration, navigational landmarks and even regions where supplemental feeding grounds could occur. According to Morato et al. (2010), seamounts are hotspots of pelagic biodiversity in the open ocean. Vitória-Trindade Seamounts Chain are known for the presence of baleen whales, such as the use by humpback whales as a breeding ground, especially those seamounts closer to Abrolhos Bank, the main breeding ground of the species in Brazil (Wedekin et al. 2014).

The ARS behavioural mode potentially represents different behavioural types (e.g., foraging, resting, breeding, and other social interactions), and its interpretation depends on the context in which it occurs (Jonsen 2016). In our study ARS behavior and higher occupancy by sei whales in productive areas such as regions with upwelling systems, submarine canyons and seamounts can indicate that these areas may serve as a critical stopover for feeding during migration to low latitudes. In the continental slope of the Santos Basin, copepods represent the most abundant and diverse taxon, accounting for approximately 33% of all recorded zooplanktonic invertebrate species. Additionally, Amphipoda (7%) and Euphausiacea (3%) are also present (Nogueira JR & Brandini 2018). These three zoological groups represent the main prey of sei whales in the South Atlantic (Cooke 2018). Although the hypothesis of feeding in the breeding area was not directly approached in this work, ARS behavior and high occupancy in specific areas, highlighting their importance as critical habitats.

CONCLUSIONS

This study provides the largest data-set on the sei whale in the low latitudes of the Southwestern Atlantic Ocean. The results were derived from a comprehensive collection of sightings through systematic boat-based surveys in Santos Basin, rigorous taxonomic identification, and the tagging of 26 individuals with satellite transmitters. The distribution and concentration of sightings revealed a high use of the shelf-break, particularly near two submarine canyons and an area off Cabo Frio, where the coastline and shelf-break change orientation. Sei whales movements indicate broad latitudinal use, spanning the southern and southeastern offshore and shelf-break waters of Brazil. These areas may be considered critical breeding habitats for the sei whale. Additionally, movement modeling revealed areas of restricted search (ARS) behavior and high occupancy around productive areas in southern and southeastern Brazil, including two submarine canyons (Cananéia and São Sebastião), the shelf-break off Cabo Frio, and the Vitória-Trindade Seamounts chain. The whales' high occupancy of these sites, associated with increased prey productivity–primarily driven by upwellings of the South

Atlantic Central Waters (SACW)–suggests that, in addition to breeding, these areas may also serve as important supplementary feeding sites for sei whales. Further sampling of oceanic waters off Brazil will be crucial in better defining the boundaries of breeding and calving habitats for this endangered migratory species, as well as exploring the potential role of opportunistic feeding in low latitudes. Transboundary distribution of the sei whale and the use of remote habitats, often with limited search effort, pose significant challenges for the conservation and management of this species worldwide.

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Table 1. Summary of sei whales tagged in the Southwestern Atlantic Ocean between 2016 and 2024.

Whale Id (PTT*)	**Start (Date)**	**End (Date)**	**Duration (days)**	**Group size**	**Sex**	**Distance Track (km)**	**Distance/Day (km)**
158546	25/08/16	30/08/16	6	10	NI	268.50	44.75
162629	31/08/16	08/09/16	9	3	Male	507.35	56.37
162630	01/09/16	08/10/16	38	2	NI	2,756.79	72.54
34638	06/08/18	13/09/18	39	15	NI	2,653.58	68.04
34755	07/08/18	18/08/18	12	32	NI	635.59	52.96
58005	08/08/18	05/10/18	59	15	Male	4,313.98	73.11
179332	28/07/19	30/07/19	3	4	Female	95.32	31.77
179339	28/07/19	07/0919	42	4	NI	2,628.35	62.57
58007	29/07/19	31/0819	34	6	Male	2,282.94	67.14
179337	29/07/19	30/08/19	33	6	NI	2,148.50	65.10
197762	22/07/20	11/08/20	28	3	NI	1,948.08	69.57
197766	02/08/20	23/09/20	53	6	Male	3,785.81	71.43

197765	02/08/20	21/08/20	20	6	Male	862.89	43.14
179336	03/08/20	09/08/20	7	5	Male	535.26	76.46
179338	03/08/20	06/08/20	4	5	Female	112.63	28.15
179334	03/08/20	10/08/20	7	2	NI	338.69	48.38
197767	22/07/20	29/08/20	39	3	NI	2,795.26	71.67
224119	12/07/22	17/07/22	6	8	NI	500.11	83.35
224122	10/07/22	17/07/22	8	8	Male	427.40	53.42
235338	28/07/22	05/0822	9	3	NI	472.89	52.54
235340	25/07/22	08/08/22	15	3	NI	1,076.82	71.78
244905	22/07/24	26/07/24	5	3	NI	128.26	25.65
244909	20/07/24	09/08/24	21	2	NI	1,295.11	61.67
244910	20/07/24	03/08/24	15	2	NI	825.24	55.01
244911	21/07/24	26/08/24	37	4	NI	2,388.02	64.54
244913	23/07/24	10/08/24	19	8	NI	985.29	51.85
244914	19/07/24	12/08/24	25	8	NI	1,911.02	76.44
Mean± SD			22.5 ± 16.9	3.4 ± 4.1		1,522.19 ± 1,179.59	59.2 ± 15.1

* Platform Transmitter Terminal (PTT), which is the code for each sei whale. NI = Sex not identified, Mean± SD when applicable.

Figure 1. Aerial image captured by an UAV showing twelve sei whales (*Balaenoptera borealis*) from a group of 32 individuals, as well as one killer whale (*Orcinus orca*).

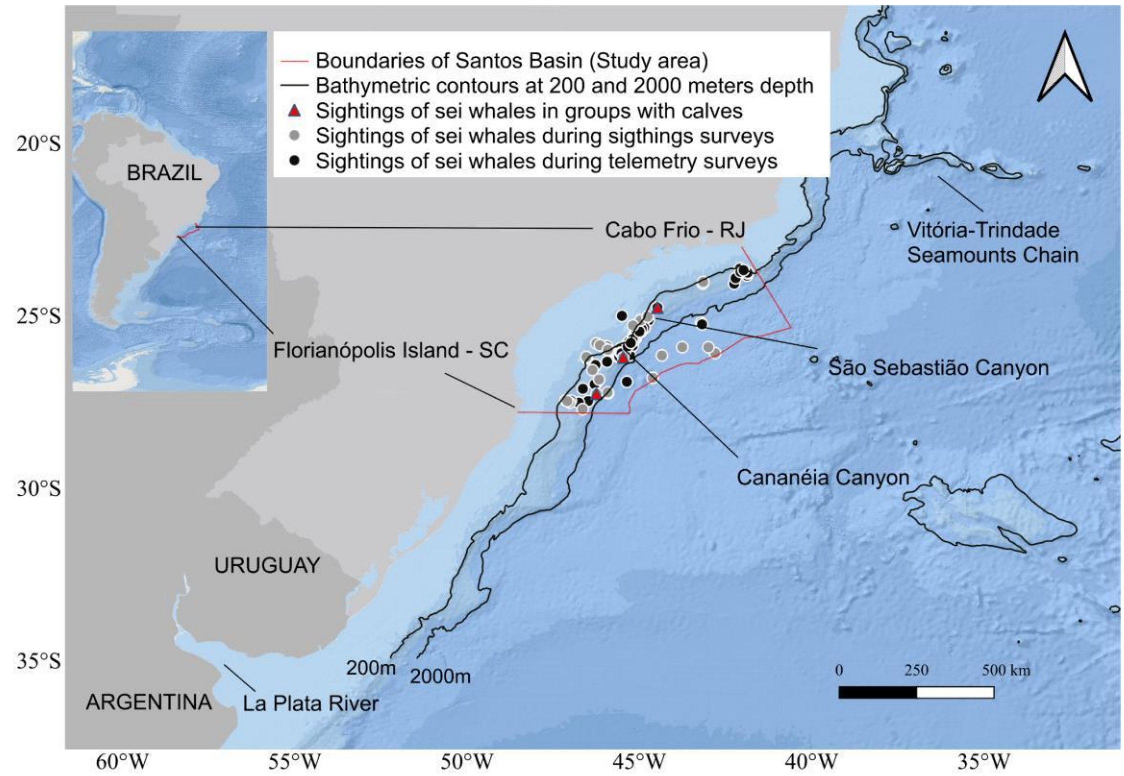

Figure 2. Study area showing the boundaries of the Santos Basin and location of the sei whale records in the Southwestern Atlantic Ocean.

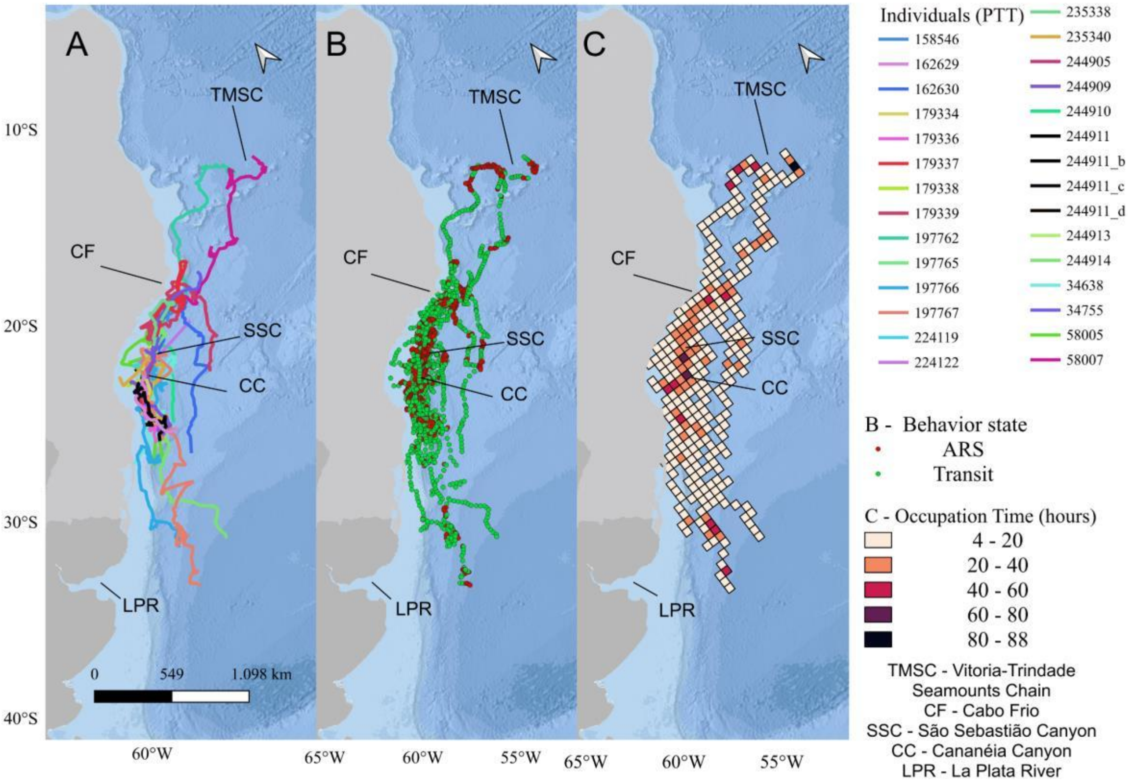

Figure 3. A) Tracks of 26 sei whales, *Balaenoptera borealis* tagged with satellite transmitters and modeled by continuous-time correlated-random-walk (CTCRW) models. The PTTs 244911, 244911_b, 244911_c and 244911_d represent different segments of the same individual. B) Behavioral states estimated by the Hidden Markov Model and applied to satellite tags data for sei whales, *B. borealis*, on the Southwestern Atlantic Ocean. C) Time of occupancy is defined as the total number of hours spent in each 50 km^2 grid square divided by the number of whales in that grid square and expressed in hours/whale.

SUPPLEMANTARY MATERIALS

Table S1. Summary of sei whales recorded in the Southwestern Atlantic Ocean between 2016 and 2024 by two different survey types.

Survey type	Date	Latitude	Longitude	Depth of sightings (n)	Group size (n)	Calves (n)
Line-transect	08/06/2016	-25.9189	-43.7582	2193	4	0
Line-transect	30/09/2016	-27.254	-45.9095	1958	2	0
Line-transect	30/09/2016	-27.231	-45.9236	1934	2	0
Line-transect	23/10/2016	-26.0919	-42.8041	2349	1	0
Line-transect	28/08/2017	-27.2703	-46.248	1620	10	1
Line-transect	03/09/2017	-25.0419	-44.7629	329	1	0
Line-transect	01/10/2017	-26.2175	-45.4704	1281	5	1
Line-transect	02/09/2018	-27.5245	-47.0258	585	1	0
Line-transect	08/09/2018	-25.809	-46.2495	145	4	0
Line-transect	08/09/2018	-25.8625	-46.1489	164	1	0
Line-transect	08/09/2018	-25.9948	-45.9152	351	1	0
Line-transect	06/09/2019	-24.0741	-43.1633	452	2	0
Line-transect	06/09/2019	-24.0284	-43.1495	320	10	0
Line-transect	06/10/2019	-26.1609	-44.3493	2270	1	0
Line-transect	26/08/2020	-26.5826	-46.3634	387	1	0
Line-transect	26/08/2020	-26.2397	-46.5291	173	2	0
Line-transect	26/08/2020	-26.2057	-46.5406	173	1	0
Line-transect	25/09/2020	-25.9215	-42.9995	2198	2	0
Line-transect	08/11/2020	-25.1435	-44.9717	158	1	0
Line-transect	09/07/2021	-27.716	-46.6474	1355	2	0
Line-transect	14/07/2021	-26.8092	-44.6148	2100	1	0
Line-transect	05/10/2022	-26.8574	-46.1719	592	1	0
Line-transect	10/09/2023	-25.0351	-44.7656	319	3	0
Line-transect	27/08/2024	-27.4596	-47.1454	408	2	0
Line-transect	27/08/2024	-27.485	-47.0926	537	1	0
Line-transect	03/09/2024	-25.2886	-45.1877	107	1	0
Telemetry	23/08/2016	-23.8461	-41.8771	702	2	0
Telemetry	24/08/2016	-23.7224	-41.9663	466	1	0

Telemetry	24/08/2016	-23.7196	-41.9949	463	2	0
Telemetry	24/08/2016	-23.6587	-42.0576	303	3	0
Telemetry	24/08/2016	-23.6583	-42.0696	298	3	0
Telemetry	25/08/2016	-23.6427	-42.0842	252	10	0
Telemetry	25/08/2016	-23.7649	-42.0431	572	2	0
Telemetry	25/08/2016	-24.0806	-42.2498	1171	1	0
Telemetry	29/08/2016	-25.4735	-44.9529	652	1	0
Telemetry	31/08/2016	-25.764	-45.2595	259	3	0
Telemetry	31/08/2016	-25.7727	-45.2477	328	2	0
Telemetry	01/09/2016	-26.1492	-45.2772	1739	2	0
Telemetry	01/09/2016	-26.0775	-45.5864	587	15	0
Telemetry	07/07/2017	-27.5155	-46.5441	1508	2	0
Telemetry	07/07/2017	-27.4818	-46.4885	1551	2	0
Telemetry	14/07/2017	-26.0187	-45.4808	842	1	0
Telemetry	14/07/2017	-26.0028	-45.4735	786	1	0
Telemetry	14/07/2017	-25.9861	-45.4758	763	1	0
Telemetry	14/07/2017	-25.9869	-45.4483	862	1	0
Telemetry	15/07/2017	-25.6523	-45.1699	208	2	0
Telemetry	21/07/2017	-23.9209	-42.2089	807	2	0
Telemetry	06/08/2018	-25.5868	-45.1759	160	15	0
Telemetry	06/08/2018	-25.6145	-45.1001	370	1	0
Telemetry	06/08/2018	-25.5959	-45.1251	259	1	0
Telemetry	07/08/2018	-25.5905	-45.1283	240	32	0
Telemetry	08/08/2018	-25.7205	-45.2444	214	15	0
Telemetry	08/08/2018	-25.8378	-45.3039	496	8	0
Telemetry	08/08/2018	-25.8739	-45.3859	792	12	0
Telemetry	28/07/2019	-23.7348	-42.0615	526	4	0
Telemetry	28/07/2019	-23.7354	-42.0694	528	2	0
Telemetry	29/07/2019	-23.7776	-41.8559	617	6	0
Telemetry	29/07/2019	-23.7683	-41.8714	573	15	0
Telemetry	29/07/2019	-23.7571	-41.8602	475	6	0
Telemetry	29/07/2019	-23.7607	-41.8614	527	7	0
Telemetry	20/07/2020	-25.9486	-45.5466	559	1	0
Telemetry	20/07/2020	-26.0175	-45.5444	714	1	0
Telemetry	20/07/2020	-26.0063	-45.5385	687	2	0
Telemetry	21/07/2020	-26.1347	-45.6592	558	1	0
Telemetry	21/07/2020	-26.1413	-45.6174	602	2	0
Telemetry	22/07/2020	-25.7905	-45.3232	188	3	0
Telemetry	22/07/2020	-25.7871	-45.2905	220	4	0
Telemetry	22/07/2020	-25.8777	-45.1937	1046	4	0
Telemetry	02/08/2020	-25.6011	-45.1402	222	1	0
Telemetry	02/08/2020	-25.6638	-45.1037	527	1	0
Telemetry	02/08/2020	-25.6628	-45.1275	335	1	0
Telemetry	02/08/2020	-25.6628	-45.1275	335	4	0
Telemetry	02/08/2020	-25.6642	-45.1401	260	6	0
Telemetry	02/08/2020	-25.6688	-45.1525	254	2	0
Telemetry	02/08/2020	-25.7389	-45.1846	390	1	0
Telemetry	02/08/2020	-25.7486	-45.1929	417	2	0

