Interannual shifts in sea surface temperature and chlorophyl drive the relative abundance and group size of common bottlenose dolphins *Tursiops truncatus* on the Southeast Gulf of California

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Abstract

Despite being one of the most common odontocetes off Sinaloa (Mexican Pacific coast), basic studies on the ecology of common bottlenose dolphins (*Tursiops truncatus*) are scarce in the region. This study aimed to describe changes in the relative abundance, group size, and behavior of this species during 2007 – 2012. We used boat-based surveys and satellite images of sea surface temperature (SST) and chlorophyll-a (Chl-a) to model changes in dolphin relative abundance (RA) over time, using correlations in time series analyses. Overall, mean RA was 3.6 dolphins h^{-1} (SD = 8.0), and significantly higher RA (6.4 −16.7 dolphins h^{-1}) occurred in 2008, 2011, 2012, which was concurrent with hydrographic effects of La Niña oceanographic conditions, as well as during the upwelling season (February – April) (SST: 17.3 – 25.0 °C; Chl-a: 3.7 – 21.4 mg m^{-3}). Conversely, significantly lower RA values (0.5 – 3.8 dolphins h^{-1}) occurred in 2007 and 2010 that were likely associated with El Niño effects on the biological productivity of the area (Chl-a: 0.3 – 7.6 mg m^{-3}). We found significant correlations between monthly Chl-a and SST average values with mean bottlenose dolphins RA, and lags (22 – 29 days) in the trophic response to variations of the hydrographic parameters. Significantly larger dolphin groups were recorded during La Niña years possibly because of the higher availability of their prey. This hypothesis is supported by higher feeding frequencies (35 – 73%) observed during the upwelling seasons, especially during La Niña conditions, whereas the most frequent behavior throughout all other years was traveling (28 – 69%). Our results show that RA and group size of bottlenose dolphins inhabiting the waters off Sinaloa, Mexico, are likely influenced by the changes in hydrographic parameters, especially during extreme climatic events.

Introduction

Climate-driven changes to the physical-chemical properties of the water column alter biological productivity and food availability in marine ecosystems affecting the trophic web including top predators (Camphuysen *et al.*, 2006). Thus, spatial and temporal distribution patterns of common bottlenose dolphin (*Tursiops truncatus*) populations are influenced by such environmental variations (Ballance, 1992; Defran and Weller, 1999; Baird *et al.*, 2009; Bearzi *et al.*, 2009; Pardo *et al.*, 2013; Sprogis *et al.*, 2018). The continuous presence of this species in highly productive areas, such as coastal lagoons and river mouths, has been well documented, in which individual home ranges are somewhat well defined and populations are well-structured (Ballance, 1992;

Reza-García, 2001; Morteo *et al.*, 2004; Rodríguez-Vázquez, 2008). However, in open coastal waters, bottlenose dolphins have wider distributions and home ranges, which result in potential differences associated with population dynamics and social structure (Defran and Weller, 1999; Morteo *et al.*, 2004; Bearzi *et al.*, 2009; Defran *et al.*, 2015; Bolaños-Jiménez *et al.*, 2021). Coastal bottlenose dolphins in the Gulf of California (GoC) region have a complex population structure and are hypothesized to have originated from an oceanic ecotype (Segura *et al.*, 2018). Morphological, genetic, and trophic data have identified several stocks within the GoC (Segura *et al.*, 2006; 2018; Morteo *et al.*, 2017). While individuals belonging to these coastal stocks have the capacity to travel extended distances, many maintain high site fidelity to localized areas and defined home ranges presumably due to preferred habitat conditions (Delgado-Estrella, 2015; Morteo *et al.*, 2019).

Marine predators (*e.g.* dolphins, and birds) often shift distribution patterns in response to seasonal variations in oceanographic conditions, and predator abundance commonly decreases, especially during El Niño South Oscillation (ENSO) (Tershey *et al.*, 1991; Velarde *et al.*, 2004); this pattern has been identified for Indo-Pacific coastal bottlenose dolphins (*T. aduncus*) off Australia (Sprogis *et al.*, 2018). Despite being the most commonly observed cetacean species in the GoC, there is no information on important population parameters (*e.g.* abundance, group size, and behavior) of the common bottlenose dolphin, or how temporal variations in environmental conditions (*e.g.* . sea surface temperature and chlorophyll-a concentrations) might influence the occurrence of dolphins in the southeast GoC. This study uses standardized cetacean ecotourism surveys and satellite data on environmental parameters to model temporal changes in relative abundance.

