Bryde's whales off the central coast of Ecuador: Distribution, behaviour and ecological insights

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ABSTRACT

The Bryde's whale is a lesser-known baleen whale. Surveys were conducted to assess the presence and ecology of Bryde's whales along the central coast of Ecuador during the months of December–May between 2021 and 2024. The study area covered 6,700 km² of coastal and open waters, with depths reaching up to 1,000 m. The effort included 46 trips, covering 5,018 km, during which 100 whales were sighted in 62 groups. Whales were found in all surveyed areas, with the majority (58%) detected in waters between 41–60 m depth and only two records made in waters shallower than 30 m. The average relative abundance was estimated at 0.016 whales/km of survey (SD = 0.057). The average group size included 1.61 whales (SD = 1.13). Mother-calf pairs were observed in eight groups (12.9%). Feeding behaviour was noted in 13 groups (20.9%) and coincided with a larger group size compared with other behavioural states ($P = 0.02$). We used generalised linear modeling (GLM) with a negative binomial distribution to explain the variability of whale relative abundance. Six explanatory variables (month, depth, SST, chlorophyll *a*, ONI and ICEN) and effort as an offset variable were used to fit models. The model that best fit the data revealed a significant positive correlation with month and a negative correlation with chlorophyll *a*. Thus, whales increased abundance toward the end of the research season. The negative correlation with chlorophyll *a* suggests that other ecological factors, including the lagged response of prey to productivity, and shifts in prey distribution, may play a more critical role and warrant further investigation. The coastal distribution of Bryde's whales exposes them to fishing gear and vessel collisions, underscoring the need for management strategies to mitigate these interactions.

KEYWORDS: BRYDE'S WHALE; ECOLOGY; DISTRIBUTION; RELATIVE ABUNDANCE; BEHAVIOUR; ECUADOR

INTRODUCTION

The Bryde's whale (*Balaenoptera edeni*) is distributed in tropical and subtropical waters around the world between 40°N and 40°S (Kato & Perrin, 2018). While Bryde's whales are not known for long-distance migrations, they may exhibit seasonal movements in response to changes in water temperature, prey distribution and breeding activity (Cooke & Brownell Jr., 2018). However, taxonomic uncertainty persists around the species because some populations have not been evaluated in detail, given the difficulty of detecting and identifying them at sea. At the international level, both the International Whaling Commission (IWC) and the Taxonomy Committee of the Marine Mammal Society (2024) recognise a single species *Balaenoptera edeni* with two subspecies: *B. e. brydei*, a large oceanic form, and *B. e. edeni*, a smaller coastal form. In some places, such as South Africa (Best, 1977; 2001; Penry *et al*., 2018), Peru (Ramírez, 1986) and the Northwest Pacific–Indian Ocean

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(Kanda *et al*. 2007; Kershaw *et al*. 2013), both forms have been reported simultaneously. In Peru, in contrast to elsewhere, the neritic form, distributed up to 100 nm from the coast, is longer than the oceanic form inhabiting oceanic waters beyond 100 nm (Ramírez, 1986). Wada *et al*. (2003) proposed both subspecies to be recognised as different species based on their molecular relationships and morphology. Recent molecular analyses with samples from Peru, Chile and Brazil showed a closer relationship of South American Bryde's whales with *B. e. brydei* than *B. e. edeni*, as proposed by Wada *et al*. (Pastene *et al*., 2015). Although the species at the global level is considered 'Least Concern' (Cooke & Brownell Jr., 2018), a low gene flux shows some population structure that demands tailored conservation strategies (Kanda *et al*., 2007).

The Bryde's whale was reported for the first time in the Southeast Pacific in 1960 at a whaling station in Iquique, Chile (Clarke & Aguayo, 1965). Previously, the species was not easily distinguished from the sei whale (*B. borealis*). The authors also reported that there were two credible earlier cases of Bryde's whales in the region reported by a Norwegian whaling manager on Gorgona Island, Colombia (2°54'N, 78°13'W) and on La Plata Island, Ecuador (1°20'S, 81° 05W) in 1914 (Norsk Hvalfanngst-Tidente, 1925, cited by Clarke & Aguayo, 1965). The doubt about the identity between sei and Bryde's whales has therefore persisted for a long time in the region. The two species were separated in whaling records from Peru only after 1974, even though whaling from coastal stations in the area began in 1951 (Ramírez, 1989a, b). Nonetheless, the Peruvian whaling focused on sperm whales (*Physeter macrocephalus*), with only 67 sei whales taken until 1967. From 1968 onwards, sei and Bryde's whales were taken regularly. Between 1968 and 1974, a total of 3,263 whales identified as Bryde's + sei were taken, and 3,263 Bryde's whales and 215 sei whales between 1974–1985 (Ramírez, 1989b). Assuming that the sei:Bryde's proportion was constant since the beginning of whaling activities, it can be inferred that approximately 2,910 Bryde's whales were taken during the period 1968–74. Consequently, the cumulative count from three coastal Peruvian whaling stations stands at 6,173 Byde's whales. When the moratorium on commercial whaling came into effect in 1985/86, the Southeast Pacific Bryde's whale stock showed signs of depletion and catches per unit of effort had decreased by half (Ramírez, 1989a).

A significant number of Bryde's whale sightings have been made in the Eastern Pacific in the last four decades, including Southeast Pacific countries, such as Colombia, Ecuador (including the Galápagos Islands) and Peru, by the United States National Oceanic and Atmospheric Administration (NOAA) during its monitoring programme on cetacean populations in the eastern tropical Pacific (Hamilton *et al*., 2009). The population abundance in an area of 19 million km^2 of the eastern Pacific was estimated at 13,000 (CV = 20) individuals during 1985–90 (Wade & Gerrodette, 1993). NOAA sightings also demonstrated that the distribution of the species in the Southeast Pacific was continuous from Colombia to northern Chile, as suggested at the time by Clarke & Aguayo (1965) and Ramírez (1989a). Information regarding the movements of individuals within the Southeast Pacific is limited, yet efforts to compare catalogues between Panama, Ecuador and Peru are ongoing (Castro *et al*., 2017).

Overall, the presence of Bryde's whales in Ecuadorian waters is still poorly known given the limited research effort towards the species. A first attempt to evaluate whale stocks in the country was carried out in the late 1950s, when Clarke (1962) reported 21 sei whales during a whale research campaign in 1959 between the coast of Ecuador and around the Galápagos Islands, also indicating they could have been Bryde's whales. Three whaling survey cruises carried out between 1963 and 1964 in Ecuador and the Galápagos by Japanese whalers from the Taiyo Gyogyo company and personnel from national fishing institutions of Ecuador also reported the presence of 'sei' whales and sperm whales (Loesch, 1966). Since the 1980s, reports of Bryde's whales in the Galápagos have been relatively frequent (e.g., Merlen, 1995; Palacios & Salazar, 2002, Denkinger *et al*., 2013; Biggs *et al*., 2017). However, on the continental coast of Ecuador, the first records of the species date back to the 1990s and were associated with strandings (Chiluiza *et al*., 1998; Félix *et al*., 2011), vessel collisions (Félix & Van Waerebeek, 2005; Félix, 2009), opportunistic observations aboard tourist boats during the humpback whale breeding season (Castro *et al*., 2017), and observations from land (Museo de Ballenas, 2024).

In 2021, we initiated systematic surveys along Ecuador's central coast to evaluate the Bryde's whale population status, expanding the information previously collected opportunistically onboard whale-watching vessels (Castro *et al*., 2017). These efforts have yielded new insights into seasonality, behaviour and relative abundance. Given the threats identified over the last two decades in the country, we expect this information will help shape management strategies for this poorly known species.