Telemetry	03/08/2020	-26.3208	-45.9379	532	3	0
Telemetry	03/08/2020	-26.3411	-45.938	540	3	0
Telemetry	03/08/2020	-26.4626	-46.2816	451	2	0
Telemetry	03/08/2020	-26.4364	-46.2774	429	5	0
Telemetry	04/08/2020	-27.1259	-46.6405	471	2	0
Telemetry	05/09/2021	-25.7115	-45.2327	211	4	0
Telemetry	05/09/2021	-25.753	-45.2972	179	1	0
Telemetry	30/09/2021	-25.1717	-44.8278	299	2	0
Telemetry	02/10/2021	-25.731	-45.1753	372	1	0
Telemetry	08/07/2022	-25.99	-45.423	1037	1	0
Telemetry	09/07/2022	-25.9864	-45.5419	591	4	0
Telemetry	09/07/2022	-25.0112	-45.5079	100	8	0
Telemetry	20/07/2022	-25.2155	-43.2094	2200	1	0
Telemetry	20/07/2022	-25.2582	-43.1828	2228	1	1
Telemetry	21/07/2022	-23.6872	-41.978	383	1	0
Telemetry	25/07/2022	-25.691	-45.1999	230	3	0
Telemetry	26/07/2022	-26.1356	-45.5192	945	2	0
Telemetry	19/07/2024	-24.7733	-44.4781	452	3	1
Telemetry	19/07/2024	-25.1453	-44.7373	573	8	0
Telemetry	20/07/2024	-25.364	-44.8454	930	2	0
Telemetry	20/07/2024	-25.3591	-44.8594	850	3	0
Telemetry	20/07/2024	-25.3937	-44.9334	502	1	0
Telemetry	20/07/2024	-25.4643	-44.9997	318	2	0
Telemetry	21/07/2024	-25.8877	-45.3271	786	4	0
Telemetry	21/07/2024	-26.1543	-45.557	719	2	0
Telemetry	21/07/2024	-26.1724	-45.5727	708	6	0
Telemetry	21/07/2024	-26.2093	-45.5569	892	3	0
Telemetry	21/07/2024	-26.2093	-45.5911	774	2	0
Telemetry	21/07/2024	-26.1847	-45.5895	706	1	0
Telemetry	21/07/2024	-26.0804	-45.5477	839	2	0
Telemetry	21/07/2024	-26.0604	-45.4235	1193	2	0
Telemetry	22/07/2024	-26.0985	-45.5183	936	2	0
Telemetry	22/07/2024	-26.9231	-45.3644	2237	2	0
Telemetry	22/07/2024	-25.8938	-45.3404	789	2	0
Telemetry	22/07/2024	-25.7956	-45.2514	485	8	0
Telemetry	23/07/2024	-25.8964	-45.9486	212	3	0
Telemetry	26/07/2024	-25.8964	-45.9486	212	3	0
Telemetry	26/07/2024	-25.9044	-45.9405	222	3	0
Telemetry	26/07/2024	-25.9682	-45.9549	283	6	0
Telemetry	27/07/2024	-26.9631	-46.2494	658	1	0
Telemetry	27/07/2024	-26.9939	-46.2992	653	3	0
Telemetry	27/07/2024	-27.5264	-46.7601	1028	3	0
Telemetry	27/07/2024	-27.4723	-46.9909	643	3	0

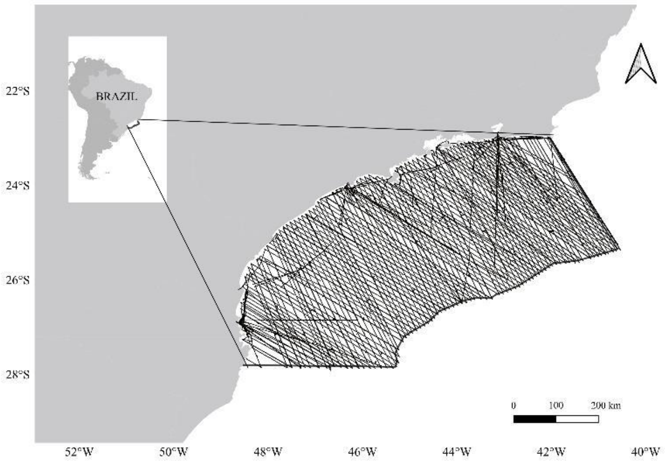

Figure S1. The survey lines of 16 surveys were arranged in a zigzag pattern, shifting between 60 and 90 km from one campaign to another to minimize spatial sampling bias. These lines were oriented perpendicular to the coastline, traversing the depth gradient of the study area.

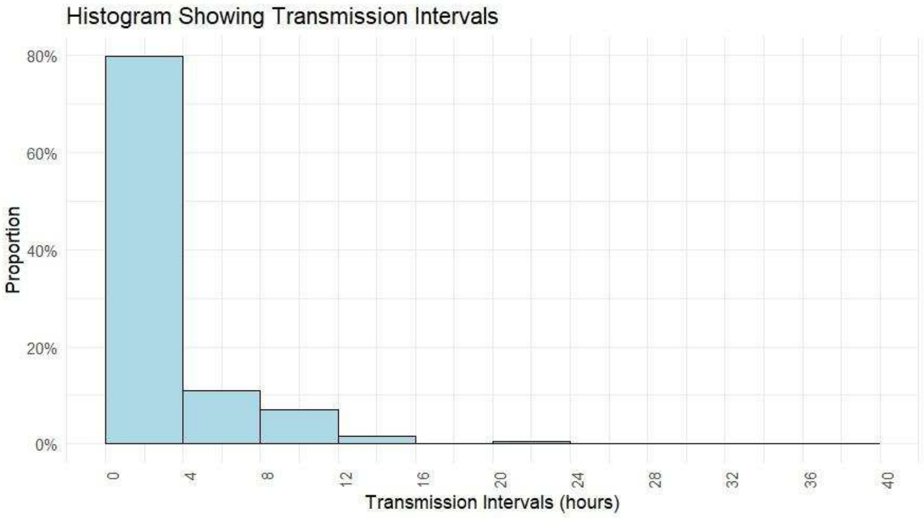

Figure S2. Transmission intervals of ARGOS-derived surface locations from the sei whales used in fitting the continuous-time correlated-random-walk model

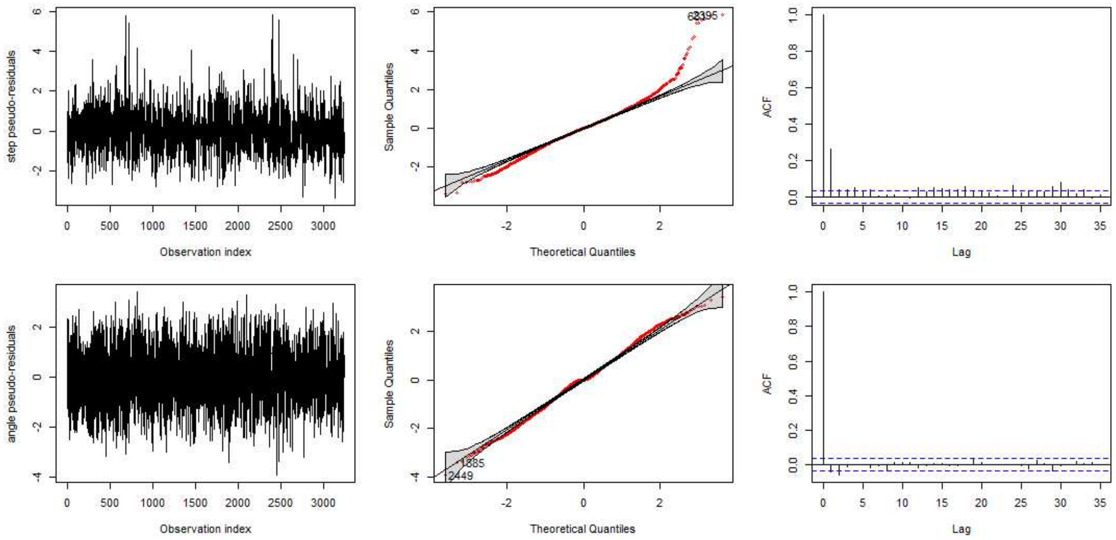

Figure S3. Column 1 (Pseudo-residuals over time): Indicates that the residuals are approximately random, indicating that the model fits temporal trends well. Column 2 (Q-Q plots): This shows that there is a violation of normality in the extreme values, which may indicate the presence of outliers or a poor prediction of the distribution of the residuals. Column 3 (ACF): The absence of autocorrelation in the residuals indicates that the model is capturing temporal dependencies well.

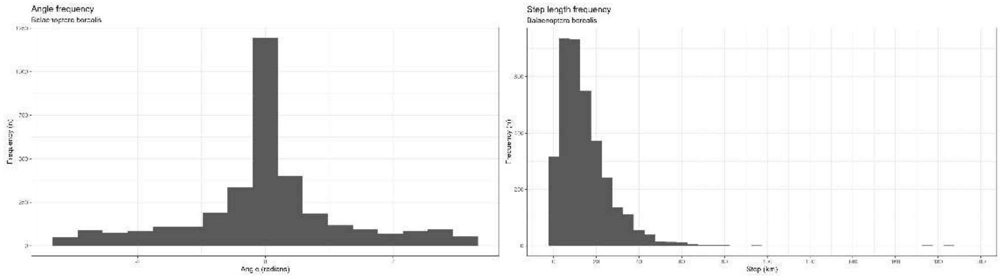

Figure S4. Frequency and distribution of the values of each parameter (angle and step) respectively, after the continuous-time correlated-random-walk (CTCRW) model.

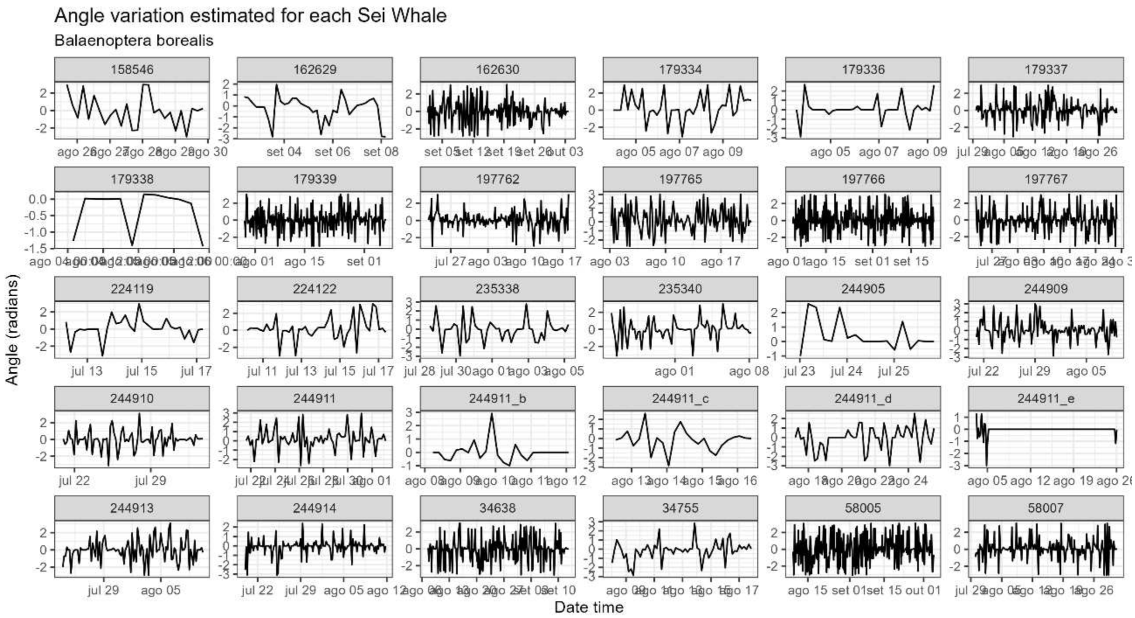

Figure S5. Graphs showing the frequency and individual distribution of the angle parameters of the 26 monitored sei whales. The track segments PTT244911, PTT244911_a, PTT244911_b, PTT244911_c and PTT244911_d represent the same individual.

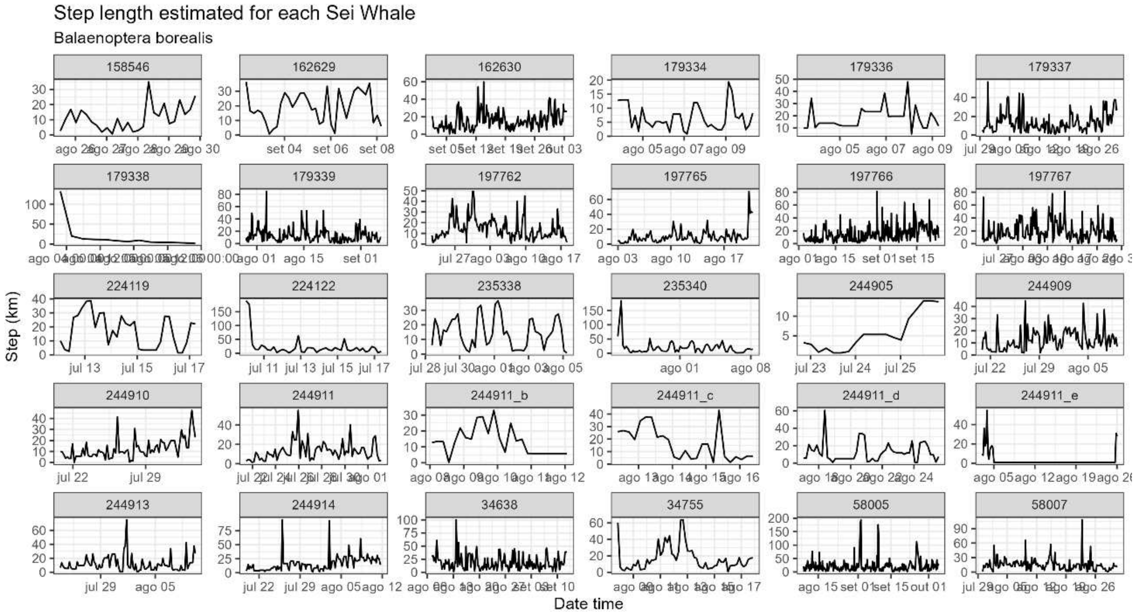

Figure S6. Figure S4. Graphs showing the frequency and individual distribution of the step parameters of the 26 monitored sei whales. The track segments PTT244911, PTT244911_a, PTT244911_b, PTT244911_c and PTT244911_d represent the same individual.

Figure S6. Aerial image captured by an AUV showing sei whales (*B. borealis*) from a group of 32 individuals in association with two killer whales (*Orcinus orca*).

CHAPTER 3. Living near the surface: dive behaviour of sei whales (*Balaenoptera borealis*) in the southwestern Atlantic Ocean

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Key words: Dive behavior, sei whale, satellite tags, non-invasive tags.

ABSTRACT

Understanding the diving behavior of baleen whales in tropical breeding areas is essential for evaluating both ecological functions and anthropogenic threats. In this study, we combined non-invasive tags data, satellite transmitters and generalized additive mixed models (GAMMs) to investigate the dive behavior of sei whales (Balaenoptera borealis) in Santos Basin (SB), off southeastern Brazil. A total of 9,963 dives were analysed, revealing a strong dominance of shallow diving, with 93% of dives occurring at depths ≤20 m. Environmental variables such as sea surface temperature, local bathymetry, and chlorophyll concentration significantly influenced dive depth and duration. Cooler waters and deeper offshore areas were associated with longer and deeper dives, while high surface productivity appeared to compress prey layers and shorten dive times. Behavioral and temporal covariates further modulated diving patterns, including diel period, lunar phase, and dive shape. Non-invasive tags data indicated instances of possible shallow lunge feeding and surface skin-feeding, suggesting that opportunistic foraging may occur in this presumed breeding habitat. The prevalence of shallow diving behavior within the depth range of vessel drafts (≤ 30 m) raises significant conservation concerns, particularly regarding the risk of ship strikes in high-traffic areas such as the Santos Basin. Our findings highlight the behavioral plasticity of sei whales in low-latitude habitats and emphasize the importance of integrating fine-scale behavioral data into marine spatial planning and mitigation strategies. Reducing vessel speed and rerouting traffic in key whale habitats should be considered to reduce the risk of anthropogenic impacts on this vulnerable species.

INTRODUCTION

Dive behavior plays a fundamental role in the ecology and survival of numerous marine species, including air-breathing mammals, birds, fish, and reptiles (Roncon et al. 2018). Among marine mammals, dive patterns vary widely: sea otters typically dive to depths of less than 20 meters (Costa et al. 2001), whereas sperm whales can descend to around 3,000 meters (Watwood et al. 2006). Dive depth and duration are influenced by species-specific traits such as body size, physiological adaptations, and ecological requirements (Kooyman & Ponganis 1998; Kavanagh et al. 2017).

The collisions between vessels and baleen whales is a globally recognized conservation concern and represent a significant source of anthropogenic mortality for several endangered species (McKenna et al. 2015, Keen et al. 2019). As maritime traffic continues to grow in size, speed, and geographic coverage, the likelihood and severity of ship strikes is expected to increase (Silber et al. 2010). Understanding the behavioral ecology of whales in different habitats, especially the use of the water column, is essential to assess where and when individuals are most vulnerable to vessel interactions (Keen et al. 2019). Fin whales (*Balaenoptera physalus*) in the California Current System, for instance, spent significantly more time near the surface at night, thereby increasing overlap with shipping activity during periods of reduced visual detection (Keen et al. 2019). Such pattern is critical because whales are at risk only when they are within vessel draft depths, typically the upper 20 meters of the water column (Silber et al. 2010). Integrating these behavioral parameters into spatially explicit risk models improves mortality estimates and highlights temporal windows of increased collision probability (Rockwood et al. 2017). In addition, Silber et al. (2010) demonstrated through hydrodynamic experiments that vessel speed is a key factor influencing both the probability and lethality of collisions. Their findings reveal that whales struck at higher speeds experience significantly greater accelerations upon impact, which are used as a proxy for collision severity. Moreover, submerged whales may be drawn toward the hull or propeller by pressure differentials and suction forces, increasing the risk of injury or death (Silber et al. 2010). This particularly concerns endangered populations, where individual losses have population-level implications (Silber et al. 2010, Soldevilla et al. 2017). Thus, understanding species-specific dive behavior is essential for refining ship strike risk models and informing evidence-based mitigation strategies, such as vessel speed restrictions or dynamic management zones. Addressing the behavioral and physical mechanisms underlying these interactions is critical for reducing ship-related mortality and ensuring the recovery of vulnerable whale populations worldwide.

The sei whale (*Balaenoptera borealis*) is the third largest member of the Balaenopteridae family and is one of the least known mysticete whales (Mizroch et al. 2016, Horwood 2009). It is currently listed on the IUCN Red List as a globally endangered species mainly because of the whaling industry exploitation (Cooke, 2018). An estimated 205,000 sei whales were caught within Southern Hemisphere waters during the 1900s, particularly between the 1950s and 1970s (Rocha et al. 2014).