Materials and method

Study site

The coastal region off Mazatlán, Sinaloa, is an open water habitat on the northwestern Pacific coast of Mexico (Fig. 1), with low influence of riverine inputs (Rubio-Rocha and Beltrán-Magallanes, 2003). The oceanographic characteristics in this saline, open water environment are driven by three different currents with large seasonal variations: 1) the California Current (January – April), 2) the Mexican Coastal Current (May – October), and 3) the GoC Current (November – December) (Wyrtki, 1966; De la Lanza-Espino, 2001; Kessler, 2006; Lavín *et al.*, 2006). Sea surface temperature (SST) ranges from 17 to 31°C (De la Lanza-Espino and Flores-Verdugo, 2003), and the area has two climatic seasons: 1) the dry period (Winter – Spring) characterized by N – NW winds that promote coastal upwelling in the area (De la Lanza-Espino and Flores-Verdugo, 2003); and 2) the rainy season (Summer – Autumn) with the effect of the "Mexican monsoon associated" and S – SE humid winds (Jáuregui-Ostos, 2003).

Surveys

From 2007 to 2012, we used small (6 – 9 m) outboard-powered motorboats (commonly known as "pangas") owned and piloted by "Onca Explorations", a locally-based ecotourism and whale-watching company to estimate cetacean abundance, behavior, distribution, and group size; however, only data on bottlenose
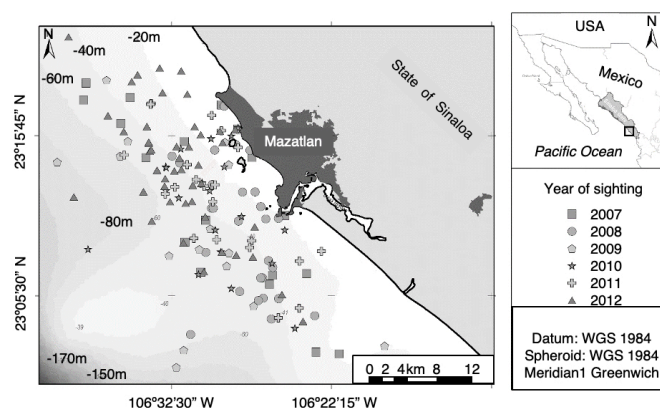

Figure 1. Geographical location of the study area and sighting records of bottlenose dolphins *Tursiops truncatus* in the coastal waters of Mazatlán, Sinaloa, Mexico, during the study period 2007 – 2012.

dolphin sightings were used in the subsequent analyses. Surveys were intended to maximize area coverage (approximately 1,400 km²) in search for cetaceans and thus commonly reached deep waters 10 – 20 km offshore. The orientation for the first 60 minutes of the survey was chosen at random heading NW – SE, and survey speed was approximately 27 (± 5) km h⁻¹. Mean daily survey distance was 59.6 (± 17 SD) km, and surveys were conducted across all years and seasons, under favorable weather conditions (Beaufort Sea State ≤ 3). All sightings were georeferenced with a GPS (Garmin eTrex Vista HCx, Garmin International, Inc., Schaffhausen, Switzerland). Due to technical difficulties across the survey period, GPS tracks were not obtained. According to standardized protocols, the crew included at least three observers with experience searching for marine mammals (*i.e.* scanning the front and sides of the boat, thus having a 180° panoramic view). Cetacean sighting data included species identification, group size, behavior, and dorsal fin/body photographs (see Morteo *et al.*, 2017).