MATERIALS & METHODS

Study area

The study area encompasses two polygons with surface areas estimated at 5,600 km² and 1,100 km² along the central coast of Ecuador (Fig. 1). Nested within a vast bay, the southern polygon spans from Puerto Cayo in the north to Salinas in the south, a distance of 100 km. To the northwest, the area extends 40 km into the Pacific Ocean, roughly 10 km west of La Plata Island. On its west side, the area extends about 150 km southward from the north of La Plata Island to the northern Gulf of Guayaquil, 50 km south of Salinas. Due to the narrow continental shelf along Ecuador's coastline, the eastern side is predominantly shallow, ranging from 10 to 60 m in depth, while the western side transitions to deeper ocean waters, ranging between 100 and 1,000 m in depth. The smaller polygon is located west and north of Bahía de Caráquez, approximately 80 km north of the large polygon and includes mostly shallow areas (20–30 m).

The study area is characterised by a tropical climate with two seasons throughout the year, a warm and rainy season between December and May and a colder, dry season between June and November. The yearly average sea surface temperature (SST) along the Ecuadorian coast is 25.3°C in the warmer months, while in the dry season, it can drop to approximately 20°C (Chinacalle-Martínez *et al.*, 2021). The oceanographic dynamic in the

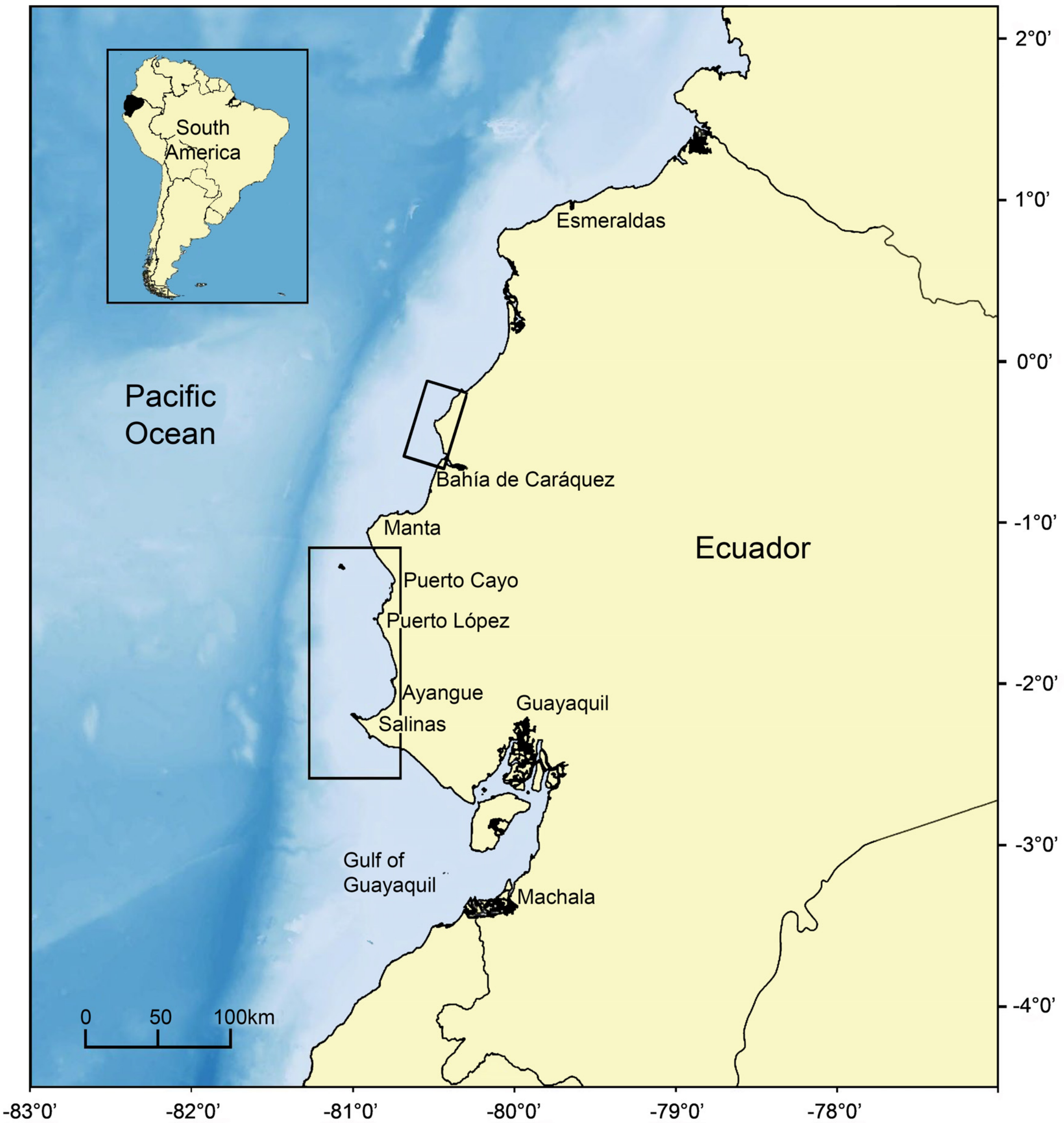

Figure 1. The study area on the central coast of Ecuador and the two polygons where surveys were conducted. The map also includes the location of Ecuador in northwest South America.

area is associated with the Equatorial Front, caused by the confluence of the Peruvian or Humboldt Current coming from the south, characterised by colder waters, high salinity and high productivity, and tropical waters in the north characterised by warm waters, lower salinity and lower productivity (Wyrtki, 1966). The area is also affected by the El Niño Southern Oscillation (ENSO) Phenomenon, whose warm phase 'El Niño' increases SST by up to 4 °C above the average, and its cold phase 'La Niña' when SST can decline up to 2 °C below the average (Fielder, 2002). This cycle is also associated with changes in the average wind speeds, rainfall, thermocline depth, circulation and biological productivity, with notable impacts on the distribution of marine species, including birds, small pelagic fish and marine mammals (Barber & Chávez, 1983; Ramírez & Urquizo, 1985; Fielder, 2002).

Surveys

Since early opportunistic and Peruvian whaling records showed that Bryde's whales were more abundant during the warm season (December–May) (Ramírez, 1989a; Castro *et al*., 2017), survey effort concentrated on those months between 2021 and 2024. A 12 m length fiberglass boat with an upper deck 2 m above the water surface and powered by twin 150-HP outboard engines was used as the research platform. Surveys were conducted at 18.5–28 km/h. Puerto López in the north of the study area was used as the main launching site, although four trips departed from Salinas. Survey effort concentrated along the coast between the north of Puerto Cayo and Ayangue in the south, approximately 70 km apart, and from Puerto López north-westward to La Plata Island, 40 km apart (Fig. 2). These areas are characterized by shallow waters (20–50 m depth). In the deeper southwest part (Salinas and Gulf of Guayaquil), surveys covered mostly deeper areas (100–1,000 m depth). Nonetheless, an extended area within the largest polygon between Puerto Cayo and Salinas, south and west of Ayangue, remained un-surveyed (Fig. 2).