Sei whales exhibit remarkable ecological flexibility, capable of switching between lunge-feeding and skim-feeding strategies. This trait functionally places them between the specialized feeding modes of other rorquals and balaenids (Segre et al. 2021). Their feeding is tightly linked to the diel vertical migration of zooplankton, particularly calanoid copepods such as *Calanus finmarchicus*, which rise to surface waters at night (Baumgartner & Fratantoni 2008). Sei whales are believed to exploit these nighttime surface aggregations for efficient foraging, as supported by evidence of nocturnal skim-feeding and daytime reductions in vocalization activity (Baumgartner et al. 2008). Given their ecological plasticity, cosmopolitan distribution, and reliance on prey exhibiting diel vertical migration, sei whales may experience variable exposure to anthropogenic threats such as ship strikes depending on their diving behavior.

Understanding the diving behavior of sei whales is essential for understanding their foraging habits, accurately assessing ship strike risk, and guiding effective conservation efforts for this vulnerable and understudied species.

MATERIALS & METHODS

Information about sei whales was obtained during the Cetacean Monitoring Project in Santos Basin (PMC-BS), south and southeastern Brazil, executed by PETROBRAS as demanded by IBAMA (Brazilian Institute of Environment and Renewable Natural Resources) in the federal environmental licensing of oil and gas production and transportation at the Santos Basin. The project included ship-based line transect with distance sampling surveys to estimate density and identify the cetacean community, and telemetry surveys to locate species that could potentially be tagged with satellite transmitters.

Study area

The Santos Basin (SB), spanning approximately 350,000 km², extends from Cabo Frio in the State of Rio de Janeiro (~23°S) to the Island of Santa Catarina in the State of Santa Catarina (~28°S), encompassing the coastal regions of four southeastern Brazilian states (Hercos et al. 2023) (Figure 1). The basin exhibits distinct hydrographic dynamics across its extent. In its northern portion, the continental shelf and slope are primarily influenced by the Brazil Current, which transports warm, tropical, and oligotrophic waters southward along the continental margin (Brandini et al. 2018).

Located along the central slope of the SB, the Cananéia Canyon is a well-developed submarine feature formed through successive retrogressive slumping events. It is characterized by a broad, stepped head measuring approximately 23 km in width and rising 370 meters in height (Hercos et al. 2023). About 150 km to the north lies the São Sebastião Canyon, a similarly elongated and linear formation that begins on the continental shelf at depths around 150–200 meters and extends beyond 1,500 meters. Both canyons significantly influence the sediment dynamics of the Santos Basin shelf, acting as conduits for nutrient-enriched deep waters and enhancing the geological and ecological complexity of the region (Figueiredo Jr et al., 2023).

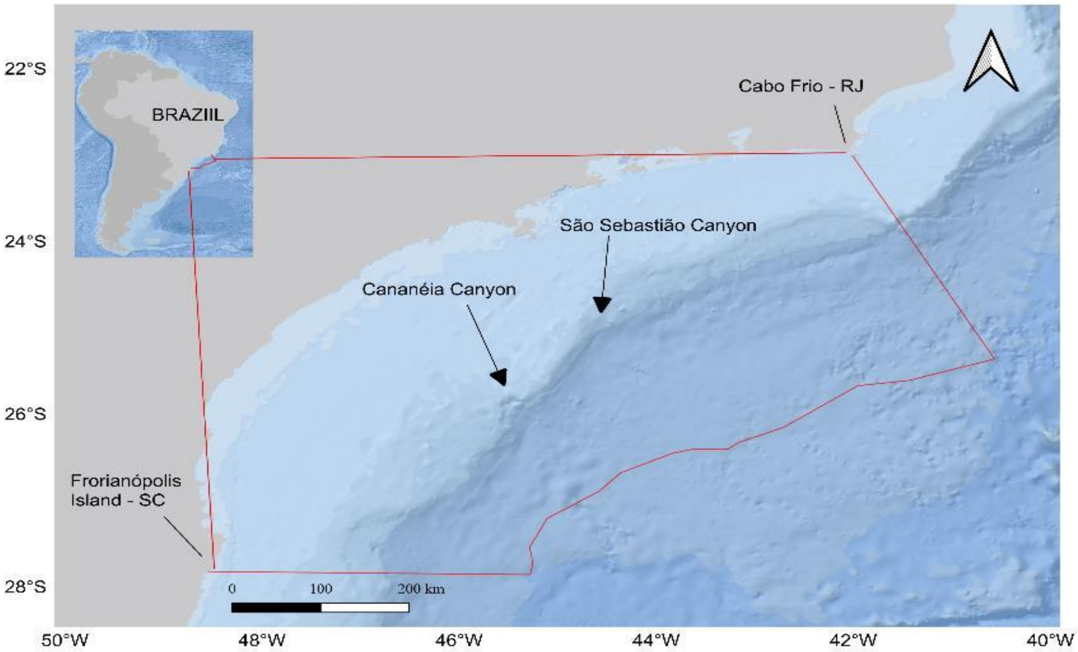

Figure 1. Map of the study area located off the southeastern and southern coasts of Brazil, highlighting key submarine geomorphological features. The red outline represents the monitored area where data collection occurred. The Cananéia and São Sebastião Canyons are indicated, along with coastal reference points such as Florianópolis Island (SC), representing the southern limit, and Cabo Frio (RJ), representing the northern limit of the study area. Bathymetric relief illustrates the presence of topographic gradients.

Data collection

All data collected and presented in this study occurred within the scope of the "Cetacean Monitoring Project at the SB (PMC-BS), executed by PETROBRAS and SOCIOAMBIENTAL as required by IBAMA in the federal environmental licensing of PETROBRAS's oil and Gas production and transportation at the Santos Basin. The project included line transect surveys using a ship-based (23.7-m-long vessel) to estimate and identify the cetacean community, with coverage distributed throughout the year on the coastal and oceanic waters of the Santos Basin (PETROBRAS, 2019). These surveys were used to identify spatio-temporal "hotspots" suitable for targeted tagging efforts. And telemetry surveys whose objective was to locate cetacean groups with potential for satellite tagging and/or Non-invasive suction cup tags deployment, covering as much of the SB area as possible.

Satellite SPLASH10 tags

A SPLASH10 version of the remotely deployed Low Impact Minimally Percutaneous External-electronics Transmitting (LIMPET) tag was used, manufactured by Wildlife Computers, Inc. (Redmond, WA). Tags were deployed using a 180 lb crossbow (Excalibur Vixen II) at ranges of 4-10 m and attached on or near the dorsal fin using two sterilized 6.7 cm long titanium darts with backwards-facing 'petals' (Andrews et al. 2005). The tags relayed data through the Argos satellite system and operated using a saltwater-activated switch. They were set to transmit daily during time windows with optimal Argos satellite coverage over the region, amounting to approximately 10 to 11 hours per day. Each tag was restricted to a maximum of 450 transmissions per day. When possible, biopsy samples were simultaneously collected from the tagged individual. We deployed the tags from a 6.4m rigid-hulled boat with a 150 hp power stroke. Before tagging, we attempted to photograph the dorsal fin and body of all individuals in the group for identification.

All transmitters were programmed to transmit daily. Dives were defined as any submergence that exceeded 5 m depth and lasted longer than 30 seconds. Dive duration, depth profiles, and surface time were generated using the Behavior Log function (Wildlife Computers, 2012) and 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 ("Square", "U", and "V"). Geographic locations of transmitters were determined by Service Argos (CLS America) using the Doppler shift created by the satellite passing overhead.

Analysis of location data and behavioral state

PTT uplink locations were estimated by the Argos satellite system, and a measure of locational accuracy, defined by a location class (3, 2, 1, 0, A, B and Z in order of decreasing accuracy), was assigned to each estimated location (Argos, 2016). The 'momentuHMM' package (McClintock & Michelot 2018) of R software (R Core Team, 2025) was used to fit a continuous-time correlated random walk model, CTCRW, to estimate and regularise the time interval between observed satellite uplinks. The fitting of these models allowed the frequency of estimated locations along the tracks to be regularised into a defined time interval. To standardize and minimize possible biases when estimating behavioral states, tracks with transmission intervals greater than 24 hours were segmented, thus preventing state models from generating pseudo linearity space during the standardization of intervals by CTCRW models. Tracks and/or track segments with less than 10 location points have been removed. As model parameters, the time interval was set to 4 hours, a value that comprises 80% of the transmission intervals recorded in the raw data (Prieto et al. 2014).

With the tracks regularized by CTCRW, a Hidden Markov Model (HMM) was fitted to model the behavioral states using the 'prepData' function from the 'momentuHMM' package. This function calculates step length (modeled with a "*gamma*" distribution) and turning angle (modeled with a '*wrpcauchy'* distribution) intervals which are the variables used as predictors of two behavioral modes of whales: 'Area Restricted Search' (ARS) was characterized by short step length and low turn angle concentration; and 'Transit' was characterized by a long step length and high turning angle. These behavioral modes were applied to model and predict dive behavior (Table 1).

To estimate dive positions with greater accuracy, a continuous-time correlated random walk model was applied using the 'momentuHMM' package. The model incorporated latitude, longitude, datetime, and a parameter to estimate datetime (predTime) as inputs. This approach enabled the estimation of a location point for each dive event, using datetime as a predictor of position. A time step of 20 minutes, corresponding to the median interval between consecutive dives was applied, resulting in a dataset containing both dive and location information for each transmitter.

Non-invasive tags

DTAGs (Johnson & Tyack 2003) and CATS tags (Cade *et al.* 2016) were used on sei whales. Tags were attached to focal animals using a 6-meter-long carbon fiber pole. The attachments were approached using a 6.4m rigid-hull inflatable boat. Focal follows of tagged animals, consistent with techniques described by Altman (1974), were attempted. Once the tag detached from the focal animal, it was located using a directional YAGI antenna and retrieved with a dip net. Tags and suction cups were inspected for skin samples suitable for biopsy, using the protocol described by Miller et al. (2010). Dtag data were offloaded from the tag using infrared (IR) data transmission (Dtag2). CATS tag data was offloaded via WiFi using the tag manufacturer's software (https://www.cats.is). Data from the tags was field-inspected to ensure sensor data and audio and visual recordings were consistent with expectations from field deployment. Post-processing procedures, necessary to convert the tag's frame of movement reference to that of the tagged whale and mathematically translate those values to the pitch, roll, and heading of the tagged animal (Johnson & Tyack 2003), were performed for DTAG data. The computed animal pitch, roll, and heading values form the basis for kinematic analysis, from which inferences about diving behaviors (e.g., foraging) may be made (Goldbogen et al. 2006). These data were analyzed using Dtagtools in MATLAB.

Diving and kinematic profiles were analyzed for possible foraging behaviors, characterized by one or more of the following characteristics (according to Goldbogen et al. 2006): 1) rapid acceleration (increased fluke rate, acoustic detection of increased flow noise characteristic of rapid swimming); 2) large changes in left or right roll angles coincident with rapid acceleration; 3) rapid deceleration (decreased fluke rate, acoustic detections of rapid decrease in flow noise intensity); 4) rapid increases in the magnitude of one or more synthetic kinematic measures (i.e., jerk or ODBA, overall dynamic body acceleration). In Goldbogen *et al.* (2006), there were repeated bouts of foraging evident in the tag data.

Predictors of diving behavior

Differences in dive parameters were analyzed about daylight and moon phases to assess whether these factors influenced the whales' diving behavior. Dive times, originally recorded in UTC, were converted to local time before the integration of telemetry and illumination data.

Information on solar elevation was obtained from the ‘oce’ package version 1.1-1 (Kelley & Richards 2019). These data were used to categorize the predicted whale locations into four groups (diel variation) : (1) “dawn” was defined as solar elevation from - 12 to + 6 degrees about 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).

Lunar phases were obtained from the ‘suncalc’ package, version 0.5.0 (Thieurmel & Elmarhraoui, 2019). Moon luminosity was extracted for each location based on the predicted latitude, longitude, and time of 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 last quarter and full moon and 0.75 – 1.

Chlorophyll-a and daily Sea Surface Temperature (SST) data were extracted using the R package “rerddapXtracto” v.1.1.045, which accesses the ERDDAP server at the NOAA/SWFSC Environmental Research Division.

Bathymetric data were used to extract two environmental variables: depth and seafloor slope. These variables were derived from a digital elevation model (DEM) of the seafloor obtained from the General Bathymetric Chart of the Oceans (GEBCO 2023, https://www.gebco.net). The raster layer was imported into QGIS (version 3.34 where depth values were extracted for each dive location using the "Point Sampling Tool" plugin.

To calculate slope, the bathymetric raster was first processed using the "Slope" algorithm available in the Raster Terrain Analysis tools in QGIS. This tool computes the maximum rate of change in elevation between each cell and its neighbors, generating a raster layer representing the slope in degrees. Slope values were then extracted at each dive location using the same point sampling method.

All environmental layers were projected in a common coordinate reference system (WGS 84) before analysis to ensure spatial consistency.

GAMM modeling approach

To investigate how environmental and behavioral factors influence the diving patterns of sei whales (*B. borealis*), we fitted Generalized Additive Mixed Models (GAMMs) using the 'mgcv' package in R (Wood 2023). Separate models were developed for two response variables: dive duration and dive depth, both modeled assuming a Gamma distribution with a log link function, appropriate for continuous and strictly positive data (Wood 2017).

Models included both continuous and categorical predictor variables. Continuous variables were sea surface temperature (°C), Chlorophyll-a concentration (mg/m^3), local bathymetric depth (m) and seafloor slope (degrees). These variables were centered and scaled before modeling to improve interpretability and numerical stability. Smooth terms (s ()) were applied to these predictors to capture potential nonlinear relationships, and their partial effects were visualized using smooth plots. In addition, categorical predictors were included as fixed effects, such as: dive shape (Square, U-shaped or V-shaped), behavioral state (ARS or transit), diel variation (dawn, day, dusk and night) and lunar phase (new moon, first quarter, full moon and last quarter). To quantify the influence of these factors on dive behavior, we calculated and compared estimated percentage changes in dive duration and depth for each level relative to a baseline.

A two-dimensional smooth term of latitude and longitude was included to account for spatially structured residual variation.

Random intercepts were included for individual whales to account for repeated measures (~1 | ID).

The GAMM was fitted using the 'mgcv' package in R, which allows simultaneous inclusion of smooth terms for nonlinear predictors and random effects for individual whales (PTT). Multicollinearity was checked by a variance inflation factor (VIF) and Pearson correlation.

The model used a Gamma distribution with log link function, suitable for modeling positively skewed duration data. All models were fitted using restricted maximum likelihood (REML) to improve the robustness of smooth term estimation (Wood 2017).

Model validation was performed using gam.check(), assessing the degree of smoothing (k-index), the significance of smooth effects (edf vs. k'), the residual structure, and visual inspection of diagnostic plots (S1 and Tables 3, 4, 5 and 6).

Table 1. Description of environmental and behavioral variables used as candidate predictors in the GAMM models to evaluate the diving behavior of sei whales (*Balaenoptera borealis*).

Candidate predictor variables (PVs)	Working name	Definition and method
Temperature	temp	Sea surface temperature (˚C) as monthly composites at 4 km resolution. Derived from the NASA OceanColor Web service (https://oceancolor.gsfc.nasa.gov/l3/)

Chlorophyll-a concentration	chlor	Chlorophyll-a concentration (mg m-3) as monthly composites at 4 km resolution. Derived from the NASA OceanColor Web service (https://oceancolor.gsfc.nasa.gov/l3/)
Local depth	Depth_local	Water depth (m) extracted from the GEBCO grid (GEBCO Compilation Group, 2025).
Local slope	Declive_local	Degrees of slope of the seabed. Derived from the GEBCO grid using QGIS.
Dive shape	Shape	Categorical classification of dive profile: U-shaped or V-shaped, from tag data by ARGOS
Behavioral state	state	Categorical behavioral state classification: ARS or Transit, inferred from HMM model
Diel period	Diel	Time of day (Day, Dusk, Night and Dawn) based on solar position
Lunar phase	Fase_lunar	Lunar phase at time of dive (Full moon, Last quarter, New moon, Fisrt quarter)
Individual ID	Ptt	Random effect term for individual identity (tracking tag code)
Spatial coordinates	long, lat	Longitude and latitude used for spatial smoothing (thin plate regression splines)

RESULTS

A total of 26 sei whales were tagged and biopsy samples were obtained from eight individuals, seven males and two females. But one individual, a female, was excluded from the analysis due to the short time the transmitter remained (three days) (Table 2). Transmission duration ranged from three to 59 days (mean = 22.5 ± 16.9). Total track length ranged from 112.6 to 4,313.7 km (mean = 1,522.1 ± 1,179.5).

Dive behavior inferred by satellite transmitters

For 26 sei whales equipped with satellite tags, 9,963 individual dives were recorded.

Dive depths ranged from 5 to 191 meters, with a mean depth of 10.8 ± 8.7 meters. The majority of dives (93%) were shallower than 20 meters (Figure 2A and 3). Dive durations varied from 30 seconds to 21.8 minutes, with a mean duration of 3.9 ± 3 minutes (Figure 4). The most frequent dives lasted between 30 seconds and 2 minutes (37.1%), followed by dives between 2 and 4 minutes (23%) (Figure 2B). All dive profiles from the 26 sei whales can be found in the supplementary material (Figures S4 to S11).

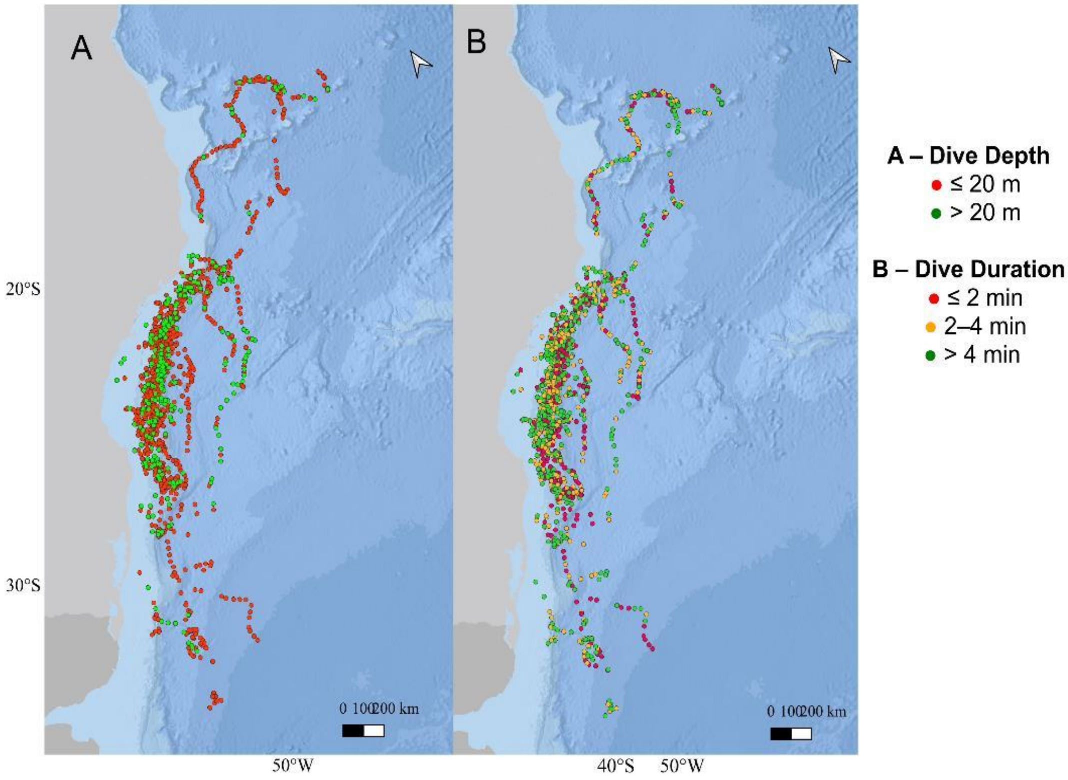

Figure 2. Spatial distribution of dive locations recorded from 26 tracked sei whales along the southeastern coast of Brazil. A - Dive depth classification: shallow dives (≤ 20 m, red) and other dives (> 20 m, green). B - Dive duration classification: short (≤ 2 min, red), intermediate (2–4 min, yellow), and long (> 4 min, green).