Effort and relative abundance

Survey effort was measured as the effective time (h) in search for cetaceans, by subtracting the sighting time for data collection from total survey time (Morteo *et al.*, 2004; 2012). Only surveys with effective searching time ≥ 2 h were used to compute the relative abundance (RA) of bottlenose dolphins. This criterion was empirically derived to homogenize the area coverage from effort data (since survey tracks were unavailable) and thus, all these surveys covered > 75% of the study area (measured from the coast and divided into regions based on bathymetric contours). This procedure also allowed minimizing the chances of biases by atypical values (such as the occasions where captains were notified about the location of the marine mammals, which were not included here) (Zepeda-Borja, 2017).

Daily relative abundances (dolphins h⁻¹) were computed, and temporal comparisons in different scales (*i.e.* annual, seasonal, and monthly) were tested via ANOVA or Kruskal-Wallis tests in R-Studio Desktop (R-Core-Team, 2015).

Correlations to hydrographic parameters

Monthly composites of night-time sea surface temperature (SST) (15 – 31 °C) and chlorophyll-a concentration (0 – 22 Chl-a mg m⁻³) were obtained from the MODIS-Aqua database (http://

www.conabio.gob.mx/informacion/gis/). SST and Chl-a pixel values were extracted for each bottlenose dolphin sighting using its GPS location with the function "Extract MultiValues to Points" in ArcGIS 10.3 (ESRI, 2014), and then averaged by month. We then used the Southern Oscillation Index (SOI) and the Oceanic Niño Index (ONI) to classify our study period; in summary, positive anomalies above 0.5 from typical values (using data from the last 40 years) are identified as "El Niño" conditions, whereas negative deviations classify "La Niña" events (see van Oldenborgh *et al.*, 2021). Despite efforts to reduce the presence of highly atypical values (*i.e.* based on survey time filtering such as RA > 20 dolphins h⁻¹, and according to literature Chl-a > 22 mg m⁻³, Lopez-Sandoval *et al.*, 2009), these were still found within the database (< 1% of the records), and thus discarded from the analyses (see Figs 2 and 3). Correlations among the hydrographic parameters and bottlenose dolphin monthly RA were identified using Pearson tests and a time-series approach was used to search for lagged correlation between the variables through a local similarity analysis fastLSA (Durno *et al.*, 2013). This latter procedure provides a measure of the lag at which a significant correlation may be found and can be used under no normality assumptions. It also prevents permutations that are computationally intensive, while protecting results against false positives.

Group size

For each sighting, an estimate of mean group size was determined by averaging the total count of individuals observed by all experienced crew members, based on the chain rule (*i.e.* all individuals present within two body lengths) following Shane *et al.* (1986). All sightings, regardless of survey duration and group size, were used to determine the general statistical distribution within the study area. The predominant group size was summarized using a Kernel density test ($K_{(x)}$) (Rosenblatt, 1956; Silverman, 1986), and then temporal differences (*i.e.* annual, seasonal, and monthly) were evaluated using Kruskal-Wallis tests available at R-Studio Desktop.

Behavior

We used five categories to classify behavior (Transit = Tr, Feeding = Fd, Socialization = Soc, Evasion = Ev and Bow-riding = Bw) (criteria defined in Guzmán-Vargas, 2015). The primary
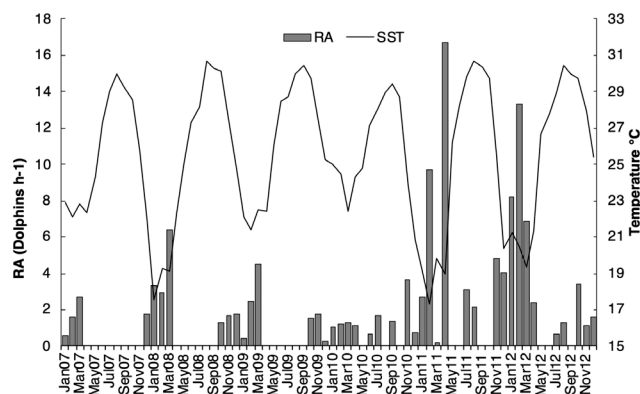
activity for the sighting was agreed upon by all experienced crew members. Behavioral data were pooled by season (*i.e.* dry-wet), and yearly/seasonal to search for temporal patterns, and differences were tested using Chi-square tests (χ^2) on contingency tables (Guzmán-Vargas, 2015) with *XLSTAT* for Excel (Microsoft Office 2016).