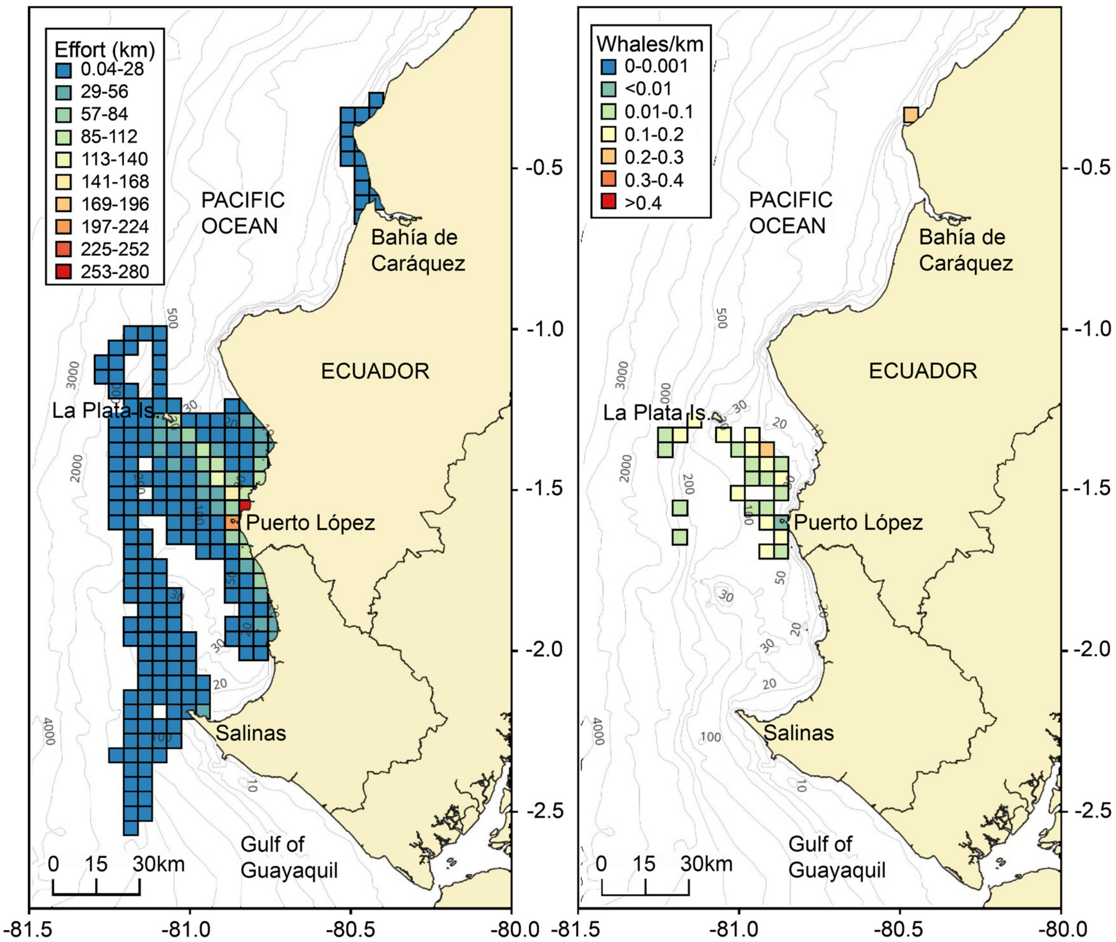

Figure 2. Survey effort per 25 km^2 cell grid in the study area (left) and relative abundance (whales/km of survey) weighted by survey effort (right). In both cases, colours indicate the intensity according to their respective scale.

The crew, consisting of three to five researchers and two sailors, scanned the horizon on both sides of the boat, searching for whales. Upon detection, the boat cautiously approached the area to gather data on group size, age/sex composition and behaviour. Whales that did not maintain a clear association pattern but were within an area of a few hundred meters and displayed similar behaviour were considered part of the same group. Whales were considered adults, juveniles or calves according to the size estimated by eye agreed between researchers in the field. Juveniles were visually 30–50% smaller than adults. Calves corresponded to an evidently smaller animal seen on the side of a large whale, presumably its mother.

We defined three behavioural states in the whales: (1) travelling – when the whales moved in a straight direction at a relatively fast speed (around 10–12 km/h); (2) milling – when whales stayed around the sighting area with back-and-forth movements and slower speed; and (3) feeding – when whales completed short, fast movements within a small area, generally conducting side swimming and exposing the whiter ventral coloration. Feeding was also associated with marine birds dive-bombing and surface feeding, and, in some cases, small schooling fish breaching above the surface.

Spatial analysis

The encounter rate (number of whales/km of survey) was used as an indicator of relative whale abundance in the study area. Although this index is sensitive to sampling conditions, such as weather and the height of the sighting point, these effects were minimised by conducting surveys on similar boats during periods when weather conditions along the coast of Ecuador are relatively uniform.

Sighting coordinates and track surveys were recorded with a handheld Garmin 60 GPS. Positions and survey tracks were used to estimate survey effort and relative abundance using vectorial tools implemented in Q-GIS v.3.4 (QGIS Development Team, 2018). Before conducting the spatial analysis, parts of the tracks corresponding to the sighting period were considered off-effort and removed from the survey track. A polygon data layer of 5 km * 5 km grid cells (25 km^2) covering the study area was used to calculate individual cell effort units. The total length of survey tracks was calculated in each polygon cell using the geoprocessing tool 'intersect'. The number of whales was calculated in each cell using the data management tool 'join attributes by location'. Finally, the relative abundance of whales per unit of effort in each cell (whales/km of survey) was calculated using the 'field calculator' tool. Maps of effort and relative abundance were also created with Q-GIS. Only cells with a greater effort than the diagonal of a cell (7 km) were considered to mitigate the potential bias due to the low effort in those areas (Gnome *et al*., 2023).

Ecological modelling

Generalised linear modelling (GLM) was employed to discriminate between the potential factors influencing the relative abundance of whales within the study area. The negative binomial distribution was chosen because it better addressed the over-dispersed data by incorporating a variance function, $\mathrm{Var}(Y) = \mu + \mu 2 / \theta$, where theta ($\theta$) is the dispersion parameter and quantifies how much of the observed variance exceeds what is expected under a Poisson distribution (Zuur *et al*., 2009). Thus, the negative binomial distribution can be viewed as a generalisation of the Poisson distribution, where the variance is allowed to be greater than the mean. Theta values between 1 and 5 are indicative of a moderate overdispersion, suitable to be addressed with the binomial distribution.

The analysis utilised the number of whales as the dependent variable and the effort (km of survey) as the offset variable to balance the uneven coverage of the study area. Explanatory variables included one temporal variable (month), two continuous variables associated with environmental data (SST [°C] and chlorophyll *a* [mg/m^3]), one physiographic variable (depth), and two indexes associated with El Niño Southern Oscillation (ENSO) Phenomenon (the Oceanic Niño Index [ONI] and the Coastal Niño Index [ICEN; Spanish acronym]). The ONI is a minimum of five consecutive three-month running averages of SST anomalies in the central Pacific Ocean in the Niño 3.4 region (5°N–5°S, 120°–170°W) as defined by NOAA's Climate Prediction Center.[4] The ICEN was developed in Peru to monitor the El Niño phenomenon with a local index because the thermic conditions in the Eastern Pacific are different from the Central Pacific (Takahashi *et al*., 2014; IMARPE, 2024). The ICEN index is

[4] *http://www.cpc.ncep.noaa.gov/*

calculated in a similar way to the ONI index, with three-month average of SST anomalies in the Niño 1 + 2 region (80–90 °W) but only spans the 0–30 °S latitude range with associated climatology data for the 1981–2019 period, using ERSST v5 real-time data (Quishpe-Ccalluari *et al.*, 2018).[5]

A value for each explanatory variable was extracted for each sighting. In surveys with multiple sightings, the sum of all group sizes was used to estimate the relative abundance for that trip. Additionally, the values of SST, chlorophyll *a* and depth were averaged. In trips with no sightings, a value of '0' was assigned to the dependent variable, and values for SST and chlorophyll *a* were obtained by averaging the values within a polygon (N: –1.3, S: –1.8, E: –80.8, W: –81) covering approximately 1,500 km^2 of the study area.

Variables were evaluated for multicollinearity using the variance inflation factor (VIF) from the *car* package in R, with values greater than 10 indicating high multicollinearity (Fox & Weisberg, 2011). All variables used in our analysis had a VIF of 2 or lower. Data were also evaluated for spatial autocorrelation (SAC), which can significantly affect GLM modeling by violating independence assumptions, inflating error rates and biasing results. Spatial autocorrelation (SAC) occurs when observations collected in close proximity exhibit similar values (Dormann *et al*., 2007). To ensure no significant SAC remained in the data, Moran's I test was applied, as implemented in the *spdep* package (Bivand & Wong, 2018). This test evaluates the residuals of the model to identify any unaccounted spatial autocorrelation. We confirmed no SAC was present in our dataset.