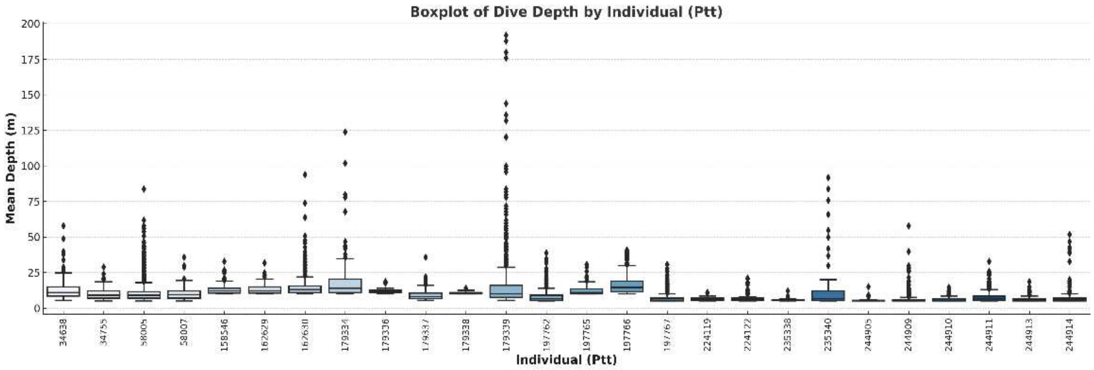

Figure 3. Boxplot of dive depth (in meters) recorded for each sei whale (*B. borealis*) identified by PTT code. Boxes represent the interquartile range, the horizontal line within each box indicates the median, and whiskers are plotted as outliers

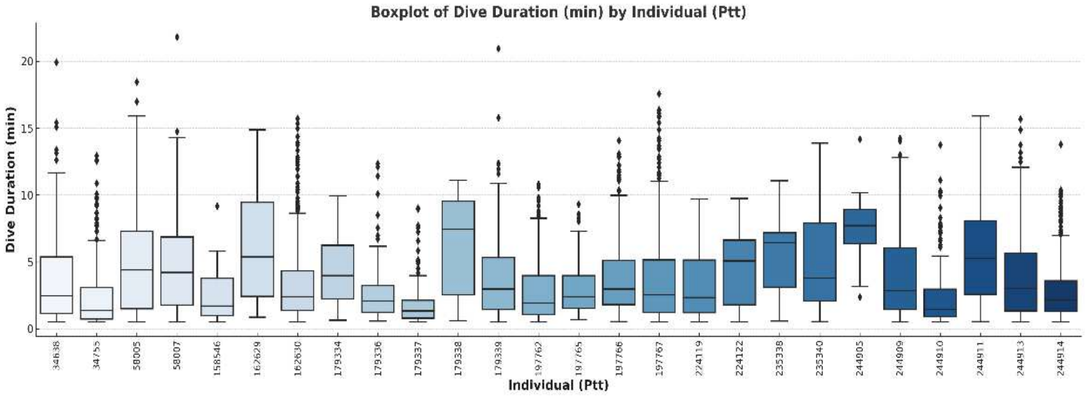

Figure 4. Boxplot of dive duration (in minutes) recorded for each sei whale (*B. borealis*) identified by PTT code. Boxes represent the interquartile range, the horizontal line within each box indicates the median, and whiskers are plotted as outliers.

Dive depth and duration showed a very weak correlation (Person's correlation coefficient, r=0.06; $p < 0.001$) (see supplementary material, Figure S1).

Dive behaviour inferred by DTAG/CATS

Archival tags remained attached for 5hs, 4hs27min, and 9hs21min, recording a maximum depth and maximum dive duration of 29m (mean=10m ± 4.1m) and 11.2min (mean=4.8min ± 2.6min), 15.4m (mean=7.4m ± 2m) and 8.6min (mean=4.8min ±

2.3min), 11.5m (mean=6.1m ± 1.8m) and 15.2min (mean=7.3min ± 2.3min), respectively (Table 2 and Figure 5).

Table 2. Summary of sei whales tagged in the Southwestern Atlantic Ocean with digital suction cup tags.

Tag ID	Date	Duration of TAG	Mean (SD) Dive Duration (min)	Max Dive Duration (min)	Mean (SD) Dive Depth (m)	Mode Dive Depth (m)	Max Dive Depth (m)
bb16_244a	2016-08-31	5h 3m	4.6 (3.0)	11.1	13.9 (4.8)	10.2	28.9
bb19_209a	2019-07-28	4h 27m	3.8 (2.3)	8.8	7.5 (2.0)	5.26	15.4
bb20_202a	2020-07-22	9h 21m	7.3 (4.3)	15.2	6.1 (1.8)	5.04	11.5

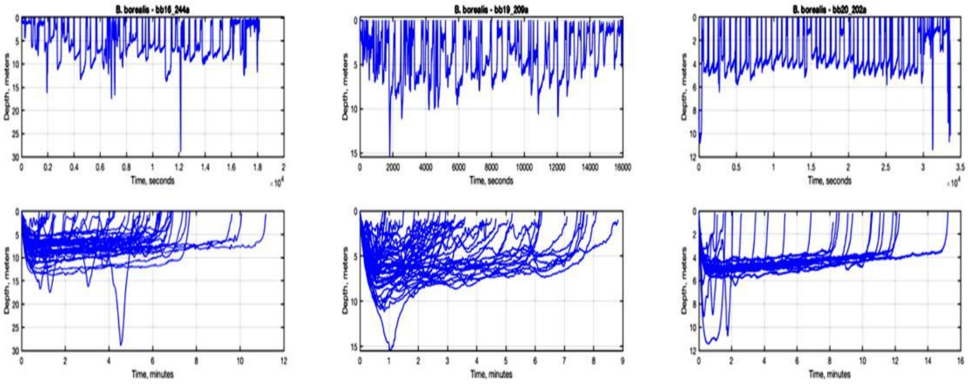

Figure 5. General patterns observed in these dive profiles show a trend among *B. borealis* (*n* = 3) to limit most of their activity to the top 10 meters of the water column.

The sei whale (bb16_244a) engaged in numerous subsurface, shallow water dives (*n* = 584), and analysis of sensor data revealed many instances of possible lunge feeding events, which are marked by rapid increases in fluke rate, followed by rapid increases in roll rate and rapid decreases in fluke rate, according to the literature. One occasion of possible sub-surface lunge feeding was marked by (Figure 6): a) a change in heading, followed by b) an increase in fluke rate, c) a right-then-left side roll, and d) movement at a depth exceeding 10 meters. This event is followed by three possible examples of surface skin-feeding events (one in Figure 7 and two in Figure 7). These potential surface feeding events stand out as likely foraging activity due to a) increased fluke rate, b) rapid changes in pitch and roll, and c) a depth of less than a meter or two. In the data collected in sei whale bb16_244a data, we did not see repeated bouts of possible foraging events.

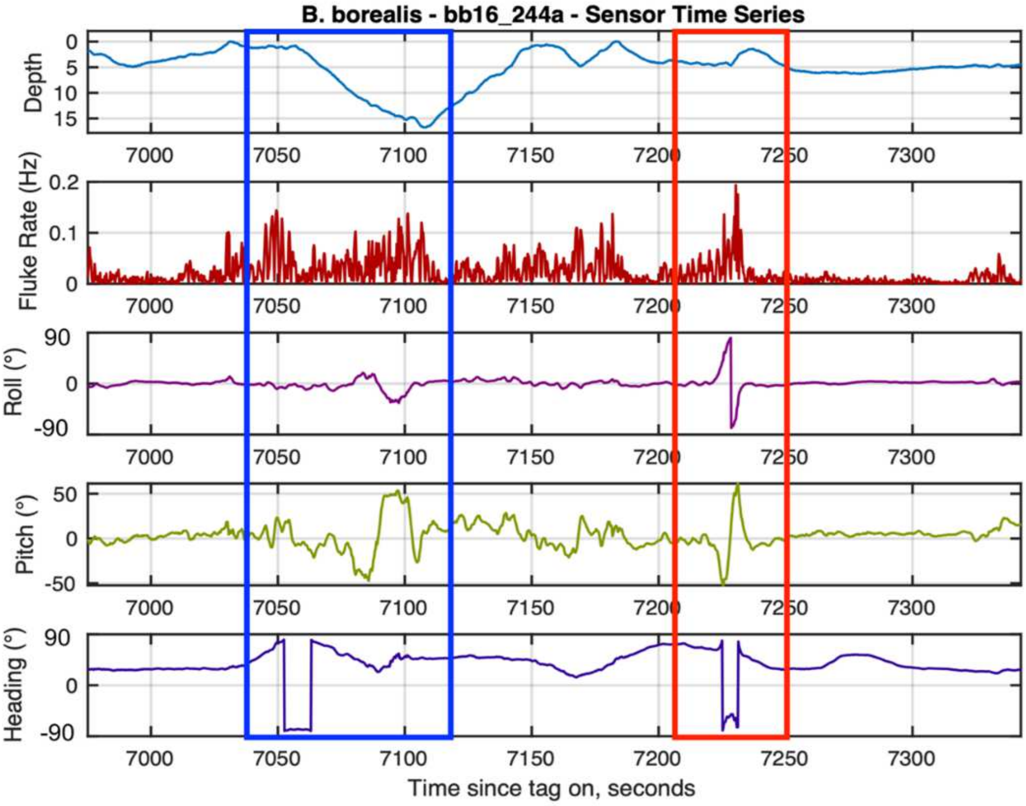

Figure 6. Time series of depth, fluke rate, roll, pitch, and heading recorded by a DTAG deployed on a sei whale (*Balaenoptera borealis*, tag ID: bb16_244a). The blue rectangle highlights a possible subsurface lunge feeding event, characterized by a sudden shift in heading, a sharp increase in fluke rate, a right-to-left roll maneuver, and movement at depths exceeding 10 meters. The red rectangle indicates a potential surface-lunge feeding event marked by elevated fluke rate, rapid pitch and roll changes, and shallow depth (<2 meters).

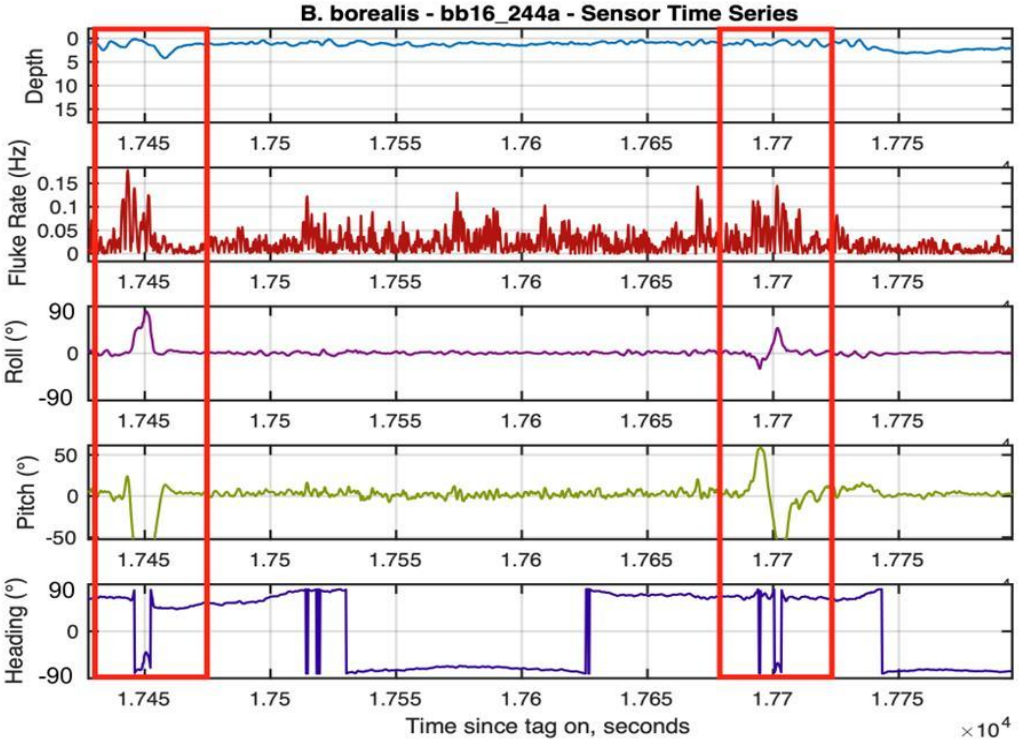

Figure 7. Additional sensor data from the same sei whale (bb16_244a), showing two more potential surface-lunge feeding events highlighted by red rectangles. These are characterized by increased fluke rate, rapid changes in pitch and roll, and maintenance of very shallow depths (typically <2 meters). These isolated events may indicate opportunistic foraging or alternative behaviors, such as exploratory or investigative movements.

Modeling dive behavior: effects of environmental and behavioral variables

The effective degrees of freedom (edf) adhered well to the basis dimension (k): all important terms showed acceptable k-index values or were manually adjusted as needed. Convergence and Hessian positivity were verified: all models achieved full convergence with positive-definite Hessians. Residual distribution: Diagnostic plots did not indicate any severe violations of model assumptions (see supplementary material, Figure S2 and S3).

The models demonstrated good statistical performance, with explained deviance of 29.3% for the duration model and 44.6% for the depth model.

Modeling of Dive Depth

The generalized additive mixed models (GAMMs) revealed distinct patterns in how environmental variables influence dive depth (Figure 8 and Table S2).

Temperature exhibited a clear negative relationship with dive depth, with deeper dives occurring in colder waters. As the temperature increased beyond ~15°C, the partial effect steadily decreased.

In contrast, chlorophyll concentration showed a weak positive effect on dive depth, particularly at higher productivity values. This may indicate that in more productive areas, prey availability at depth encourages deeper foraging dives. However, the overall effect was modest, and increased uncertainty was observed at the upper chlorophyll range.

Local depth had a pronounced positive association with dive depth. Deeper dives occurred in areas with greater bathymetric depth, but the relationship showed a nonlinear trend, with the most significant increases between 5,000 m and 3,000 m. Beyond this range, the effect stabilized, suggesting bathymetric constraints or behavioral preferences.

Finally, local slope exhibited significant effect on dive depth. The effect of local slope on dive depth showed a non-linear pattern. At low slope values (0–5°), the partial effect remained close to zero, indicating little influence of slope on dive depth in flatter areas. As slope increased beyond approximately 5°, there was a positive association, with dive depth increasing and reaching a peak effect at around 10°. Beyond this point, the effect declined, suggesting that steeper slopes were associated with shallower dives.

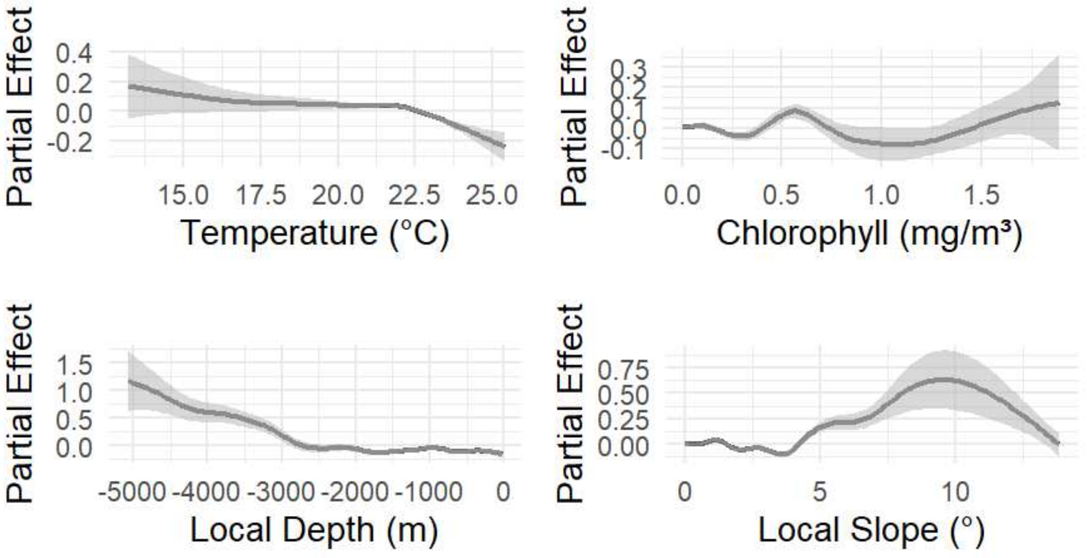

Figure 8. Partial effects of environmental covariates on mean dive depth from the GAMM model. Each panel displays the smoothed relationship between a predictor variable and the response variable (mean dive depth), while holding other variables constant. Shaded areas represent 95% confidence intervals. Temperature and local depth showed strong non-linear effects, with dive depth decreasing at higher temperatures and in shallower regions. Chlorophyll concentration exhibited a slight positive effect, while dive depth increases with slope up to approximately between 5° to 10°, followed by a decline at steeper slopes.

Modeling of Dive Duration

The generalized additive mixed models (GAMMs) revealed distinct patterns in how environmental variables influence dive duration (Figure 9 and Table S3). Dive duration was affected differently by the same environmental covariates.

Temperature showed a nonlinear relationship, with a peak around ~15 °C and lower durations observed at both higher and lower extremes. This “hump-shaped” pattern suggests that intermediate thermal conditions may support longer dives, possibly through optimized physiological performance or favorable prey distributions.