Results

Survey effort

From 2007 to 2012, 568 surveys were conducted with 1,225 h of effective search effort ($\bar{x}$ = 2.19 h ± 1.04 SD per survey) (Table 1). Only 302 surveys met the specified criteria for effort (≥ 2 h), accounting for 894.6 h of search time ($\bar{x}$ = 2.96 ± 0.69 SD) and were included for subsequent analyses. The temporal scales of surveys were not homogeneous across years, with more surveys during the period 2009 − 2010, and months with less surveys from April to October (Tables 1 and 2).

Relative abundance

A total of 152 dolphin groups were observed in 302 surveys, resulting in an overall mean RA of 3.6 (± 8.0 SD) dolphins h⁻¹. Significantly higher monthly mean RAs occurred between January and March (6.4 − 16.7 dolphins h⁻¹), and larger RAs (9.9 - 13.8 dolphins h⁻¹) were more common in February 2011 and 2012, respectively (ANOVA, *p* < 0.05). However, this pattern was not consistent across all years (Table 2, Figs 2 and 3).

Correlation of hydrographic parameters

SST values were negatively correlated with Chl-a concentrations (Pearson R^2 = 0.64, *p* < 0.01). The *post hoc* analysis showed that this was especially true between November and May (Pearson R^2 = 0.87, *p*< 0.001). This pattern repeated annually in most years, except for 2007 and 2010 during El Niño warm conditions, where Chl-a values remained low (1.6 − 7.6 and 0.6 − 2.8 mg m⁻³, respectively) and SST was high (23.2 − 25.5°C). Time-series analyses with fastLSA identified that the best possible correlation for these variables was achieved at a 22-day lag (*p* < 0.0001).

After removing sightings with atypical group size (> 20 individuals) and SST outliers, a low and negative association

Figure 2. Monthly averages of bottlenose dolphin *Tursiops truncatus* relative abundance (dolphins h⁻¹) and sea surface temperature (°C) in the coastal waters of Mazatlán, Sinaloa, Mexico, 2007 − 2012.
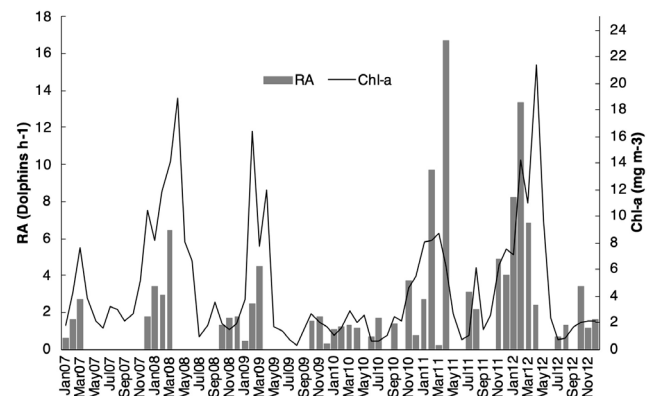

Figure 3. Monthly averages of relative bottlenose dolphin *Tursiops truncatus* abundance (dolphins h⁻¹) and chlorophyll-a concentration (mg m⁻³) off the waters of Mazatlán, Sinaloa, Mexico, 2007 − 2012.

Table 1. Total number of surveys during 2007-2012 in the coastal waters of Mazatlán (n = 302), Sinaloa, Mexico. The values inside the parenthesis show the effort (eff) in hours (h) during each month. Significant annual differences are denoted in letters such that column with "a" is different from columns with "i".