Model selection was based on the Akaike Information Criterion corrected for small sample sizes (AICc). AICc is a measure that balances the goodness of fit of a model with its complexity, penalising models that are more complex to avoid overfitting (Burnham & Anderson, 2002). All calculations and data processing were carried out using the R statistical environment (R Core Team, 2024).

Datasets used in the ecological analysis include the following:

1. SST: NOAA ACSPO Daily Global 0.02° (2.2 km) Gridded Super-collated SST and Thermal Fronts Reanalysis, 2012–present, Daily (L3S-LEO degrees). Downloaded from NOAA Environmental Research Division Data Access Program (ERDDAP).[6]

2. Chlorophyll *a* (Gap-filled DINEOF): NOAA S-NPP NOAA-20 VIIRS and Copernicus S-3A OLCI, Science Quality, Global 2 km, 2018–recent. Downloaded from NOAA Environmental Research Division Data Access Programme (ERDDAP).[7]

3. The ONI index: Downloaded from the NOAA Climatic Prediction Center.[8]

4. The ICEN index: Downloaded from the Peruvian Institute of Geophysics (IGM)'s website.[9]

5. Depth: Downloaded from the IHO-UNESCO Global Bathymetric Chart of the Oceans GEBCO with a 15 arc-second (250 m) grid resolution.[10]

RESULTS

Survey effort

The survey effort encompassed 251.8 hours at sea, including 26.2 hours spent observing whales, covering a distance of 5,018.5 km. A total of 62 groups, including 100 whales, were recorded during the study (Table 1). As the effort doubled in 2023, compared to the first two years, the number of groups and whales recorded increased 10 times. While survey effort was comparable in 2023 and 2024, the number of groups and the number of whales were higher in 2024 by 2.6 and 2.3 times, respectively. 2024 coincided with an extension of monitoring areas, as surveys extended towards deeper areas west of Puerto López and southward to Salinas.

[5] The ICEN is available at *http://met.igp.gob.pe/datos/icen.txt*
[6] *https://coastwatch.pfeg.noaa.gov/erddap/index.html*
[7] *https://coastwatch.pfeg.noaa.gov/erddap/index.html*
[8] *https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php*
[9] *http://met.igp.gob.pe/datos/ICENr.txt*
[10] *https://download.gebco.net/*

Table 1

The effort made during the study period (trips, distance and time) and number of groups and whales recorded between 2021 and 2024.

	2021	2022	2023	2024	TOTAL
Number of trips	3	8	18	17	46
Total distance (km)	357.3	661.9	1,824.2	2,175.1	5,018.5
Total time (h)	17.3	36.6	91.4	106.5	251.8
Sighting time(h)	1.2	1	9.7	14.2	26.2
Groups	2	1	16	43	62
Whales	2	1	27	70	100

Whale distribution and depth

Bryde's whales were found in all surveyed areas, in shallow and deep waters, although rarely in depths of less than 30 m. Most sightings were made in shallow waters in the northeast (Puerto López to La Plata Island), but also along the west side of the study area and in the northwestern part of the Gulf of Guayaquil at 500–1,000 m depth. Figure 3 shows the sighting frequency distribution at different depth ranges. In coastal waters, the majority (58%) of sightings were made in water depths ranging between 41 and 60 m, with only two (3.2%) in waters less than 30 m, including one sighting recorded in less than 20 m at Bahía de Caráquez, where the continental shelf narrows. There is a lack of whales immediately off Puerto Cayo, an area with high effort but shallow water. Twelve sightings occurred in waters over 100 m deep, with a maximum recorded depth of 900 m.

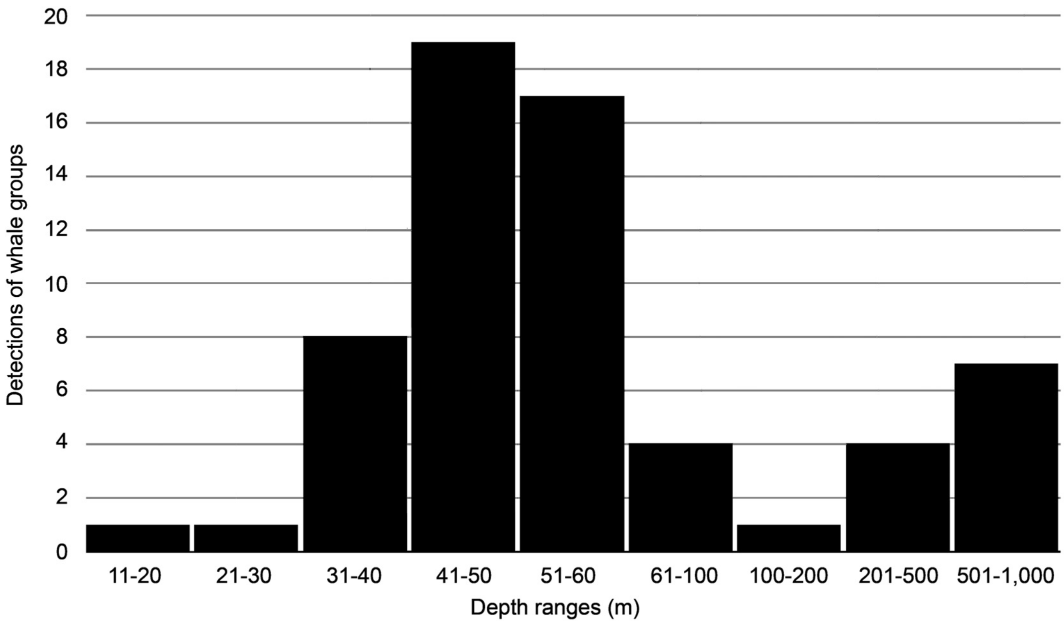

Figure 3. Sightings of whale groups in relation to depth during the study period.

Whale encounter rate

The encounter rate per 25 km^2 grid ranged between 0 and 0.622 whales/km of survey (average 0.016 whales/km, SD = 0.057, n = 226 grids with effort) with most surveyed grids not including any sightings (n = 196, 76%) (Fig. 2). Thirteen surveyed grids (43.3%) recorded an encounter rate between 0.01 and 0.1 whales/km of survey, primarily between Puerto López and La Plata Island on the western side of the study area. A slightly increased encounter rate was found around La Plata Island, north between Puerto López and La Plata Island, and south near Puerto López (between 0.1 and 0.2 whales/km of survey). Other areas with encounter rates between 0.1 and 0.2, but with a lower survey effort, were located southwest of Puerto López. Overall, 86.7% of grids with sightings (26/30) resulted in 0.01 and 0.2 whales/km of survey.

Group size and composition

Most sightings included only one animal (n = 35, 56.4%), followed by pairs (n = 22, 35.4%), and then trios (n = 4, 6.4%). Besides these small groups, we recorded one aggregation of nine animals (1.6%). The average group size was 1.61 whales (SD = 1.13).

Eighty-five of 100 recorded animals were assigned to an age class: 77 adults, one juvenile and eight calves. Most singletons and groups recorded included adult animals (45 groups, 72.5%). The second most recorded group class was mother and calf (n = 7, 11.3%), followed by juveniles (n = 1, 1.6%) and mother/calf with other adults (n = 1, 1.6%). In eight groups (12.9%), the class composition was not determined because the sighting did not last long enough to allow for proper assignment.

Behaviour

The behavioural state was established in 55 of 62 groups (88.7%). In 13 groups (20.9%), whales were observed feeding or there was indirect evidence of feeding, i.e., dolphins and/or marine birds were feeding in the immediate area. In 24 groups (38.7%), whales showed milling behaviour, and, in 19 groups (30.6%), whales were travelling. The average group size (whales/group) of feeding groups was significantly larger (2.3 ind./group, SD = 2.09) than milling (1.33 ind./group, SD = 0.56) and travelling groups (1.47 ind./group, SD = 0.61) (One-Way ANOVA $F = 3.79$, $p = 0.02$).