Chlorophyll concentration had a negative relationship with dive duration. While moderate concentrations were associated with longer dives, higher values led to a sharp decline. This pattern may reflect ecological saturation or prey vertical redistribution in highly productive zones, limiting the effectiveness of extended dives.

Regarding local depth, dive duration followed a complex nonlinear pattern with oscillating effects. Longer dives were more likely at depths around 4,000 m, consistent with access to mesopelagic prey layers. The variability observed may reflect interactions between prey distribution and bathymetric heterogeneity.

The effect of local slope on dive duration exhibited no significant and a positive, approximately monotonic relationship. At lower slope values (0 -5°), the partial effect remained close to zero, indicating minimal influence of slope on dive duration in flat areas. As slope increased beyond approximately 5°, dive duration progressively increased, with the strongest positive effect observed at the highest slope values above 10°.

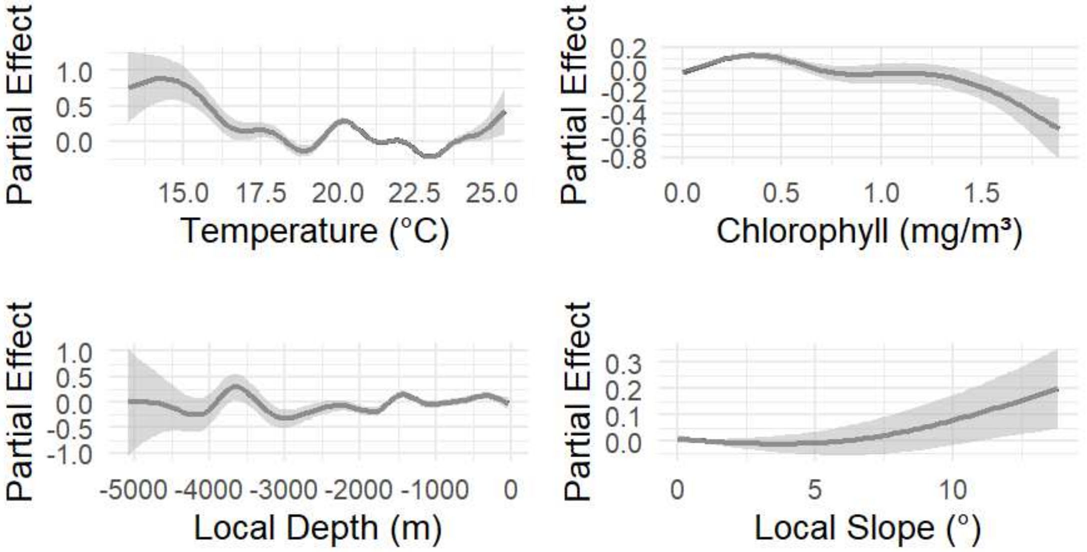

Figure 9. Partial effects of environmental predictors on dive duration from the GAMM model. Each panel illustrates the smoothed relationship between a environmental variable and dive duration, with other variables constant. Shaded areas indicate 95% confidence intervals. Dive duration was positively associated with lower temperatures and showed a non-linear response to local depth. Chlorophyll concentration had a slightly negative effect, while local slope tended to have longer dive durations in areas with steeper slopes.

3.3.3 Predicted Effects on Dive Depth and Duration

The relative influence of behavioral and temporal variables on dive metrics revealed distinct and interpretable patterns (Figure 10, Tables S4 and S5). The results showed that behavioral state and dive shape were among the strongest predictors, particularly for dive duration.

The U-shaped dives were associated with a marked decrease in dive duration (~ 35%), while having no observable effect on depth. In contrast, V-shaped dives had a strong dual effect: they significantly reduced dive duration (~ -20%) but led to a substantial increase in dive depth (~ +40%), indicating distinct functional roles of dive shapes in foraging or transit strategies.

Dives classified as being in transit behavioral state led to a moderate reduction in duration (~15%), with only a slight positive effect on depth, suggesting limited foraging activity or quick relocation behaviors during these dives.

The night period showed a increase in dive depth (~10%), with a smaller influence on duration, while dusk and day had minor positive effects on both metrics.

These findings support the hypothesis of nocturnal foraging behavior, with cetaceans diving deeper during nighttime likely in response to prey vertical migrations.

Lunar illumination also played a role, especially in modulating dive duration. During the last quarter, dive duration increased significantly (~+25%), while full moon dives showed moderate duration increase (~+10%) but a slight reduction in depth. New moon conditions had minimal effects on both metrics, indicating that intermediate lunar light levels may optimize conditions for extended diving activity.

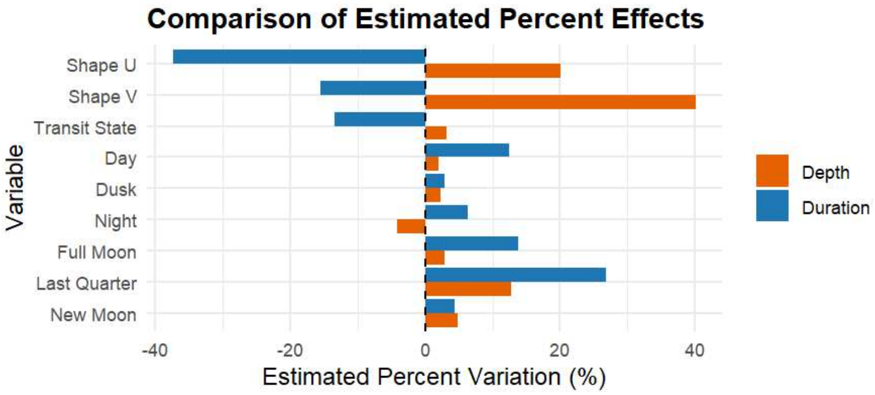

Figure 10. Comparison of estimated percent variation explained by categorical predictors in the GAMM models for dive depth and duration. Bars represent the relative effect size (in percentage) of each factor on the response variables. Positive values indicate an increase in the variable relative to the reference level, while negative values indicate a decrease. Dive shape ("V Shape" and "U Shape") and lunar phase ("Last Quarter", "New Moon") had substantial effects on both dive depth and duration. Notably, "V Shape" contributed the highest percent variation in dive duration, while diel period ("Night") and behavioral state ("Transit") showed moderate but distinct effects across the two models.

DISCUSSION

Dive behavior

The analysis of dive behavior across baleen whale species reveals a spectrum of vertical strategies, shaped by prey distribution, body size, foraging mechanics, and environmental context (Fortune et al. 2020, Friedlaender et al. 2020, Dong et al. 2022). In this study, sei whales (*Balaenoptera borealis*) exhibited predominantly short duration (mean = 3.9 min) and shallow dives (mean = 10m), with 93% occurring above 20 meters, although dives up to 191 m have occurred. Different dive patterns may be related to foraging, breeding, movements at certain depths or even rest. Ishii et al. (2017) reported average dive depths of 14-18 meters and durations of approximately three minutes and suggested that sei whales may favor epipelagic prey layers such as *Neocalanus* copepods or small schooling fish like anchovy, especially near frontal systems or productive shelf regions. In this study area, there are three main productive zones: Cananéia and São Sebastião submarine canyons and Cabo Frio upwelling systems. Similar dive depths were encountered in the coastal waters of China, for bryde's whales (*B. edeni*) performing very shallow dives (mean ~ 4 m; max ~16 m) during tread-water feeding bouts targeting surface fish schools. Such shallow foraging reduces energetic expenditure and may allow for more frequent prey encounters in stratified surface layers (Dong et al. 2022).

In contrast, fin whale (*B. physalus*) and blue whales (*B. musculus*) demonstrate foraging patterns concentrated at much greater depths, frequently exceeding 150 -200 meters. These species employ lunge-feeding tactics in deep krill aggregations, maximizing energy intake per dive despite the higher cost of oxygen use (Croll et al. 2001, Goldbogen et al. 2006, Friedlaender et al. 2020). Dive durations for these species can reach 10-15 minutes, with multiple lunges per dive recorded at depth. Humpback whales (*Megaptera novaeangliae*) exhibit highly plastic dive behavior, ranging from shallow surface lunge feeding to deep pelagic dives exceeding 500 meters, especially in offshore or oceanic habitats (Derville et al. 2020).

Sei whales in the present study showed a weak positive correlation between depth and dive duration. The maximum dive duration was 21 minutes and is related to a dive of 15 meters. The bryde's whale also presents a weak correlation between depth and dive duration (Dong et al. 2022). Fin whales demonstrated a consistent pattern in which deeper dives were associated with longer durations and a higher number of foraging lunges per dive (Friedlaender et al. 2020). Dive duration and maximum depth were positively correlated, possibly reflecting the time required to descend, forage, and ascend when targeting prey layers located deeper in the water column (Goldbogen et al. 2006). Whales in feeding areas adjust their dives according to the depth of available prey patches, increasing the efficiency of energy gain (Friedlaender et al. 2020).

The sei whales tracked in this study were in a region of the southwestern Atlantic that is considered a potential breeding habitat (Heissler et al. 2016), similar in ecological function to the breeding grounds described for humpback whales in the South Pacific (Derville et al. 2020). In such reproductive areas, baleen whales typically display shallow, low-energy dive behavior, often avoiding energetically costly foraging activities. Indeed, In New Caledonia, humpback whales commonly performed dives shallower than 80 meters and of short duration, consistent with behaviors such as resting, socializing, and calf rearing. However, some dives reached depths of up to 600 meters (Derville et al. 2020).

Another possible explanation for the predominance of shallow dives observed in sei whales is that these behaviors may not be exclusively linked to foraging or surface-related ecological functions. Instead, shallow diving could reflect a biomechanically optimized swimming strategy. Large whales such as pygmy blue whales (*Balaenoptera musculus brevicauda*) tend to swim at or just below a depth threshold where drag from surface turbulence is minimized (Owen et al. 2016). This optimal transit depth allows whales to reduce energetic expenditure during horizontal displacement. In this context, the shallow dives observed in sei whales could reflect energy-conserving transit behavior, especially during migration or when prey is not densely aggregated.

Possible Foraging Dives

The DTAG sensor data recorded in sei whale *bb16_244a* provide valuable insights into the fine-scale biomechanics of shallow dive foraging behavior. The identification of lunge-feeding-like events, characterized by sharp increases in fluke rate, sequential rolling motions, and rapid deceleration patterns, closely aligns with kinematic signatures described by Goldbogen et al. (2006) for fin whales, particularly during deep lunges. However, in this study, the sei whale exhibited these kinematic cues at much shallower depths, typically between 10 and 20 meters, and occasionally near the surface (<2 m), suggesting a modified form of subsurface or surface-oriented lunge feeding.

The three possible examples of surface lunge-feeding described here are strongly supported by Segre et al. (2021), who used multi-sensor tags to demonstrate that sei whales exhibit surface lunges with subtle rolling and pitch maneuvers. In their study, foraging occurred primarily near the surface and was marked by brief but frequent events, consistent with energetically efficient, opportunistic feeding on patchy prey such as amphipods.

Although direct observations of lunge feeding in sei whales are relatively scarce in the literature, Ishii et al. (2017) reported dive profiles consistent with lunge feeding behavior in two tagged individuals off Japan. These whales performed U-shaped dives at depths averaging 14-18 meters, often aligned with subsurface prey layers (e.g., *Neocalanus* spp.). Although the tags used in that study lacked high-resolution kinematic sensors (such as accelerometers or gyroscopes), the dive shapes and their temporal alignment with prey patches strongly suggested lunge feeding as a likely foraging strategy. However, no direct confirmation of lunges was possible.

In contrast, the present study provides high-resolution DTAG data that capture the kinematic hallmarks of lunge feeding, including rapid increases in fluke rate, sequential roll motions, and abrupt deceleration in shallow waters (< 20 m). These behaviors occurred both below 10 m (subsurface lunges) and in near-surface waters. This strongly supports the idea that sei whales can execute lunge feeding events in the epipelagic zone, particularly when prey is aggregated near the surface.

Segre et al. (2021) provide further support for this interpretation, having identified both subsurface lunge-like feeding events and surface skim-feeding behaviors in sei whales off the Falkland Islands. Using high-resolution biologging data, they showed that sei whales are capable of rapid, shallow lunges and short-duration filtering events that differ biomechanically from the deep, repeated lunges seen in larger rorquals. Importantly, they also observed no sustained sequences of foraging, but rather discrete, energetically efficient events, a pattern mirrored in the DTAG data presented here. Together, these findings suggest that sei whales possess a foraging strategy that is highly adaptable and responsive to ephemeral prey particularly suited to dynamic surface-layer habitats.

The convergence between the dive profiles in Ishii et al. (2017), the findings from Segre et al. (2021) and the DTAG derived behavior observed here reinforces the interpretation that sei whales can adopt rorqual-like lunge feeding mechanics even at shallow depths, potentially maximizing foraging efficiency in areas where dense prey aggregations are found close to the surface. This capacity may be especially relevant in low-latitude or tropical environments, such as the Brazilian coast, where prey availability is patchy and transient.

Further tagging efforts of sei whales in this region, coupled with behavioral focal follows and collection of video or photographic evidence of foraging, would provide evidence to support or refute the hypothesis that these kinematic cues are consistent with foraging events.

Modeling Dive Behavior

Smoothed Effects on Dive Depth

The results from the GAMM analysis revealed that shallow diving behavior in sei whales off the Brazilian coast is influenced by environmental gradients, particularly sea surface temperature, chlorophyll concentration, and bathymetric depth.

The negative effect of temperature on dive depth suggests that deeper dives are more likely to occur in cooler waters, which may correspond to regions where prey aggregates below the surface thermocline. In warmer waters (>15°C), whales performed consistently shallower dives. This pattern aligns with optimal foraging theory, which predicts that prey availability in stratified tropical waters is compressed toward the surface, making shallow foraging energetically advantageous (Doniol-Valcroze et al. 2011).

The positive association with chlorophyll was weak but present, suggesting a modest relationship between productivity and the tendency for whales to dive deeper, potentially to access prey below surface blooms. However, this effect was not linear or strong, reinforcing the idea that sei whales may rely on patchy, ephemeral prey distributions, a pattern consistent with opportunistic foraging rather than targeted deep feeding seen in other rorquals in feeding areas.

Bathymetric depth, on the other hand, showed a pronounced nonlinear effect, with deeper dives occurring over waters between ~3,000 and 5,000 meters, after which the relationship plateaued. This may reflect pelagic foraging strategies influenced by prey fields associated with oceanographic features such as fronts or upwelling zones, which often occur near continental slopes.

Local slope had significant effect on dive depth, with sei whales performing deeper dives primarily at moderate slope values between 5° and 10°. These results suggest that sei whales may exploit bathymetric features such as the upper flanks of submarine canyons and seamount chains, where moderate slopes can enhance prey aggregation through topographic effects without requiring highly complex or steep bathymetric structures. This is consistent with deep-diving odontocetes and some mysticetes like Rice's whales, which associate foraging with slope-related features (Kok et al. 2023).

Given that the study area coincides with a suspected reproductive ground for the species (Heissler et al. 2016), as with humpbacks in New Caledonia (Derville et al. 2020), one might expect reduced feeding behavior. However, the presence of lunge-feeding-like signatures captured in DTAG data suggests that opportunistic feeding is occurring, likely when prey patches are accessible with minimal energetic cost. This behavior reflects the dual role of this tropical habitat: serving both reproductive and foraging functions, depending on environmental conditions and individual energetic needs.

Finally, it's worth noting that shallow diving could also reflect energy-efficient transit behavior. As proposed by Owen et al. (2016), large whales may swim just below the surface to reduce drag while maintaining optimal cruising speed, termed "optimal displacement depth". Such dives, though not directly linked to feeding, may still contribute to the energetic efficiency of movement within and between activity areas in warm, low-productivity systems.

Smoothed Effects on Dive Duration

The GAMM analysis revealed that the duration of sei whale dives in tropical waters is shaped by a complex and non-linear interplay of environmental conditions. Unlike dive depth, which was most strongly influenced by temperature and bathymetry, dive duration appears to be governed by a broader set of ecological and physiological factors, including thermal conditions, productivity accessibility, and seafloor structure.

The hump-shaped relationship between temperature and dive duration, with a peak around 15 °C, suggests that intermediate thermal environments may support longer dives. This could be due to optimal metabolic performance at these temperatures (Kooyman & Ponganis 1998) or to increased prey patch stability in thermally stratified waters (Bollens & Frost 1989, Costa 2001). In warmer waters (>20°C), surface productivity may increase but prey layers tend to become vertically compressed, leading to shorter, more frequent dives. Conversely, at colder temperatures, the metabolic costs of extended submergence may increase, leading whales to reduce dive duration even if prey are deeper. The observed variability in dive duration may also reflect physiological constraints and environmental modulation beyond direct foraging behavior. For marine mammals, dive duration is often influenced by factors such as thermoregulation, buoyancy, and locomotion efficiency about water column properties (Kooyman & Ponganis 1998; Costa & Gales 2003). In the present study, intermediate temperatures were associated with longer dives, possibly indicating thermally optimal zones for sustained submersion where oxygen stores can be used more efficiently (Costa & Gales 2003).

Chlorophyll concentration exhibited a nonlinear negative effect, with longer dives at moderate productivity but shorter dives at high chlorophyll levels. This may indicate that in highly productive areas, prey becomes more accessible near the surface, eliminating the need for prolonged dives. A similar pattern was observed in Bryde's whales which performed short-duration, high-frequency dives in coastal zones where small fish are concentrated in the upper few meters (Dong et al. 2022).

The influence of local bathymetric depth on dive duration was complex and oscillatory, but longer dives clustered around depths of ~4,000 m. This suggests that pelagic prey layers, potentially mesopelagic micronekton or vertically migrating zooplankton, are more commonly exploited in deep-oceanic regions, consistent with observations in fin and blue whales foraging near slope breaks (Goldbogen et al. 2015, Friedlaender et al. 2020). The variability in dive duration at different depths could reflect spatial heterogeneity in prey availability or oceanographic structure such as eddies and fronts (Bailleul et al. 2010, Hazen et al. 2011, Jouma'a et al. 2017; Irvine et al. 2025).