Month	2007	2008[a]	2009[i]	2010[i]	2011	2012
Jan	5 (15.4)	16 (57.0)	9 (22.5)	7 (17.7)	8 (23.0)	7 (19.6)
Feb	9 (22.2)	7 (21.5)	13 (37.9)	7 (15.8)	10 (28.9)	10 (27.3)
Mar	6 (21.5)	16 (53.2)	11 (28.1)	10 (29.0)	7 (21.6)	14 (39.1)
Apr	4 (13.9)	1 (3.5)	3 (8.4)	5 (16.3)	5 (14.5)	2 (7.3)
May	2 (7.2)	1 (4.5)	-	-	-	-
Jun	-	-	-	1 (2.9)	3 (8.3)	-
Jul	1 (3.2)	-	-	3 (7.4)	2 (5.7)	4 (14.5)
Aug	-	-	2 (7.2)	-	6 (18.9)	3 (9.6)
Sep	-	-	-	1 (3.6)	-	-
Oct	-	2 (6.5)	2 (8.6)	2 (5.7)	1 (4.4)	4 (11.0)
Nov	-	2 (7.7)	4 (12.0)	3 (8.9)	8 (22.5)	4 (12.0)
Dec	8 (24.0)	6 (15.9)	10 (25.3)	11 (31.5)	10 (30.2)	4 (10.2)
TOTAL	35 (107.4)	51 (169.8)	54 (150.0)	50 (138.8)	60 (178.0)	52 (150.6)
Eff ($\bar{x}$ ± S.D.)	(3.1 ± 0.77)	(3.3 ± 0.76)	(2.8 ± 0.72)	(2.8 ± 0.60)	(3.0 ± 0.57)	(2.9 ± 0.56)

(Pearson R^2 = 0.41, $p < 0.01$; n = 120) was found between monthly mean RA and the correspondent SST values (Fig. 2), especially from January to April (*pos hoc* Pearson R^2 = 0.68, $p < 0.001$; n = 84). The fastLSA showed a lag of 29 days ($p < 0.0001$). This pattern was more evident in 2008, 2011, and 2012, during La Niña cold conditions, where the lowest SST and highest RA values were recorded (SST: 17.3 – 19.3 °C; RA: 6.41 – 16.73 dolphins h⁻¹).

Conversely, after accounting for dolphin group size and extreme Chl-a values, the association between the monthly RA means and the Chl-a was slightly higher and positive (Pearson R^2 = 0.49, $p < 0.01$; n = 115) (Fig. 3), and both RA and Chl-a increased from November to April, being higher between February and April (*post hoc* Pearson R^2 = 0.58, $p < 0.001$; n = 72). The fastLSA showed a shorter lag (22 days) between these variables ($p < 0.0001$). It is also noteworthy that both Chl-a concentrations (0.6 – 2.4 mg
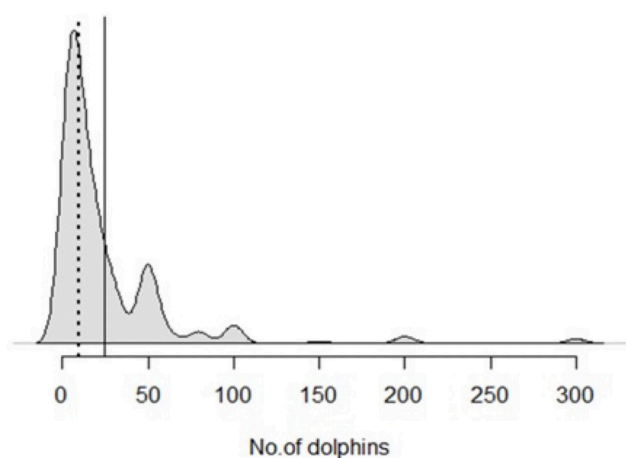

Figure 4. Kernel density analysis on group sizes for bottlenose dolphins *Tursiops truncatus* off Mazatlán, Sinaloa, Mexico, 2007 – 2012. The dotted line represents the median; the solid line represents the average.

Table 2. Monthly Relative Abundance (dolphins h⁻¹) mean (SD; sightings [surveys]) of bottlenose dolphins *Tursiops truncatus* off Mazatlán, Sinaloa, Mexico, 2007 – 2012 (n = 302 sightings). Annual significant differences ($p < 0.05$) are shown in letters such that column with "a" is different from column with "i", and monthly differences among years are also shown, such that cells with "b" are different from cells with "ii".