Ecological modelling

Among the 22 models explored, including those with up to six parameters to fit the data, the model Whales ~ offset(log(Effort)) + CHLORO + MONTH + Depth, data = data, init.theta = 3.70, link = log), showed the best fit (Table 2). The dispersion parameter theta (θ) was estimated at 3.70. Two explanatory variables, chlorophyll *a* and month, were found to significantly explain the relative abundance of whales (Table 3). The relationship between relative abundance and chlorophyll *a* was negative, indicating that whales were more abundant in areas with lower productivity. However, the *p*-value for this relationship was close to the threshold of significance (0.047). Chlorophyll *a* showed some variability during the study period (average of 0.80 mg/m^3, SD = 0.84, range 0.23 – 1.79). Most chlorophyll *a* values associated with surveys ranged between 0.23 and 0.5 mg/m^3 (57.8%, n = 26). In contrast, the temporal variable (month) was highly significant, indicating an increase in whale abundance as the research season progressed. These two parameters were also significant in all the other four top-ranked models in Table 2, demonstrating consistency. The explanatory variable 'depth' was not significant but necessary to improve the model fit across all five of the best-performing models.

Table 2

Six of 43 generalized linear models with the lowest AICc value used to explain whales' relative abundance. Statistical measures for model inference include null and residual deviances, AIC and AICc. The model with the lowest AICc, first in the list, best fits the data.

Model	Null deviance	Residual deviance	AIC	AICc
Whales ~ offset(log(Effort)) + CHLORO + MONTH + Depth, data = data, init.theta = 3.70, link = log	40.989	23.47	125.42	126.85
Whales ~ offset(log(Effort)) + CHLORO + MONTH + Depth + ICEN, data = data, init.theta = 4.21, link = log	43.626	22.723	125.19	127.24
Whales ~ offset(log(Effort)) + MONTH + Depth, data = data, init.theta = 2.77, link = log	35.246	24.145	127.74	128.67
Whales ~ offset(log(Effort)) + CHLORO + MONTH + Depth + ONI, data = data, init.theta = 3.69, link = log	40.976	23.456	127.41	129.46
Whales ~ offset(log(Effort)) + CHLORO + TEMP + Depth, data = data, init.theta = 3.03, link = log	37.009	23.848	128.25	129.68

Table 3

Results of the modeling analysis and explanatory variables for the model that fits the data best. In bold the significant values.

Coefficients	Estimate	Std. Error	*z* value	Pr(>|*z*|)
(Intercept)	–4.4770157	0.5900071	–7.588	**3.25E-14**
CHLORO	–0.7700207	0.3888531	–1.98	**0.04768**
MONTH	0.3620553	0.1188336	3.047	**0.00231**
Depth	–0.0001265	0.0009423	–0.134	0.89319

The average temperature during the study period was 26.9 °C (SD = 1.06, range: 24.08–28.74 °C). Similarly, the ENSO indexes (ICEN and ONI) did not explain the variability in whale abundance, despite the occurrence of extreme ENSO events – both La Niña and El Niño – during the study period.

DISCUSSION

Our study reveals that Bryde's whales are widely distributed along the central coast of Ecuador during the warm season (December–May), with an average relative abundance of 0.016 whales/km of survey, SD = 0.057), primarily in waters over 30 m deep. Although Bryde's whales may be present outside this period on the central coast of Ecuador, their numbers appear to decline significantly during the rest of the year. This species is rarely recorded between June and October, despite extensive research efforts focused on humpback whales during that time (e.g., Castro *et al*., 2017). Earlier whale prospecting campaigns conducted between mainland Ecuador and the Galápagos Islands in October–November 1958 (Clarke, 1962) and by Japanese whalers from January to May 1963–1964 (Loesch, 1966) reported a relative abundance of 0.9 sei/Bryde's whales per 100 n.miles, equivalent to 0.017 whales/km. These surveys, conducted before Bryde's whales became targeted by Peruvian whalers (Ramírez, 1989a), can be considered referential data. However, we acknowledge that the estimates may not be directly comparable to our data due to differences in vessel size and survey dates in the earlier studies. The relative abundance we estimated for Bryde's whales along the central coast of Ecuador is 18 to 40 times higher than the recent relative abundance reported for the Gulf of Chiriquí, Panama, during austral and boreal winters (0.04 and 0.09 whales/100 km, respectively) (Rasmussen & Palacios, 2023). The regularity of sightings during the surveyed months supports the hypothesis that the central coast of Ecuador serves as a seasonal concentration area for Bryde's whales.

The congruence in Bryde's whale seasonality between Ecuador and North Peru indicates they belong to the same population (Clarke & Aguayo, 1965; Loesch, 1966; Ramírez, 1989a). Pastene *et al*. (2015) found no genetic differences between Chilean and Peruvian Bryde's whales, suggesting that the same population would extend southward until central Chile (35 °S). While Bryde's whales mostly frequent the Southeast Pacific in the spring and summer months (Ramírez, 1989a; Pastene *et al*., 2015;), the difference in the sea surface water temperature between Ecuador and central Chile at that time could be 15 °C (ERFEN, 2023), suggesting the species is distributed along a considerable temperature gradient in this region. Since the species is widely distributed in the Eastern Pacific from Mexico to central Chile (Hamilton *et al*., 2009; Pastene *et al*., 2015), Southeast Pacific Bryde's whales may be part of a larger population inhabiting this extensive area. So far, no stock boundaries have been defined for the species in the Eastern Pacific. However, considering that the species shows a low gene flow in other populations (Kanda *et al*., 2007), more than one stock may inhabit the Eastern Pacific. This is also supported by whaling records off Peru, where two forms of the species with allopatric distribution were taken simultaneously (Ramírez, 1986). Molecular studies on phylogeography and gene flow are needed to understand the population structure of the species in the Eastern Pacific.

Whale behaviour and group structure

Bryde's whales are commonly found as singletons and less often as pairs (Kato & Perrin, 2018). Although the variability in group size was low, the number of whales per trip was highly variable even within the same week, suggesting whale movements are likely associated with prey dynamics as reported elsewhere (e.g., Alves *et al*., 2009; Biggs *et al*., 2017; Tardin *et al*., 2017; Maciel *et al*., 2018; Rasmussen & Palacios, 2023). Singletons and pairs were mostly found demonstrating milling behaviour, suggesting they were exploring feeding opportunities or resting. Larger groups of up to nine animals were observed in the same area, either a single dispersed group or multiple groups gathering, possibly for communal activities such as feeding. While Bryde's whales were predominantly observed feeding on small pelagic fish within the study area, it was not uncommon to encounter them near shrimp trawler vessels. However, the exact nature of this association remained unclear whether discarded fish attracted whales or if trawlers operated in areas where small pelagic fish congregate. According to Ramírez (1986), the neritic form of Bryde's whale off Peru feeds almost exclusively on sardines (*Sardinops sagax*), but in adverse thermic conditions can also feed on the Chilean jack mackerel (*Trachurus murphyi*). The author also pointed out that a comparable dietary shift occurred in the oceanic form during El Niño years. On the coast of Ecuador, the main schooling fish include sardines, anchovies and mackerel, among others (Canales & Jurado, 2021). Although the specific prey preferences of Bryde's whales in Ecuadorian waters remain unclear, small anchovies (*Anchoa* spp.) have been observed fleeing from the whales during feeding frenzies. These events often involve multiple predator species, including neritic spotted dolphins (*Stenella attenuata graffmani*), offshore bottlenose dolphins (*Tursiops truncatus*), blue-footed boobies (*Sula nebouxii*), red-footed boobies (*Sula sula*), and pelicans (*Pelecanus thagus*), among others. Anchovies are distributed closer to the surface and in shallower waters but are less abundant compared to other small pelagic fish species than mackerel (*Scomber japonicus*) or sardines (*Opisthonema* spp.) (Romero *et al*., 2020). In South Africa, inshore Bryde's whales mostly prey on anchovies and, to a lesser extent, on other schooling fish, such as clupeids and scombrids. Offshore, Bryde's whales prey primary on euphausiids (Best, 2001).