Local slope exhibited a positive effect on dive duration approximately monotonic relationship. At lower slope values (< 5°), the partial effect remained close to zero, indicating minimal influence of slope on dive duration in flat areas. As slope increased beyond approximately 5°, dive duration progressively increased, with the strongest positive effect observed at the highest slope values (above 10°). This finding aligns with ecological theory that moderate slopes promote prey aggregation via physical processes like upwelling, internal wave reflection, or density discontinuities, enhancing feeding opportunities (Fiedler et al. 1998; Moors-Murphy, 2014). In contrast, steep slopes may represent more dynamic or unstable environments with unpredictable prey availability, leading whales to limit time spent submerged. Additionally, the positive association between moderate seafloor slope and dive duration may relate to hydrodynamic or current-modulated factors that either aid or impede vertical movement, regardless of foraging intent. Some marine mammals may increase dive duration not due to prey pursuit but to facilitate horizontal displacement or minimize energetic costs of surfacing in certain oceanographic contexts (Watwood et al. 2006), These findings reinforce that dive duration is a multifactorial trait shaped not only by ecological demands but also by the physical structure and properties of the environment through which the animals move.

Taken together, these results indicate that sei whales modulate dive duration dynamically in response to environmental cues that likely reflect prey accessibility, water column structure, and energy optimization. The presence of longer dives in areas of intermediate temperature, gradually increasing slope, and deep bathymetry suggests that even within a tropical breeding habitat, sei whales may exploit brief windows of foraging opportunity when conditions are favourable and/or minimize energetic costs associated with surfacing under specific oceanographic conditions.

Estimated Percent Effects on Dive Depth and Duration

Dive shape

The observed effects of dive shape on dive metrics provide valuable insight into the behavioral ecology of sei whales in a tropical breeding region. In this study, square-shaped dives served as the reference category, typically associated in the literature with foraging behavior involving prolonged time at depth, where whales remain at a stable depth for more than 50% of the dive duration (Cioffi et al. 2023; Pontbriand et al. 2023). This dive type likely reflects focused behavioral states, such as active prey processing or fine-scale exploration within dense prey patches.

Square-shaped dive profiles in odontocete whales, particularly belugas (*Delphinapterus leucas*), are considered a behavioral adaptation for efficient foraging, especially on benthic prey. In a study of belugas in the Canadian High Arctic, square dives, characterized by a steady descent, an extended bottom phase, and a direct ascent, accounted for 84% of deep dives (>40 m), suggesting focused foraging activity on the seafloor (Martin et al. 1998).

In contrast, U-shaped dives showed a ~35% reduction in duration with no substantial effect on depth, suggesting a shorter engagement at depth that may still involve foraging or exploratory activity, but likely on smaller or more ephemeral prey patches. In bowhead whales, U-shaped dives are sometimes associated with surface-oriented or midwater foraging (Fortune et al. 2023), though in tropical regions, they may also represent brief resting phases or movement within the upper mixed layer, where energy expenditure is minimized. Previous studies on dive profiles of balaenid whales, including North Atlantic right whales (*Eubalaena glacialis*) and bowhead whales (*Balaena mysticetus*), found that U-shaped dives, characterized by extended bottom time, were most likely associated with foraging behavior (Baumgartner & Mate 2003, Laidre et al. 2007, Heide-Jørgensen et al. 2013)

V-shaped dives, on the other hand, produced a distinct dual pattern: a ~40% increase in dive depth and a ~20% reduction in duration. These dives lack a clear bottom phase and are often interpreted as transit or scanning dives, commonly associated with horizontal displacement, navigation, or behavioral switching (Goldbogen et al. 2006; Derville et al. 2020). In migratory or reproductive contexts, such as the southeastern Brazilian coast where this study was conducted, such dives may serve several additional functions beyond foraging. Reproductive and social exploration in breeding areas, V-shaped dives may reflect movements to locate or approach conspecifics for mating or social bonding (Cartwright et al. 2012). Navigational scanning, quick, deep descents could be used to sample environmental gradients (e.g., thermoclines, salinity fronts) for orientation or selection of travel direction (Ballard et al. 2019). Thermoregulatory dives, in warm surface waters, descending to cooler layers (10-30 m) could serve to cool the body core, especially during prolonged surface intervals associated with social behaviors (Costa & Williams, 1999). Previous studies examining the dive profiles of balaenid whales, North Atlantic right whales and bowhead whales to prey availability found that V-shaped dives were indicative of search behavior (i.e., non-feeding dives) (Baumgartner & Mate 2003, Laidre et al. 2007, Heide-Jørgensen et al. 2013). In Fin whales, V-shapes are among a broader suite of six dive types, which include exploratory, and variable-shape dives often linked to resting, traveling, or vocalization rather than feeding (Fonseca et al. 2022).

Sei whales in the North Pacific demonstrated U-shaped and V-shaped dive profiles in response to the diel vertical migration of zooplankton, with U-shaped dives aligning with high prey densities during dusk, implying prolonged bottom phases for efficient feeding (Ishii et al. 2017).

These patterns indicate a strategic use of diving forms adapted to the type of prey or in different areas (feeding or reproduction).

Influence of Behavioral State on Dive Behavior

The behavioral state classified as "transit" in the GAMM models was associated with a moderate reduction in dive duration (~15%) and only a slight increase in dive depth compared to the area-restricted search (ARS) behavior. This pattern supports interpretations that these dives are primarily functional for displacement rather than foraging. Similar results have been observed across multiple rorqual species, where transit behavior is characterized by more direct, efficient movements with reduced underwater activity compared to foraging bouts (Goldbogen et al. 2006; Owen et al. 2016).

In transit phases, cetaceans often exhibit linear horizontal movement patterns and relatively shallow, shorter dives, consistent with energy conservation strategies during relocation or migratory travel (Nowacek et al. 2001). While some studies have reported that whales may opportunistically forage during transit (e.g., Friedlaender et al. 2016), the reduced dive duration during transit behavior aligns with the idea of minimized energetic cost during locomotion in breeding or transitional areas, particularly in tropical waters where prey aggregations may be sparse or unpredictable (Derville et al. 2020).

Diel Variation in Dive Behavior

The ~10% increase in dive depth observed at night in sei whales, with only marginal changes in dive duration, suggests a diel modulation of diving behavior potentially influenced by environmental structure and behavioral strategies. One plausible ecological driver of this pattern is the diel vertical migration (DVM) of zooplankton and micronekton, a well-established phenomenon whereby prey organisms ascend to surface waters at night and descend to deeper layers during the day to avoid visual predators (Bollens & Frost, 1989; Urmy et al., 2012).

Evidence for DVM is particularly strong in tropical and subtropical waters. Nogueira Júnior et al. (2015) demonstrated this pattern in the South Brazilian Bight, where zooplankton such as medusae, ctenophores, and copepods were more concentrated in the upper mixed layer at night. This supports the interpretation that the nocturnal deepening in dive depth observed in the present study may be a response to prey becoming accessible at slightly deeper but still relatively shallow layers during the night in a stratified tropical water column.

However, evidence from other sei whale populations shows that daytime dives may also be foraging-related. For instance, Ishii et al. (2017) found that sei whales off northeastern Japan performed longer and deeper dives during daylight hours, often aligned with high-density zooplankton layers located at ~40 m. These whales demonstrated a strong spatial coupling with prey distributions detected by echosounders, with feeding dives concentrated in areas and times when prey layers were densest, mostly during the day. Thus, the diel pattern of foraging activity in sei whales may vary by region, depending on the vertical structure of prey and water column stratification.

Furthermore, Segre et al. (2021) identified sensor patterns consistent with potential surface and subsurface lunges in sei whales. While these were not clustered by diel period, they suggest that feeding may occur both day and night, particularly in tropical systems where prey layers may be patchy or less predictable.

Beyond foraging, diel differences in diving could also relate to thermoregulatory or social behavior. Cetaceans in warm tropical waters may use deeper layers during specific times of day for cooling or acoustic advantages (McKenna et al. 2015). In reproductive habitats such as the southeastern Brazilian coast, where foraging is likely secondary to breeding-related movements, diel dive shifts may reflect a mix of opportunistic foraging, physiological regulation and socialization.

Conservation Implications of Shallow Diving Behavior in Sei Whales

The predominance of shallow diving in sei whales, 93% of recorded dives in this study occurred at depths ≤ 20 meters, has significant conservation implications. This vertical habitat use increases the likelihood of ship strikes, especially in coastal and offshore areas with regular maritime traffic. Shallow depths bring whales into the vertical operating zone of most commercial ships, whose average drafts range from 7 to 15 meters in large cargo vessels and even deeper for tankers.

Sei whales spend extensive time in the epipelagic zone, which overlaps with the operational range of vessel keels and propellers. This overlap is a major predictor of lethal collisions, as highlighted by Silber et al. (2010). Their hydrodynamic modeling demonstrated that whales located at or near the draft depth of a vessel are highly vulnerable, not only to direct hull strikes but also to suction and turbulence near the bow and propeller. The study showed that whales within these zones may be drawn toward the ship's hull and struck, even if not in a direct path of travel, particularly when their vertical reaction time is insufficient for escape.

Complementing this, McKenna et al. (2015) emphasized that baleen whales, including blue and fin whales, often lack the sensory capacity or behavioral response to detect and avoid fast-moving vessels in time. Sei whales, like other rorquals, generally have slower dive responses and may not initiate avoidance behavior until a vessel is dangerously close. This latency significantly compromises their ability to escape in time, especially when engaged in shallow dives near the surface.

Studies like Wiley et al. (2011) and Conn & Silber (2013) confirm that mitigation measures such as reduced ship speeds can dramatically lower collision risk. These measures become especially relevant when whales are shown to occupy the upper water column persistently, as in this study. For example, the North Atlantic right whale, whose dive behavior has been studied in detail (Baumgartner & Mate, 2003), exhibits similar shallow dive profiles in breeding and migratory habitats and has suffered heavy population-level consequences from ship strikes.

Diel dive variation may further modulate risk for many whale species (Soldevilla et al. 2017; Calambokids et al. 2019; Caruso et al. 2020). Although the current study found slightly deeper dives at night, sei whales remained within vulnerable depths at all times of day. The implications for sei whales are particularly concerning given their tropical breeding habitat, where the proximity to ports, fisheries, and shipping lanes increases encounter rates. The Santos Basin is one of the most strategically important regions for the country's offshore oil and gas exploration (PETROBRAS, 2022). As home to extensive pre-salt reserves, the basin supports high-density industrial infrastructure, including oil platforms, support vessels, underwater pipelines, and port logistics. This concentration of extractive activity generates intense vessel traffic, particularly from large cargo and service ships that frequently transit the region at varying speeds and directions. Furthermore, the SB hosts four major ports with heavy daily traffic of cargo vessels, playing a strategic role in Brazil's maritime trade (UNCTAD, 2021)

Although ship strikes on sei whales have been recorded, the total number of strikes is likely underrepresented because of the low proportion of carcass recovery (Williams et al. 2011, Rockwood et al. 2017). Given the high overlap between sei whale shallow diving behavior and vessel operational depths, the implementation of mitigation measures such as vessel speed restrictions in key habitat areas is strongly recommended. Numerous studies have demonstrated that reducing ship speed is one of the most effective strategies to lower the probability and lethality of collisions with large whales (Silber et al., 2010; Conn & Silber, 2013, Wiley et al. 2011), and such actions are particularly urgent in regions like the southeastern Brazilian coast, where industrial and shipping activities are intensifying within known whale habitat.

CONCLUSIONS

This study presents an integrative analysis of the diving behavior of sei whales in tropical Brazilian waters using high-resolution non-invasive suction cups tags and satellite transmitters data combined with environmental modeling via GAMMs. The results reveal a consistent pattern of shallow diving, with 93% of dives occurring within the upper 20 meters of the water column. These patterns are shaped by environmental variables such as sea surface temperature, chlorophyll concentration, bathymetric depth, diel cycle, dive shape, and behavioral state.

From a conservation perspective, the predominance of shallow dives in an area of dense maritime traffic and industrial development, such as the Santos Basin, raises concern. Most cargo ships operating in Brazil have drafts between 12.3 and 15.5 meters, and the majority of sei whale dives fall within this high-risk zone. This spatial overlap exposes whales to a heightened risk of ship strikes, particularly since large whales cannot often detect and avoid fast-moving vessels.

Future conservation planning must integrate behavioral data, including dive profiles and diel patterns, into risk assessment tools. The implementation of evidence-based measures, such as seasonal vessel speed reductions and spatial zoning, is essential to mitigate collision risk and ensure the long-term viability of sei whales along the Brazilian coast.

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SUPPLEMENTARY MATERIALS

Table S1. Summary information of sei whales tracked via satellite between 2016 and 2024 along the southeastern coast of South America. The table includes transmitter ID (PTT), tracking start and end dates, tracking duration (in days), group size at tagging, sex (when available), total track distance, average daily distance, mean dive depth (in meters), and mean dive duration (in minutes).

Ptt	Start (Date)	End (Date)	Duration (days)	Group size	Sex	Distance Track (km)	Distance/Day (km)	Depth (m)	Duration (min)
158546	25/08/16	30/08/16	6	10	NI	268.5	44.75	13.3	2.3
162629	31/08/16	08/09/16	9	3	Male	507.35	56.37	13.9	6.6
162630	01/09/16	08/10/16	38	2	NI	2756.79	72.54	14.8	3.3
34638	06/08/18	13/09/18	39	15	NI	2653.58	68.04	12.6	3.7
34755	07/08/18	18/08/18	12	32	NI	635.59	52.96	9.8	2.4
58005	08/08/18	05/10/18	59	15	Male	4313.98	73.11	10.5	4.7
179339	28/07/19	07/09/19	42	4	NI	2628.35	62.57	15.1	3.5
58007	29/07/19	31/08/19	34	6	Male	2282.94	67.14	9.9	4.6
179337	29/07/19	30/08/19	33	6	NI	2148.5	65.1	9.1	1.8
197762	22/07/20	11/08/20	28	3	NI	1948.08	69.57	8.4	2.8
197766	02/08/20	23/09/20	53	6	Male	3785.81	71.43	16.2	3.7
197765	02/08/20	21/08/20	20	6	Male	862.89	43.14	12.7	3.1
179336	03/08/20	09/08/20	7	5	Male	535.26	76.46	12.2	3.1
179338	03/08/20	06/08/20	4	5	Female	112.63	28.15	10.8	6.3
179334	03/08/20	10/08/20	7	2	NI	338.69	48.38	21.3	4.4
197767	22/07/20	29/08/20	39	3	NI	2795.26	71.67	7.2	3.8
224119	12/07/22	17/07/22	6	8	NI	500.11	83.35	6.3	3.3
224122	10/07/22	17/07/22	8	8	Male	427.4	53.42	6.8	4.6
235338	28/07/22	05/08/22	9	3	NI	472.89	52.54	5.9	5.5
235340	25/07/22	08/08/22	15	3	NI	1076.82	71.78	14.6	4.9
244905	22/07/24	26/07/24	5	3	NI	128.26	25.65	5.8	7.6
244909	20/07/24	09/08/24	21	2	NI	1295.11	61.67	6.6	4.0
244910	20/07/24	03/08/24	15	2	NI	825.24	55.01	6.2	2.4
244911	21/07/24	26/08/24	37	4	NI	2388.02	64.54	8.1	5.7
244913	23/07/24	10/08/24	19	8	NI	985.29	51.85	6.3	3.9
244914	19/07/24	12/08/24	25	8	NI	1911.02	76.44	7.2	3.0

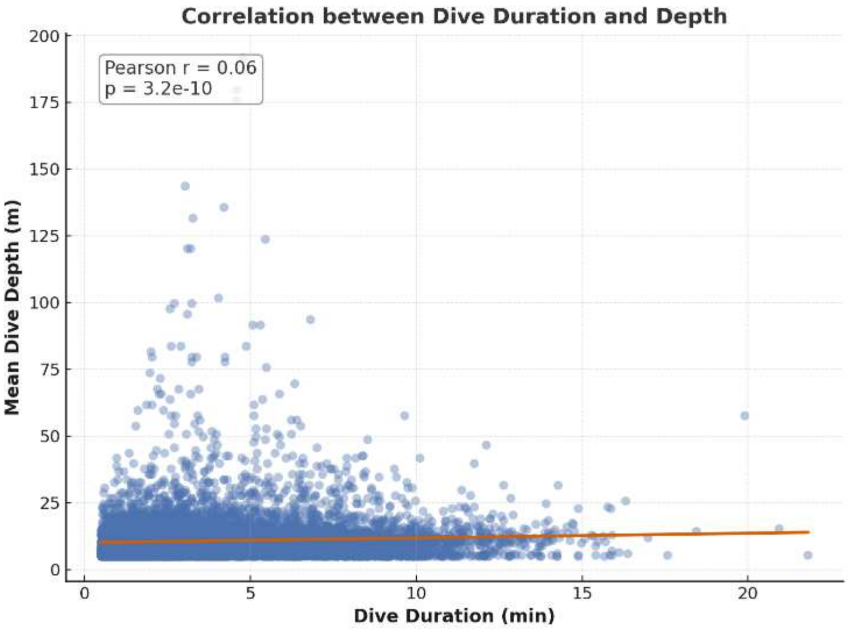


Figure S1. Relationship between dive duration and mean dive depth of sei whales. Each point represents a single dive. The plot shows a weak but statistically significant positive correlation between dive duration and depth (Pearson $r = 0.06$, $p = 3.2 \times 10^{-10}$), indicating that longer dives tend to be slightly deeper.

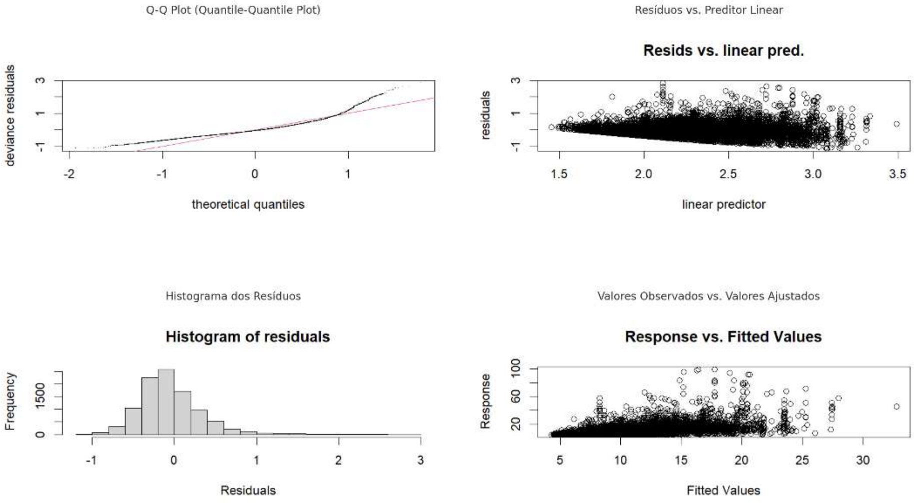


Figure S2. The plots show diagnostics of the GAMM fitted to sei whale (*Balaenoptera borealis*) dive depth analysis: the Q-Q Plot assesses the normality of residuals; the Residuals vs. Linear Predictor plot checks for patterns and heteroscedasticity; the Histogram of Residuals inspects their distribution; and the Observed vs. Fitted Values plot evaluates the model's predictive performance.