Month	2007[i]	2008	2009[i]	2010[i]	2011[i]	2012[a]
Jan	0.71 ± 1.0 (2 [5])	3.36 ± 6.0 (10 [16])	0.43 ± 1.2[ii] (1 [9])	1.08 ± 2.4 (2 [7])	2.71 ± 5.4 (2 [8])	8.20 ± 9.3 (7 [7])
Feb	1.63 ± 3.2 (3 [9])	2.91 ± 6.7 (2 [7])	2.43 ± 6.03 (4 [13])	1.19 ± 1.7 (3 [7])	9.68 ± 16.8 (3 [10])	13.33 ± 13.2[b] (13 [10])
Mar	2.68 ± 2.3 (5 [6])	6.41 ± 7.5 (11 [16])	4.49 ± 8.3 (6 [11])	1.30 ± 1.8 (5 [10])	0.19 ± 0.5 (1 [7])	6.83 ± 10.8 (9 [14])
Apr	0 0 [4]	0 0 [1]	0 0 [3]	1.12 ± 1.4 (2 [5])	16.73 ± 23.3 (4 [5])	2.38 ± 2.4 (1 [2])
May	0 0 [2]	0 0 [1]	-	-	-	-
Jun	-	-	-	0.7 (1 [1])	0 (0 [3])	-
Jul	0 0 [1]	-	-	1.66 ± 0.4 (3 [3])	3.08 ± 0.8 (2 [2])	0.67 ± 1.0 (2 [4])
Aug	-	-	0 0 [2]	-	2.12 ± 4.7 (1 [6])	1.32 ± 1.5 (2 [3])
Sep	-	-	-	1.39 (1 [1])	-	-
Oct	-	1.27 ± 1.3 (1 [2])	1.56 ± 1.6 (1 [2])	0 (0 [2])	0 0 [1]	3.43 ± 2.9 (5 [4])
Nov	-	1.69 ± 1.7 (3 [2])	1.75 ± 1.9 (2 [4])	3.67 ± 5.2 (1 [3])	4.86 ± 7.8 (5 [8])	1.16 ± 1.5 (3 [4])
Dec	1.75 ± 1.9 (8 [8])	1.78 ± 3.3 (2 [6])	0.28 ± 0.7[ii] (2 [10])	0.73 ± 1.7 (3 [11])	4.01 ± 5.3 (5 [10])	1.59 ± 1.2 (3 [4])
Average	1.42 ± 2.3 (18 [35])	3.82 ± 6.9 (29 [51])	1.91 ± 5.3 (16 [54])	1.21 ± 2.2 (21 [50])	5.21 ± 11.9 (23 [60])	6.51 ± 10.0 (45 [52])

m⁻³) and dolphin RA values (0.7 – 1.7 dolphin h⁻¹) remained low during the El Niño warm conditions in 2010 (Fig. 3).

Group size

Group sizes were obtained for 298 sightings, ranging from one to > 300 individuals (mean 24.7, SD = 7.2). The modal value obtained through the Kernel analysis was nine individuals, and the median was 10 dolphins, but there was a second modal peak of 50 individuals. Mean group size had a bimodal distribution (Fig. 4), and no monthly or seasonal differences were found (ANOVA, $p > 0.05$). However, groups were significantly smaller in 2007 and 2010 ($\bar{x}$ = 12.2 and 10.2 dolphins, respectively) during the warm El Niño phase, compared to the cold La Niña periods in 2011 and 2012 ($\bar{x}$ = 41.4 and 31.9 dolphins, respectively) ($H_{(5, 298)}$ = 29.1; $p < 0.05$).