The presence of eight mother and calf pairs in the area (12.9% of the groups) indicates that the coast of Ecuador is used for calving. Not much is known about the reproduction behaviour of the species in the Eastern Pacific. Mothers and calves have been reported in different countries of the region, including the coast and the Galápagos Islands in Ecuador, Perú, Panama and Nicaragua in different seasons (Biggs *et al*., 2017; Castro *et al*., 2017; Rasmussen & Palacios, 2023; De Weerdt *et al*., 2024). Nevertheless, it remains unclear whether the species reproduces year-round, as in South Africa (Best, 1977).

Environmental variables

The absence of correlation with water temperature suggests that its variability was too small to significantly impact whale abundance within the study area. Our study was conducted during years marked by extreme oceanographic changes due to ENSO events. These included a La Niña condition from August 2020 to January 2023 and an El Niño condition from May 2023 to the end of the study in May 2024, with short neutral periods occurring in 2021 and 2023 (Climatic Prediction Center, 2024). During the summer of 2023, the SST in the Southeast Pacific exceeded the historic average by up to 4 °C (ERFEN, 2023). Remarkably, neither the SST nor the El Niño indices (ONI and ICEN) were found to be useful in explaining variability in whale relative abundance. This contrasts previous reports in the region, where strong El Niño years triggered distributional changes in Bryde's and other large whale species toward deeper and cooler waters in northern Peru and the Galápagos Islands (Ramírez & Urquizo, 1985; Ramírez, 1986; Denkinger *et al*., 2013). Similarly, studies from the western African coast have linked Bryde's whale abundance to SSTs cooler than 20.6 °C (Weir *et al*., 2012). The SST was also relevant to explain the relative abundance of inshore Bryde's whales off South Africa (Penry *et al*., 2011). It is possible that other complex, multiscale interactions affecting habitat conditions not fully captured by ONI and ICEN indices have a more significant impact on whale distribution off the coast of Ecuador. Although SST was not a significant explanatory variable for whale relative abundance within the study area, we do not rule out its potential future relevance under a climate change scenario.

A negative correlation between the relative abundance of Bryde's whales and chlorophyll *a* was unexpected, as the presence of this species in coastal areas of the Eastern Pacific has often been linked to food availability around upwelling zones (e.g., Gallardo *et al*., 1983; Salvadeo *et al*., 2011; Biggs *et al*., 2017; Rasmussen & Palacios, 2023; De Weerdt *et al*., 2024) as well as in other parts of the world such as Brazil (Tardin *et al*., 2017) and South Africa (Best, 2001; Penry *et al*., 2011). Lagged effects on prey abundance, where productivity peaks lead to new forage biomass (Lett *et al*., 2009), may explain the observed negative correlation between productivity and whale presence off central Ecuador. Alternatively, the limited scale of our study, the resolution of the environmental data used and the dynamic nature of the region due to the influence of the Equatorial Front (Wyrtki, 1966), may have caused small-scale high-productivity processes to be overlooked. Despite studies on the ecology of Bryde's whales indicating a link with the availability of food, other physiographic or other oceanographic features, including depth and distance to shore in Brazil, (Tardin *et al*., 2017), SST and Wind speed in Oman (Penry *et al*., 2014), and distance o shore and slope in South Africa (Corkeron *et al*., 2011), might be favoured over chlorophyll *a* as significant explanatory variables.

It is not ruled out that the general conditions on the central coast of Ecuador, in terms of productivity and food availability, are suitable for Bryde's whales, since 22% of the sightings were associated with feeding events, including during the El Niño 2023–24 event. The central coast of Ecuador is considered a mesotrophic ecosystem with an average concentration value of chlorophyll *a* of 0.5 mg/m^3, with a seasonal peak between April and May, where the productivity may increase threefold (Borbor *et al*., 2019). However, chlorophyll *a* values remained relatively constant in the study area during the ENSO events, only with eventual peaks of high productivity. The highest productivity values were obtained during an intense red tide event in the northern part of the Gulf of Guayaquil in March 2024 when monitoring the area. With values of 4.6 mg/m^3, this is 10 times higher than the average but not considered in our analysis.

Management and conservation implications

Little was known of Bryde's whales on the coast of Ecuador until this research was conducted. This study therefore provides baseline information to outline future conservation and management strategies. In Ecuador, the species is considered under the IUCN category Near Threatened (NT) (Tirira, 2021). Although Bryde's whales seem to be distributed along the whole coast of Ecuador, we cannot rule out that there are zones with even higher whale concentration, particularly in the southern Gulf of Guayaquil. The gulf is the area with the largest concentration of small pelagic school fish (Romero *et al*., 2020) but still little surveyed for marine mammals. The increase of records in recent years (e.g., Castro *et al*., 2017) and the relative abundance of the species on the central coast of Ecuador reported here suggest that the species is recovering. This statement is also supported by recent records in the Galápagos Islands and Central America (Denkinger *et al*., 2013; Biggs *et al*., 2017; Rasmussen & Palacios, 2023; De Weerdt *et al*., 2024). We recommend continuing monitoring efforts across Eastern Pacific countries in the coming years to validate that this apparent increase in abundance is not a population shift.

Bryde's whales are exposed to a range of anthropogenic threats within Ecuadorian waters. Their preference for coastal habitats increases their susceptibility to entanglement in fishing gear and vessel strikes (Félix & Van Waerebeek, 2005; Félix, 2009; Félix *et al*., 2011), patterns that have also been documented in other regions globally (Ransome *et al.*, 2021; Athayde *et al*., 2022). To mitigate these risks and inform conservation and management strategies, it is essential to generate robust data on demographic trends, population structure, stock identity and responses to climate variability. We recommend the expansion of photo-identification programmes, genetics, and satellite telemetry to delineate priority habitats and characterise large-scale movement patterns.

Moreover, it is essential to enhance awareness among the public and local authorities regarding Bryde's whales to support informed conservation efforts, given that the species' presence remains poorly documented within the country. While the seasonal migration of humpback whales gains significant attention between June and October, Bryde's whales remain largely unfamiliar to the public beyond the fishing communities. The predictable presence of the species holds potential importance for tourist operators, given that whale watching is prevalent along Ecuador's coast, contributing substantially to local economies, cultural identity and whale conservation (Castro *et al*., 2022).

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REFERENCES

Alves, F., Dinis, A., Cascão I., & Freitas L. (2009). Bryde's whale (*Balaenoptera brydei*) stable associations and dive profiles: New insights into foraging behavior. *Mar. Mammal Sci*. 26(1): 202–212. [Available at: *https://doi.org/10.1111/j.1748-7692.2009.00333.x*]

Athayde, A., Cardoso, J., Francisco, A., & Siciliano, S. (2022). A vessel collision report for Bryde's whales (*Balaenoptera brydei*) off the northern coast of São Paulo, Brazil. *Aquat. Conserv. Mar. Freshw. Ecosys*. 33(2): 226–230. [Available at: *https://doi.org/10.1002/aqc.3906*]

[11] *https://whalesandclimate.org*

Best, P.B. (1977). Two allopatric forms of Bryde's whale off South Africa. *Rep. Int. Whal. Comm.* Special Issue 1: 10–38.

Best, P.B. (2001). Distribution and population separation of Bryde's whale (*Balaenoptera edeni*) off southern Africa. *Mar. Ecol. Prog. Ser*. 220: 277–289.

Biggs, D.C., Durkaccz, S.M., Martin, L.M., Narvaez, M., De la Garza, A., Lombraña, Z., & Santos, M. (2017). Bryde's whales (*Balaenoptera brydei*) in an area of upwelling off Isla San Cristóbal, Galápagos. *Neotrop. Biodivers*. 3(1): 189–195. [Available at: *https://doi.org/10.1080/23766808.2017.1368309*]

Bivand, R., & Wong, D. (2018). Comparing implementations of global and local indicators of spatial association. *TEST* 27(3): 716–748. [Available at: *https://doi.org/10.1007/s11749-018-0599-x*]

Borbor-Cordova, M.J., Torres, G., Mantilla-Saltos, G., Casierra-Tomala, A., Bermúdez, J.R., Renteria, W., & Bayot, B. (2019). Oceanography of Harmful Algal Blooms on the Ecuadorian Coast (1997–2017): Integrating Remote Sensing and Biological Data. *Front. Mar. Sci*. 6. [Available at: *https://doi.org/10.3389/fmars.2019.00013*]

Burnham, K.P., & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information – Theoretic Approach* (2nd ed.). New York: Springer-Verlag.