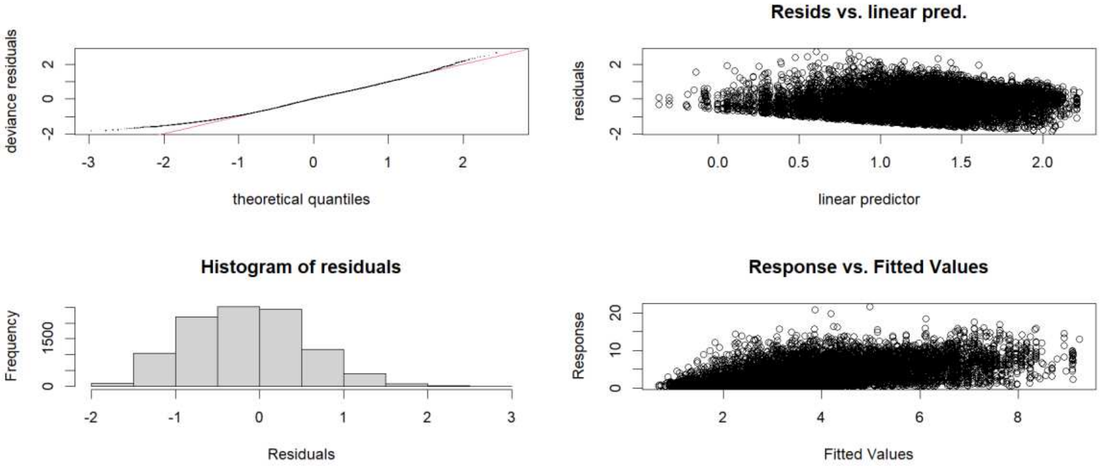


Figure S3 The plots show diagnostics of the GAMM fitted to sei whale (*Balaenoptera borealis*) dive duration analysis: the Q-Q Plot assesses the normality of residuals; the Residuals vs. Linear Predictor plot checks for patterns and heteroscedasticity; the Histogram of Residuals inspects their distribution; and the Observed vs. Fitted Values plot valuates the model's predictive performance.

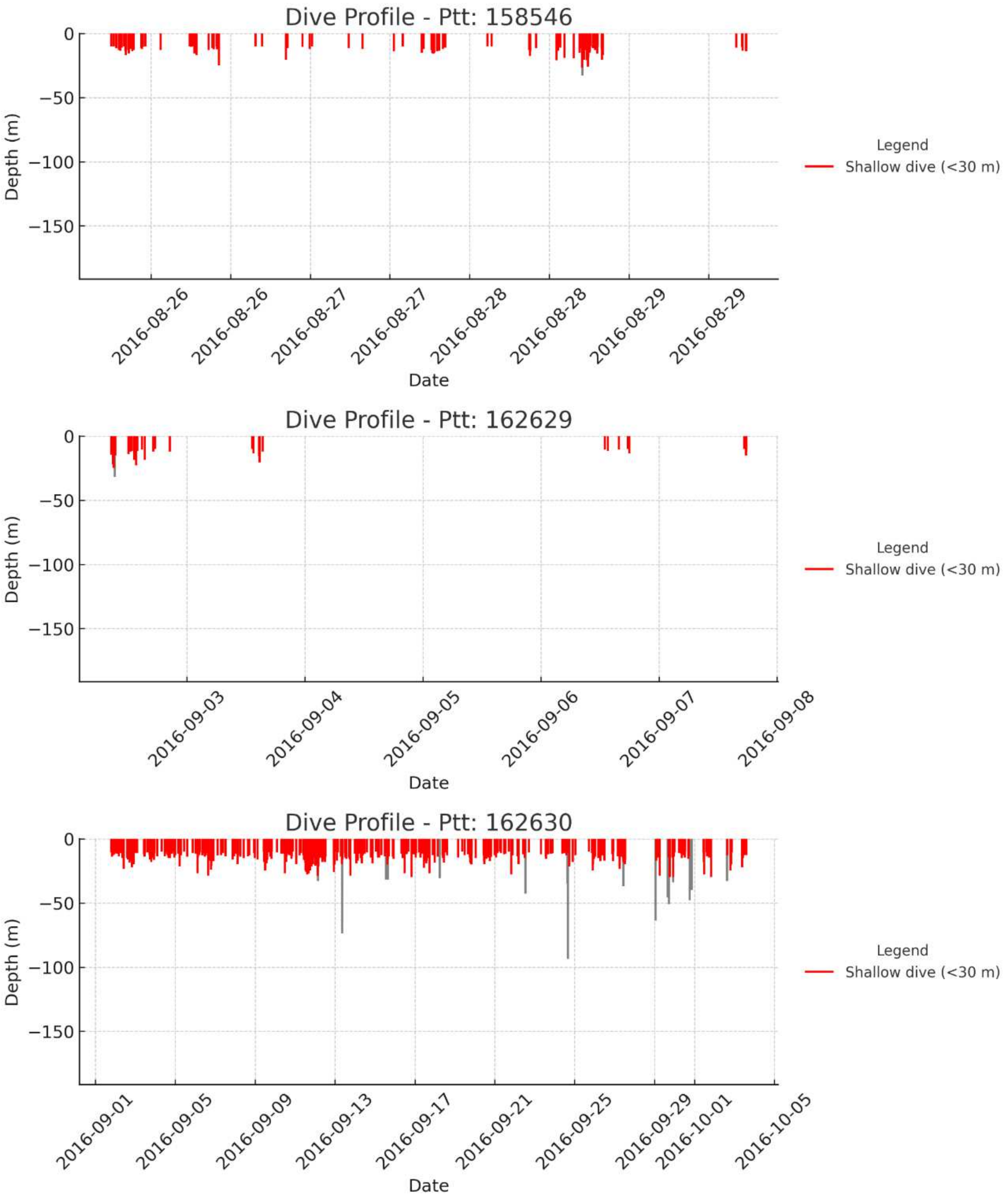


Figure S4 Dive profiles of three sei whales (*Balaenoptera borealis*) equipped with satellite transmitters in 2016. Shallow dives (<30 meters in depth) are shown in red.

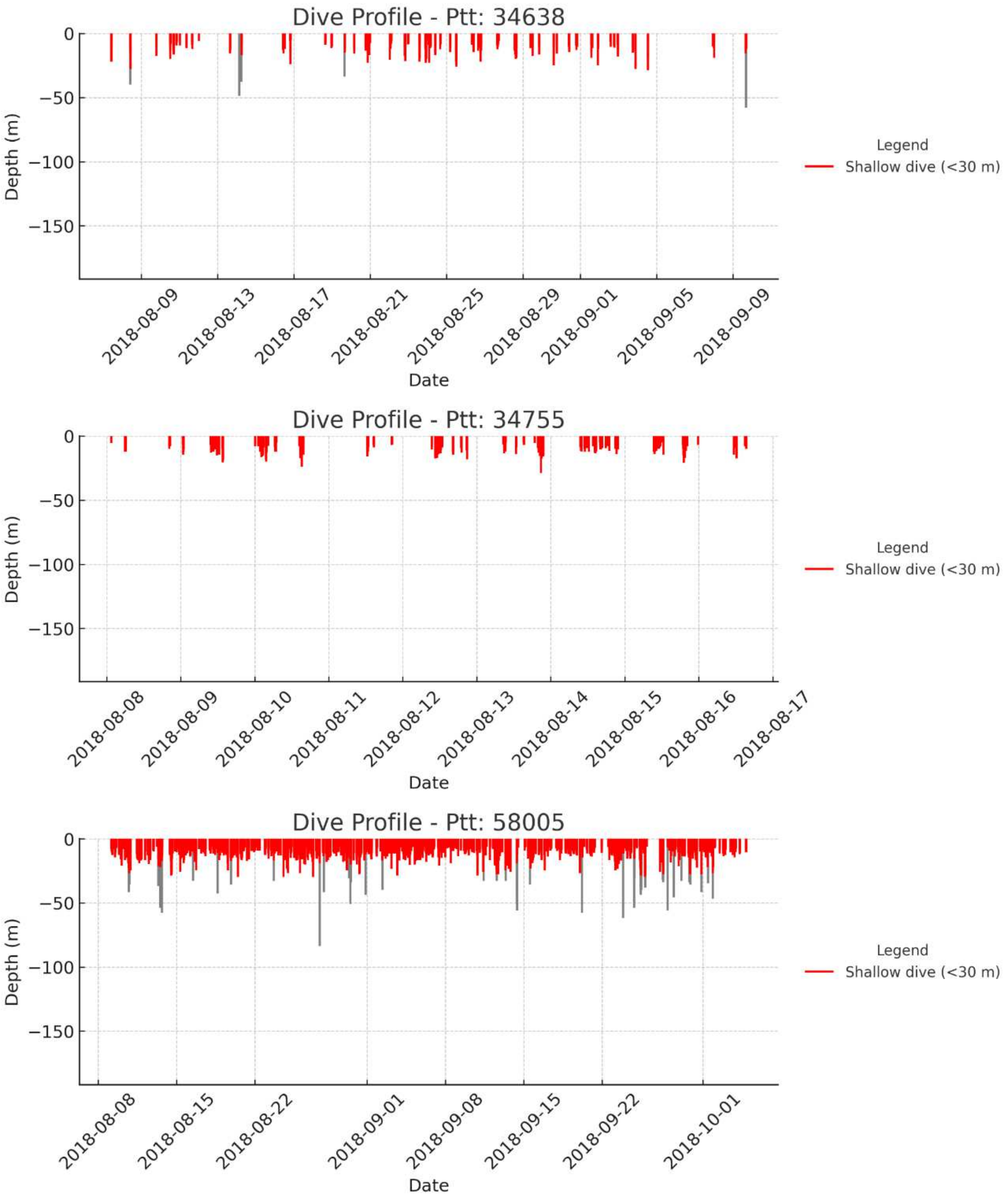


Figure S5. Dive profiles of three sei whales (*Balaenoptera borealis*) equipped with satellite transmitters in 2018. Shallow dives (<30 meters in depth) are shown in red.

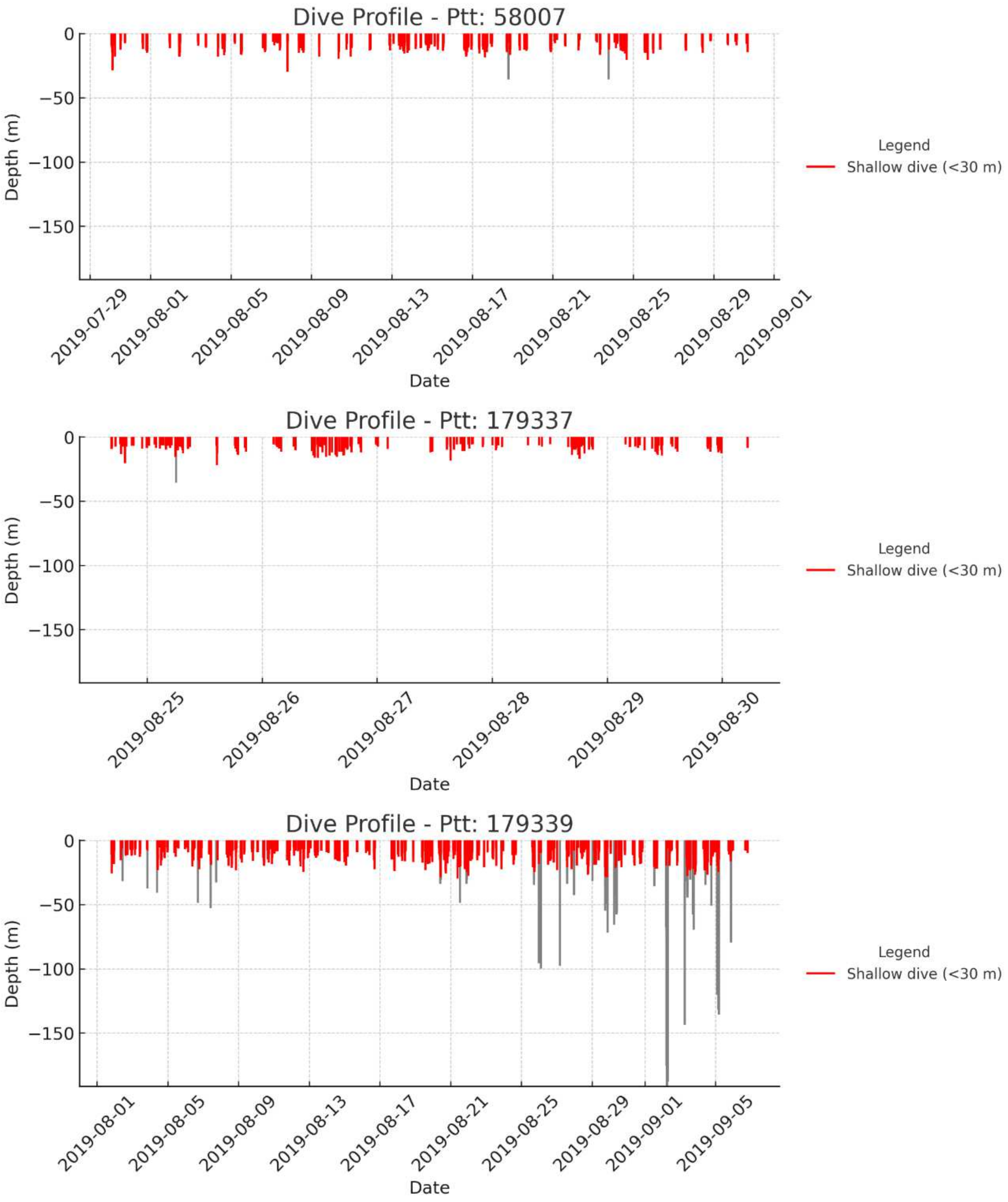


Figure S6. Dive profiles of three sei whales (*Balaenoptera borealis*) equipped with satellite transmitters in 2019 Shallow dives (<30 meters in depth) are shown in red.

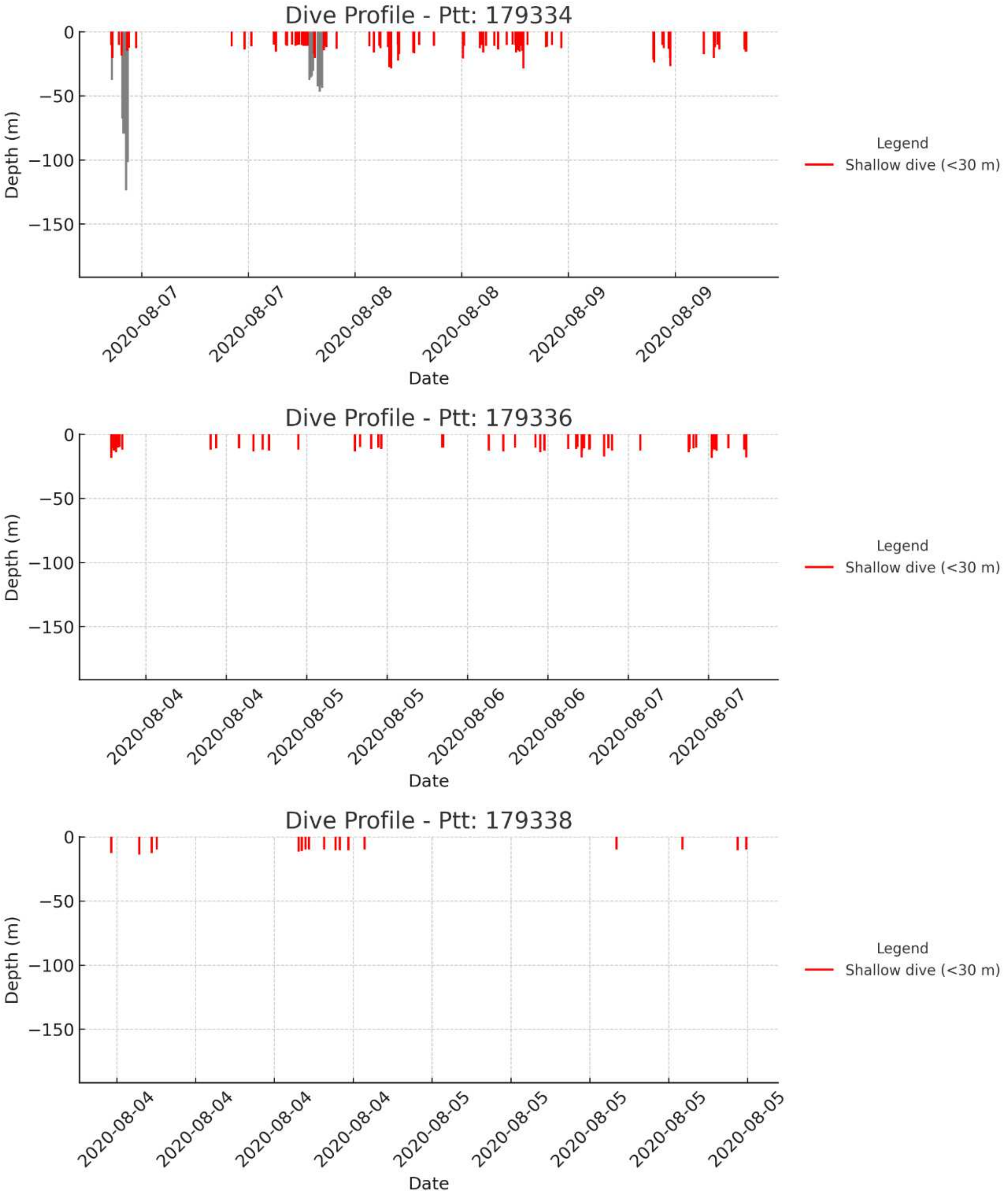


Figure S7. Dive profiles of three sei whales (*Balaenoptera borealis*) equipped with satellite transmitters in 2020 Shallow dives (<30 meters in depth) are shown in red.