Behavior

Behavioral data were available from 244 sightings between 2007 and 2012. Feeding was the most frequent behavior observed during the dry season (35 – 73%), whereas transit was dominant in the rainy season (28 – 69%). This pattern was reversed in 2007 and 2010 during El Niño warm conditions (Fig. 5). Finally, the frequency for each behavior was statistically different among seasons within the study period (χ^2 = 41.53, $p < 0.05$).
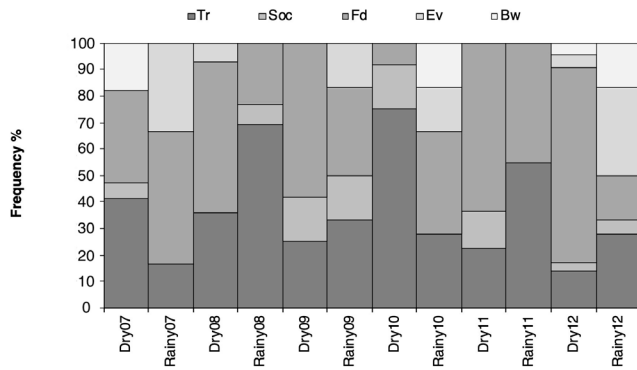
Figure 5. Seasonal behavioral frequencies in bottlenose dolphins *Tursiops truncatus* recorded during 2007 – 2012 off Mazatlan, Sinaloa, Mexico (n = 244 schools). Tr = Transit, Soc = Socialization, Fd = Feeding, Ev = Evasion, Bw = Bow-riding.

Discussion

The use of platforms of opportunity (*e.g.* ferries, ecotours and whale-watching vessels) to study marine mammals has gained popularity in the scientific community (Kiszka *et al.*, 2007; Isaac *et al.*, 2014; Lukyanenko *et al.*, 2016). Although there are some limitations to this data collection approach, these types of surveys can provide long-term data on the ecology and population structure of numerous species (Kiszka *et al.*, 2007). The systematic approach applied to this study reduced some of the most common biases associated with touristic or recreational platforms (see Isaac *et al.*, 2014), and the modifications to the daily survey areas and well-defined criteria for data in subsequent analyses allowed for a quantitative assessment of bottlenose dolphin abundance, group size, and behavior in relation to environmental parameters. The collaborative effort between researchers and the ecotourism community represents the first long-term effort to study the state of Sinaloa's cetacean populations. The results of this study suggest that, with a trained team, ecotourism vessels may be used as a platform for long-term cetacean studies (Lukyanenko et al., 2016).

Survey effort varied throughout the study period in response to varying demands from the tourism industry, particularly between autumn, winter, and spring due to peak tourism in Mazatlán, because of the arrival of humpback whales (*Megaptera novaeangliae*) (Zepeda-Borja, 2017). Nevertheless, by standardizing survey effort (*i.e.* selecting for surveys ≥ 2 h), spatial and temporal coverage were generally homogenized.

Changes in SST and surface concentration of Chl-a showed annual trends related to different oceanographic and climatic processes. Cold water (17.3 – 23.9 °C) measured between January and April is associated with the formation of coastal upwelling in the region (De la Lanza-Espino and Flores-Verdugo, 2003; Jáuregui-Ostos, 2003; Lavín and Marinone, 2003), increasing biological productivity (Kämpf and Chapman, 2016). The corresponding increase in Chl-a (3.7 – 21.4 mg m^{-3}) occurs up to three weeks later (within a 5 – 25 days window), which explains the significant but low degree of correlation between SST and Chl-a (R^2 = 0.64). Conversely, warm waters (SST: 24.0 – 30.6 °C) were recorded between June and November entering the GoC via the Mexican Coastal Current (Wyrtki, 1966; Lavín and Marinone, 2003; Kessler,

2006; Lavín *et al.*, 2006), resulting in low rainfall (700 mm, Mexican National Meteorological Service: station 00025-119, season 2006-2012), and decreased Chl-a values (0.3 – 6.1 mg m^{-3}).

The pattern described above changed in 2007 and 2010, where Chl-a concentrations remained low (1.0 – 7.6 mg m^{-3}), even during the cold months. These anomalies can be attributed to the combined effect of the oceanographic currents and the effects of El Niño (NOAA, 2020), where shifting wind patterns disrupt coastal upwelling, deepening the mixed layer and the thermocline, thus trapping the nutrients well below in the water column (Torres-Orozco *et al.*, 2005). On the other hand, during La Niña years (2008, 2011, and 2012), SST was lower (17.3 – 21.3 °C) and Chl-a increased (> 8.1 mg m^{-3}) while interacting with the California Current (Kessler, 2006; López-Sandoval *et al.*, 2009; Kono-Martínez *et al.*, 2015) between January and April. During these periods we also recorded the presence of some cetaceans that prefer colder waters and thus are not commonly seen in the area (*i.e.* common dolphin *Delphinus delphis* and gray whale *Eschrichtius robustus*).