Canales, C.M., & Jurado, V. (2021). Evaluación del stock de recursos pelágicos pequeños del Ecuador: Año 2021. Informe Técnico. Guayaquil, 2021.

Castro, C., Castrillón, J., & Gómez, W. (2022). Whale-watching tourism as a driving force for socioeconomic development in Puerto López, Machalilla National Park, Manabí, Ecuador. *Mammalia æquatorialis* 2022(4): 67–80. [Available at: *https://doi.org/10.59763/mam.aeq.v4i.51*]

Castro, C., Rasmussen, K., Pacheco, A.S., Cárdenas, D., Carnero-Huaman, R., Echeverría, G., & Kaufman, G. (2017). Bryde's whale (*Balaenoptera edeni*) occurrence and movements in coastal areas off Ecuador, Peru and Panama: A preliminary report. SC/67A/SH/15 presented to the IWC Scientific Committee, Bled, Slovenia, 2017. [Available from the IWC Publications Team]

Chiluiza, D., Aguirre, W., Félix, F., & Haase, B. (1998). Varamientos de mamíferos marinos en la costa continental ecuatoriana, período 1987–1995. *Acta Oceanográfica del Pacífico, INOCAR, Ecuador* 9(1): 209–217.

Chinacalle-Martínez, N., García-Rada, E., López-Macías, J., Pinoargote, S., Loor, G., Zevallos-Rosado, J, Cruz, P., Pablo, D., Andrade B., Robalino-Mejía, C., Añazco, S., Guerrero, J., Intriago, A., Veelenturf, C., & Peñaherrera-Palma, C. (2021). Oceanic primary production trend patterns along coast of Ecuador. *Neotrop. Biodivers*. 7(1): 1:379–391. [Available at: *https://doi.org/10.1080/23766808.2021.1964915*]

Clarke, R. (1962). Whale observation and whale marking off the coast of Chile in 1958, and from Ecuador towards and beyond the Galápagos Islands in 1959. *Norsk Hvalfangst Tidende* 51: 265–287.

Clarke, R., & Aguayo, A. (1965). Bryde's whale in the Southeast Pacific. *Norsk Hvalfangst Tidende* 7: 141–148.

Climatic Prediction Center (2024). Cold & Warm Episodes by Season. NOAA National Weather Service. [Available from *https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php*]

Committee on Taxonomy (2024). List of marine mammal species and subspecies. Society for Marine Mammalogy. [Available at: *www.marinemammalscience.org*]

Cooke, J.G., & Brownell, R.L. (2018). *Balaenoptera edeni*. The IUCN Red List of Threatened Species 2018: e.T2476A50349178. [Available at: *http://dx.doi.org/10.2305/IUCN.UK.2018-1.RLTS.T2476A50349178.en*]

Corkeron, P.J., Minton, G., Collins, T., Findlay, K., Willson, A., & Baldwin, R. (2011). Spatial models of sparse data to inform cetacean conservation planning: an example from Oman. *Endanger. Species Res*. 15: 39–52. [Available at: *http://dx.doi.org/10.3354/esr00367*]

De Weerdt, J., Patulny, C., Ruiz Pérez, N., & Blanchet, L. (2024). Sightings of Bryde's whale, *Balaenoptera edeni*, off the Pacific coast of Nicaragua. *J. Mar. Biol. Assoc. UK* 104(e40): 1–7. [Available at: *https://doi.org/10.1017/S0025315424000250*]

Denkinger, J., Oña, J., Aarcón, D., Merlen, G., Salazar, S., & Palacios, D.M. (2013). From whaling to whale watching: cetacean presence and species diversity in the Galapagos Marine Reserve. In: S.J. Walsh, C.F. Mena (Eds.) *Science and Conservation in the Galapagos Islands: Frameworks & Perspectives, Social and Ecological Interactions in the Galapagos Islands* (pp.217–235). Springer Science Business Media, LLC. [Available at: *https://doi.org/10.1007/978-1-4614-5794-7_13*]

Dormann, C.F., McPherson, J.M., Araújo, M., Bivand, R., Bollger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M., & Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30(5): 609–628. [Available at: *https://doi.org/10.1111/j.2007.0906-7590.05171.x*]

ERFEN – Comité Científico Regional para el Estudio del Fenómeno El Niño (2023). *Boletín de Alerta Climático (BAC)* 394. [Available at: *https://archivo.cpps-int.org/index.php/s/blBjsswvu3nPG1v?path=%2F394%20-%20JULIO%202023*]

Félix, F. (2009). A new case of ship strike with a Bryde's whale in Ecuador. SC/61/BC5 presented to the IWC Scientific Committee, Madeira, Portugal, 2009. [Available from the IWC Publications Team]

Félix, F., & Van Waerebeek, K. (2005). Whale mortality from ship strikes in Ecuador and West Africa. *Lat. Am. J. Aquat. Mamm.* 4(1): 55–60.

Félix, F., Haase, B., Denkinger, J., & Falconí, J. (2011). Varamientos de mamíferos marinos registrados en la costa continental de Ecuador entre 1996 y 2009. *Acta oceanográfica del Pacífico* 16(1): 61–73.

Fielder, P.C. (2002). Environmental change in the eastern tropical Pacific Ocean: review of ENSO and decadal variability. *Mar. Ecol. Prog. Ser*. 244: 265–283.

Fortin, M.J., & Dale, M.R. (2009). Spatial autocorrelation in ecological studies: a legacy of solutions and myths. *Geograph. Anal.* 41(4): 392–397. [Available at: *http://dx.doi.org/10.1111/j.1538-4632.2009.00766.x*]

Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression* (3rd ed.). Sage, Thousand Oaks CA.

Gallardo, V.A., Arcos, D., Salamanca, M., & Pastene, L.A. (1983). On the occurrence of Bryde's whale (*Balaenoptera edeni*, Anderson, 1878) in an upwelling area off Central Chile. *Rep. Int. Whal. Comm.* 33: 481–488.

Gnone, G., Bellingeri, M., Airoldi, S., Gonzalvo, J., David, L., Di-Méglio, N., Cañadas, A.M., Akkaya, A., Awbery, T., & Mussi, B., (2023). Cetaceans in the Mediterranean Sea: Encounter Rate, Dominant Species, and Diversity Hotspots. *Diversity* 15(3): 321. [Available at: https://doi.org/10.3390/d15030321]

Hamilton, T.A., Redfern, J.V., Barlow, J., Balance, L.T., Gerrodette, T., Holt, R.S., Forney, K.A., & Taylor, B.L. (2009). Atlas of cetacean sightings for southwest fisheries science center cetacean and ecosystem surveys: 1986–2005. NOAA-TM-NMFS-SWFSC-440.

Instituto del Mar de Perú (IMARPE) (2024). El Niño Costero. [Available from *https://www.imarpe.gob.pe/nino/variabilidad-climatica/el-nino-costero/*]

Kanda, N., Goto, M., Kato, H., McPhee, M.V., & Pastene, L.A. (2007). Population genetic structure of Bryde's whales (*Balaenoptera brydei*) at the inter-oceanic and trans-equatorial levels. *Conserv. Genet.* 8: 853–864. [Available at: https://doi.org/10.1007/s10592-006-9232-8]

Kato, H., & Perrin, W.F. (2018). Bryde's Whales *Balaenoptera edeni*. In: W.F. Perrin, B. Würsig, J.G.M. Thewissen, K.M. Kovacs (eds.) *Encyclopedia of Marine Mammals* (pp.143–145). Academic Press.