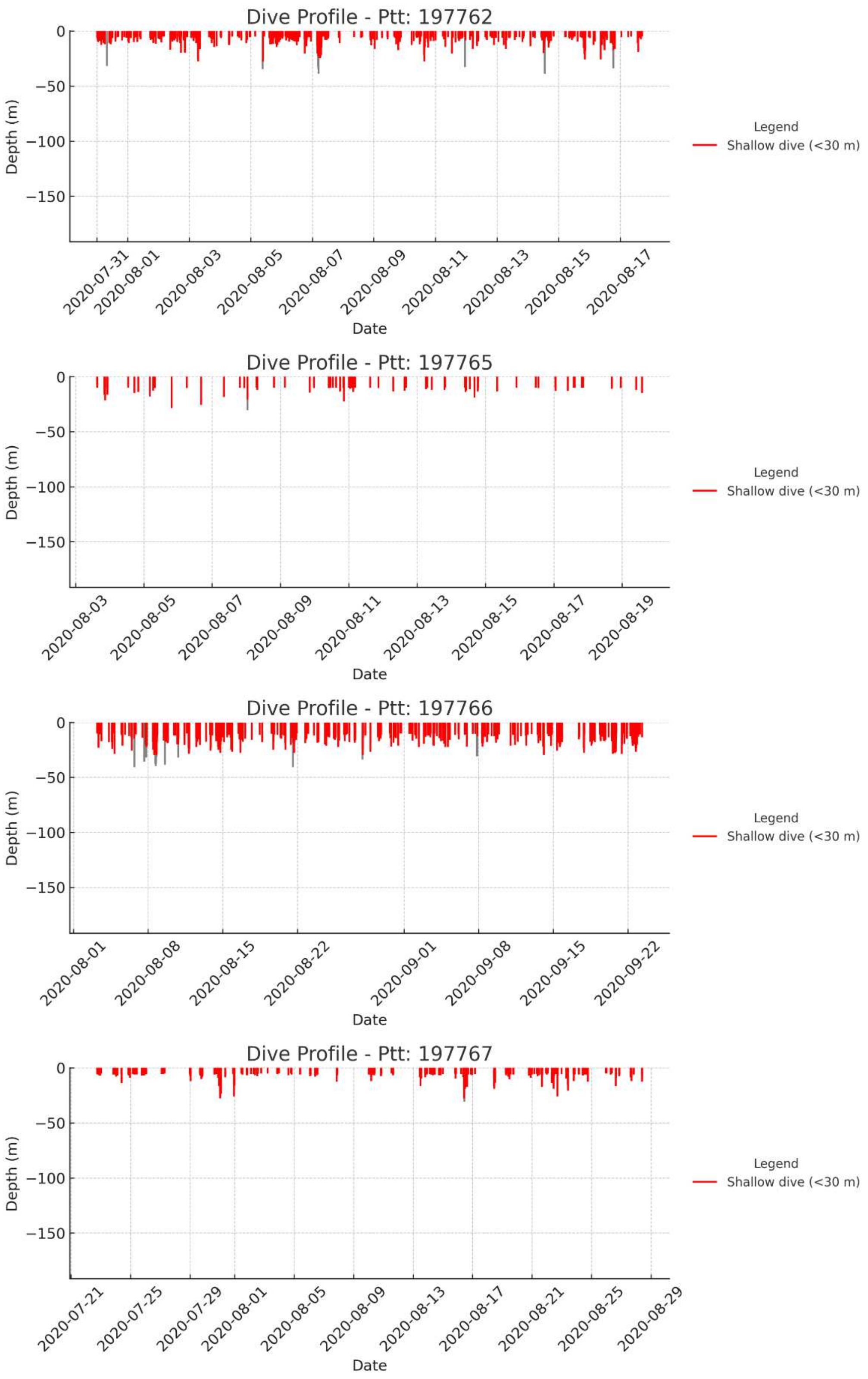
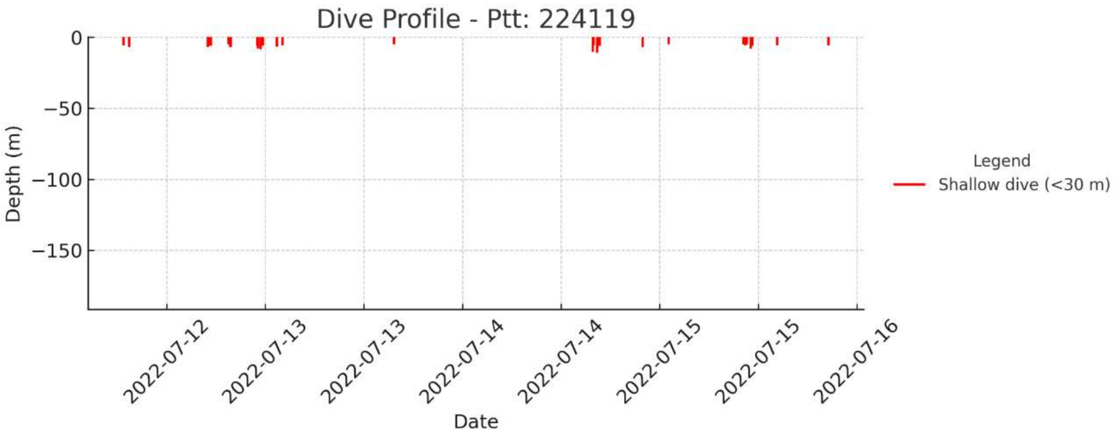
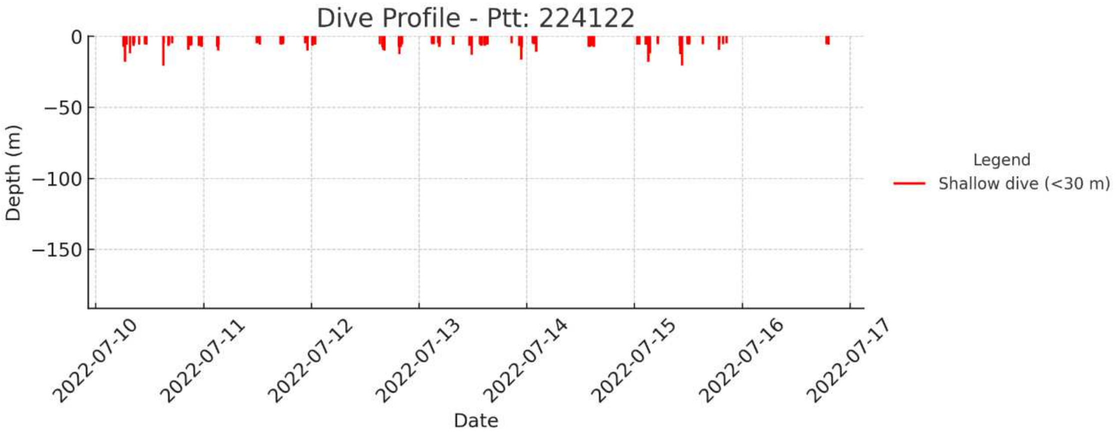
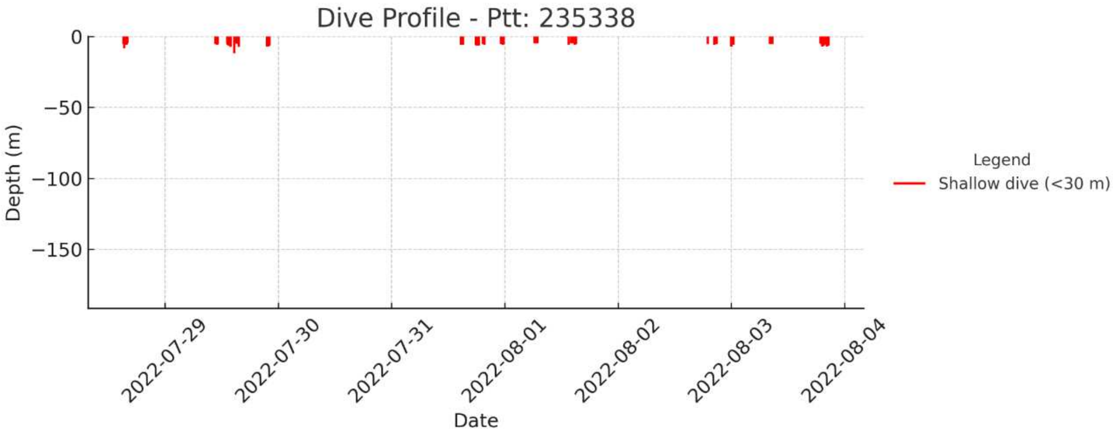


Figure S8. Dive profiles of four sei whales (*Balaenoptera borealis*) equipped with satellite transmitters in 2020 Shallow dives (<30 meters in depth) are shown in red.


Dive Profile - Ptt: 224119
Depth (m)
0
−50
−100
−150
2022-07-12
2022-07-13
2022-07-13
2022-07-14
2022-07-14
2022-07-15
2022-07-15
2022-07-16
Date
Legend
Shallow dive (<30 m)


Dive Profile - Ptt: 224122
Depth (m)
0
−50
−100
−150
2022-07-10
2022-07-11
2022-07-12
2022-07-13
2022-07-14
2022-07-15
2022-07-16
2022-07-17
Date
Legend
Shallow dive (<30 m)


Dive Profile - Ptt: 235338
Depth (m)
0
−50
−100
−150
2022-07-29
2022-07-30
2022-07-31
2022-08-01
2022-08-02
2022-08-03
2022-08-04
Date
Legend
Shallow dive (<30 m)

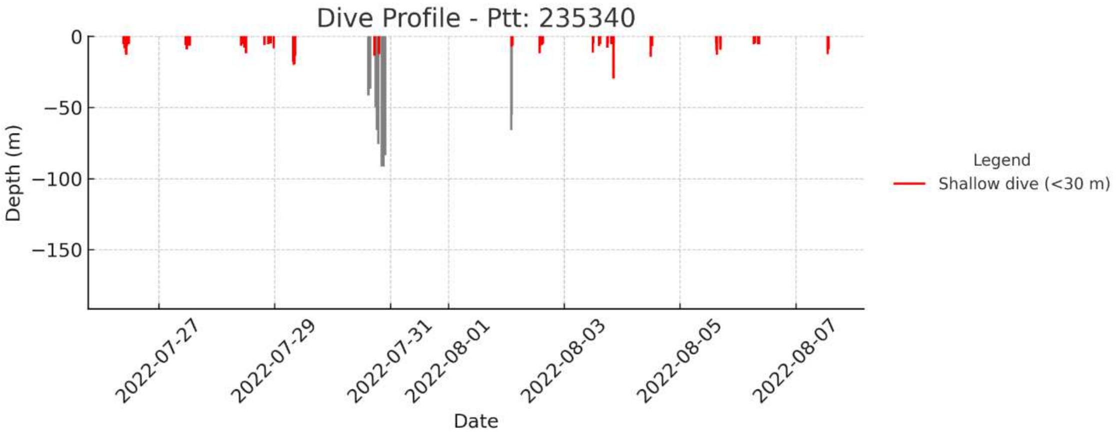

Dive Profile - Ptt: 235340
Depth (m)
0
−50
−100
−150
2022-07-27
2022-07-29
2022-07-31
2022-08-01
2022-08-03
2022-08-05
2022-08-07
Date
Legend
Shallow dive (<30 m)

Figure S9. Dive profiles of four sei whales (*Balaenoptera borealis*) equipped with satellite transmitters in 2020 Shallow dives (<30 meters in depth) are shown in red.

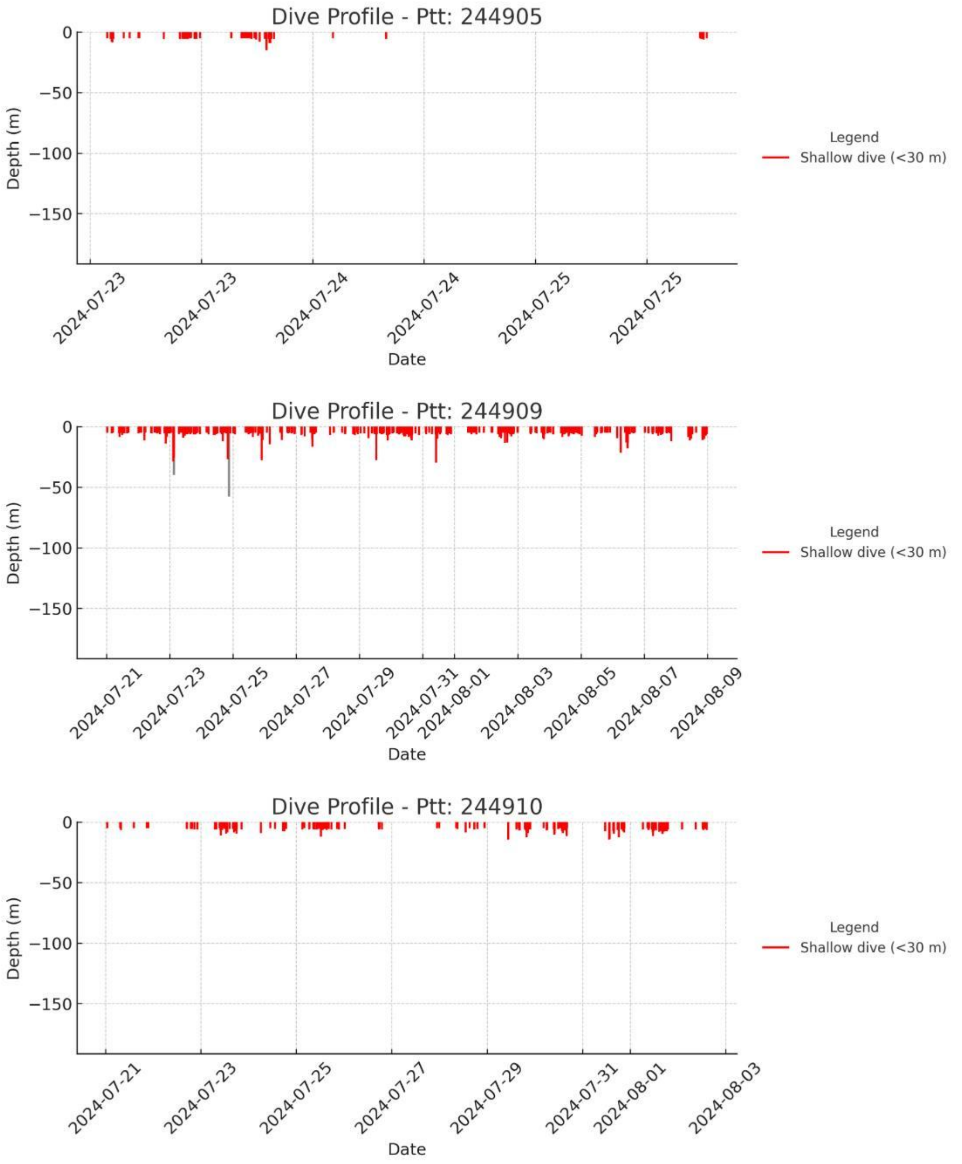


Figure S10. Dive profiles of three sei whales (*Balaenoptera borealis*) equipped with satellite transmitters in 2024 Shallow dives (<30 meters in depth) are shown in red.

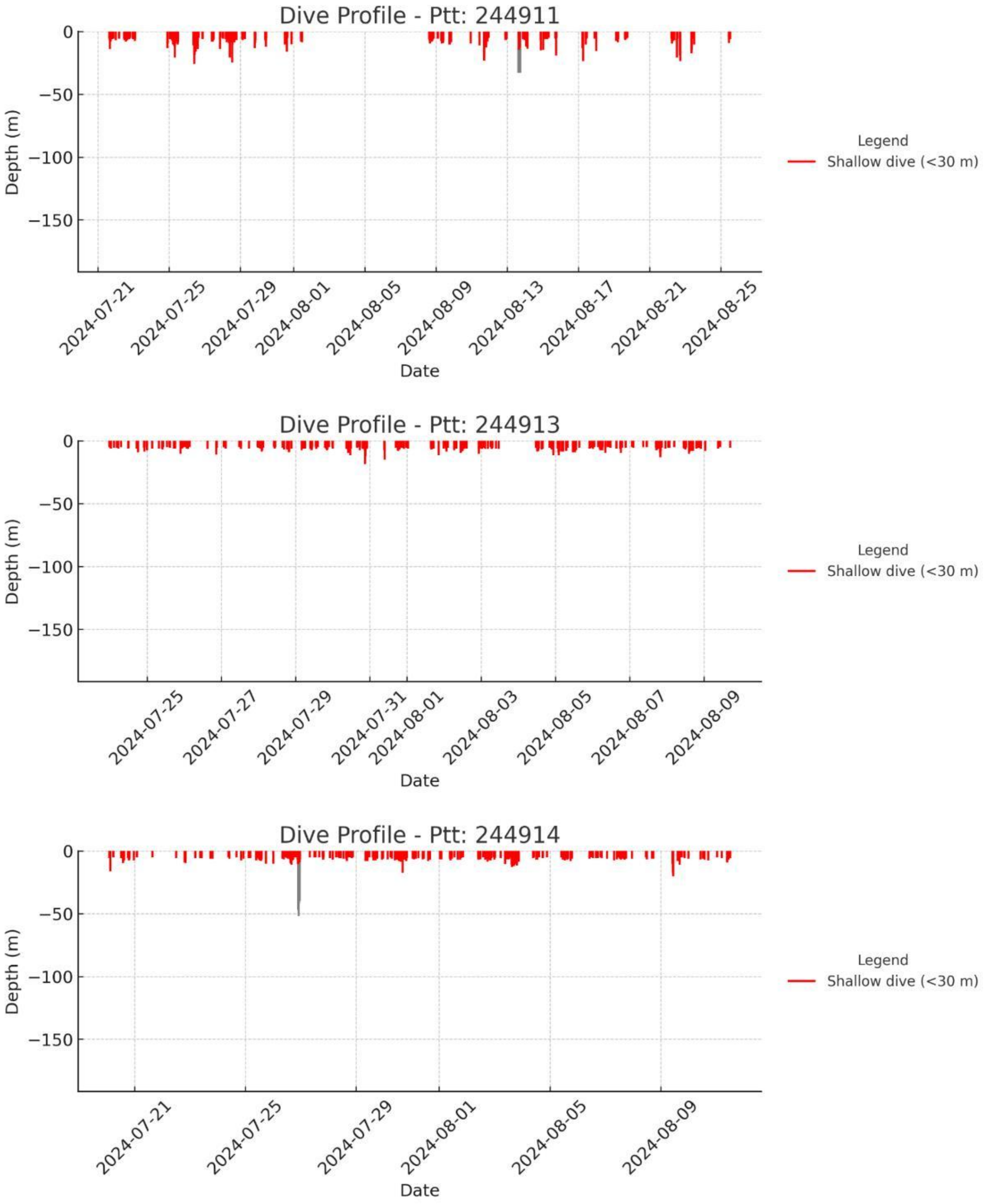


Figure S11. Dive profiles of four sei whales (*Balaenoptera borealis*) equipped with satellite transmitters in 2020 Shallow dives (<30 meters in depth) are shown in red.