Kershaw, F., Leslie, M.S., Collins, T., Mansur, R.M., Smith, B.D., Minton, G., Baldwin, R., Leduc, R.G., Anderson, C., Brownell, R.L., & Rosenbaum, H.C. (2013). Population differentiation of 2 forms of Bryde's Whales in the Indian and Pacific Oceans. *J. Hered.* 104: 755–764. [Available at: *http://dx.doi.org/10.5061/dryad.b9q73*]

Lett, C., Rose, K.A., & Megrey, B.A. (2009). Biophysical models. In: D.M. Checkley, J. Alherit, Y. Oozeki, C. Roy (eds.) *Climate Change and small pelagic fish* (pp.263–232).

Loesch, H. (1966). Observación de Ballenas en aguas ecuatorianas. Informe de Datos, mayo de 1963 y enero-febrero de 1964. Instituto Nacional de Pesca de Ecuador. *Boletín Científico y Tecnico* 4(1): 1–16.

Maciel, I.S., Tardin, R.H., & Simão, S.M. (2018). Occurrence and habitat use of Bryde's whales (*Balaenoptera edeni*) in the Cabo Frio region, South-eastern Brazil. *J. Mar. Biol. Assoc. UK*. 98(5): 1081–1086. [Available at: *https://doi.org/10.1017/S002531541600134X*]

Merlen, G. (1995). A field guide to the Marine Mammals of Galapagos. Instituto Nacional de Pesca, Guayaquil, Ecuador.

Museo de Ballenas (2024). Programa Seawatch: avistamiento de aves y mamíferos marinos desde tierra. [Available at: *https://www.museodeballenas.org/investigacion*]

Norsk Hvalfanngst-Tidente (1925). Bryde-hvalen. 14 Arg., 9: 109–110.

Palacios, D.M., & Salazar S. (2000). Cetáceos. In: E. Danulat, G.J. Edgar (Eds.). *Reserva Marina de Galápagos, Línea de Base de la Biodiversidad*. Fundación Charles Darwin/Servicio del Parque Nacional Galápagos, Santa Cruz, Galápagos, Ecuador.

Pastene, L.A., Acevedo, J., Siciliano, S., Sholl, T.G.C., de Moura, J.F., Ott P.E., & Aguayo-Lobo, A. (2015). Population genetic structure of the South American Bryde's whale. *Revista de Biología Marina y Oceanografía* 50(3): 453–464. [Available at: *https://doi.org/10.4067/S0718-19572015000400005*]

Penry, G.S., Cockcroft, V.G., & Hammond, P.S. (2011). Seasonal fluctuations in occurrence of inshore Bryde's whales in Plettenberg Bay, South Africa, with notes on feeding and multispecies associations. *Afr. J. Mar. Sci.* 33(3): 403–414. [Available at: *http://dx.doi.org/10.2989/1814232X.2011.637617*]

Penry, G.S., Hammond, P.S., Cockcroft, V.G., Best, P.B., Thornton, M., & Graves, J.A. (2018). Phylogenetic relationships in southern African Bryde's whales inferred from mitochondrial DNA: further support for subspecies delineation between the two allopatric populations. *Conserv. Genet*. 19: 1349–1365. [Available at: *https://doi.org/10.1007/s10592-018-1105-4*]

QGIS Development Team (2018). QGIS Geographic Information System. Open Source Geospatial Foundation Project.

Quispe-Ccalluari, C., Tam, J., Demarcq, H., Chamorro, A., Espinoza-Morriberón, D., Romero, C., Domínguez, N., Ramos, J., & Oliveros-Ramos, R. (2018). An index of coastal thermal effects of El Niño Southern Oscillation on the Peruvian Upwelling Ecosystem. *Int. J. Climatol.* 38(7): 3191–3201. [Available at: *https://doi.org/10.1002/joc.5493*]

R Core Team (2024). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramírez, P. (1986). Distribución y alimentación de la ballena de Bryde durante el Fenómeno "El Niño" 1982–1983. *CPPS Boletín EFREN* 17: 20–27.

Ramírez, P. (1989a). Captura y observaciones de la ballena Bryde en el norte del Perú. *Boletín de Lima* 65: 91–95.

Ramírez, P. (1989b). Captura de cetáceos mayores desde las estaciones costeras del Perú: 1951–1985. *Boletín Lima* 64: 91–95.

Ramírez, P., & Urquizo, W. (1985). Los cetáceos mayores y el fenómeno El Niño 1982–1983. In: W. Arntz, A. Landa, J. Tarazona (eds.) *El Niño: Su impacto en la Fauna Marina* (pp.201–206). Boletín IMARPE, Callao, Perú.

Ransome, N., Loneragan, N.R., Medrano-González, L., Félix, F., & Smith, J.N. (2021). Vessel Strikes of Large Whales in the Eastern Tropical Pacific: A Case Study of Regional Underreporting. *Front. Mar. Sci.* 8: 675245. [Available at: https://doi.org/10.3389/fmars.2021.675245]

Rasmussen, K., & Palacios, D.M. (2023). Bryde's Whale (*Balaenoptera edeni brydei*, Artiodactyla: Balaenopteridae) aggregation area in the Gulf of Chiriqui, Panama. *Rev. Biol. Trop.* 71(S4): e57284. [Available at: *https://doi.org/10.15517/rev.biol.trop..v71iS4.57284*]

Romero, A., Ponce, G., Hurtado, M., Prado, J., Armijos, G., Vilela, K., González, N., Aguilar, F., Muñoz, A., & Jurado, V. (2020). Estimación hidroacústica de los principales peces pelágicos pequeños en el Ecuador y su distribución geoespacial, durante diciembre de 2019 (INP 2019-12-02V). Instituto Nacional de Pesca, Ecuador.

Salvadeo, C.J., Flores-Ramírez, S., Gómez-Gallardo, A., MacLeod, C., Lluch-Belda, D., Jaume-Schinkel, S., & Urban, R. (2011). Bryde's whale (*Balaenoptera edeni*) in the southwestern Gulf of California: Relationship with ENSO variability and prey availability. *Ciencias Marinas* 37(2): 215–225. [Available at: *https://doi.org/10.7773/cm.v37i2.1840*]

Takahashi, K., Mosquera, K., & Reupo, J. (2014). El índice costero El Niño (ICEN): historia y actualización. *Boletín Técnico* 1(2): 8–9.

Tardin, R.H., Chun, Y., Simão, S.M., & Alves, M.A.S. (2017). Modeling habitat use by Bryde's whale (*Balaenoptera edeni*) off southeastern Brazil. *Mar. Ecol. Prog. Ser.* 576: 89–103. [Available at: *https://doi.org/10.3354/meps12228*]

Tirira, D.G. (ed.) (2011). *Libro Rojo de los mamíferos del Ecuador* (2nd ed.). Fundación Mamíferos y Conservación, Pontificia Universidad Católica del Ecuador y Ministerio del Ambiente del Ecuador, Publicación especial sobre los mamíferos del Ecuador 8.

Wada, S., Oishi, M., & Yamada, T.K. (2003). A newly discovered species of living baleen whale. *Nature* 426: 278–281. [Available at: *https://doi.org/10.1038/nature02103*]

Wade, P.R., & Gerrodette, T. (1993). Estimates of cetacean abundance and distribution in the eastern tropical Pacific. *Rep. Int. Whal. Comm.* 43: 477–493.

Weir, C.R., MacLeod, C.D., & Pierce, G.J. (2012). Habitat preferences and evidence for niche partitioning amongst cetaceans in the waters between Gabon and Angola, eastern tropical Atlantic. *J. Mar. Biol. Assoc. UK.* 92: 1735–1749. [Available at: *https://doi.org/10.1017/S0025315412000148*]

Wyrtky, K. (1966). Oceanography of the eastern Equatorial Pacific Ocean. *Oceanogr. Mar. Biol. Ann. Rev.* 4: 33–68.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., & Smith, G.M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer. [Available at: *https://doi.org/10.1007/978-0-387-87458-6*]