The mean RA for bottlenose dolphins at Mazatlán (x̄ = 3.56 dolphins h^{-1}) was lower compared to other areas in the GoC such as Guaymas, Sonora (12.3 dolphins h^{-1}; Guevara-Aguirre and Gallo-Reynoso, 2015) and Bahía de Banderas, Jalisco-Nayarit (20.4 dolphins h^{-1}; Rodríguez-Vázquez, 2008). However, our RAs should be considered a minimum since our surveys did not target bottlenose dolphins exclusively, and because adjacent sites may have higher quality/preferred habitats (*e.g.* productive rivers and sounds that are emptying into coastal waters) (Morteo *et al.*, 2012). Nevertheless, the frequent presence of this species implies that the coastal waters of Mazatlán are at least an important transit area. Dolphins recorded in the study area are likely part of a larger, open population as observed in other regions of the Pacific and GoC (*e.g.* Defran and Weller, 1999; Defran *et al.*, 2015). Other small cetacean species are known to transit through the study area at different distances from shore, such as the pantropical spotted dolphin (*Stenella attenuata graffmani*) (5 – 10 km offshore), and eastern spinner dolphin (*Stenella longirostris*) (10 – 20 km offshore) (Guzón, pers. obs.).

The fastLSA time-series analyses on SST and Chl-a data highlighted the importance of local and regional oceanographic features that alter biomass production, resulting in a lagged response of 22 – 29 days for the array of physical-chemical processes in the water column (Pardo *et al.*, 2013; Kämpf and Chapman, 2016). This pattern has been documented in other neighboring areas in the Pacific such as Bahía de Banderas, Jalisco-Nayarit (Cerrillo-Espinosa and Barraza-Figueroa, 2007; Rodríguez-Vázquez, 2008), and the southwestern Atlantic (Moraes *et al.*, 2012). It is also noteworthy that, although dolphin RA seemed to respond to these environmental changes within a week, higher RA could represent an influx of offshore bottlenose dolphins into the area, or that the same individuals remained in the study area and were encountered multiple times during a given survey. Even with these potential uncertainties, larger dolphin aggregations and higher residency times during upwelling periods are well-known in the GoC (Reza-García, 2001; Pardo *et al.*, 2013; Guevara-Aguirre and Gallo-Reynoso, 2015), and the Mexican North Pacific (Morteo *et al.*, 2004). These observations are particularly evident during La Niña events (De la Lanza-Espino, 2001; Jáuregui-Ostos, 2003; Lavín and Marinone, 2003; Torres-

Orozco *et al.*, 2005; Kessler, 2006; López-Sandoval *et al.*, 2009; Kono-Martínez *et al.*, 2015) and the opposite occurred during El Niño conditions (especially in 2010), which has also been observed in other regions of the Pacific (*e.g.* Sprogis *et al.*, 2018).

The Kernel density analysis showed that characteristic group sizes (*i.e.* 9 – 10 individuals) were consistent with other coastal bottlenose dolphin communities in the Mexican Pacific and within the GoC (Morteo *et al.*, 2004; Viloria-Gómora, 2007), the eastern tropical Pacific (Scott and Chivers, 1990; Defran and Weller, 1999; Morteo *et al.*, 2004; Baird *et al.*, 2009), and the Gulf of Mexico (Shane *et al.*, 1986; Martínez-Serrano *et al.*, 2011; Morteo *et al.*, 2014). Conversely, by referring to our average group size (24.2 individuals), which is more commonly used in other studies, it is similar to bottlenose dolphins in open water areas with more complex bathymetry, where groups around 30 individuals are not uncommon (*i.e.* Bahía de Banderas, Jalisco-Nayarit, Mexico by Rodríguez-Vázquez, 2008, and San Diego, California, by Ward, 1998). Nevertheless, it should be noted that our average estimate is heavily biased by atypical larger groups (*i.e.* 50, 100 and > 300 individuals).

Bottlenose dolphin groups of 300 individuals, as those found in Mazatlán are amongst the largest reported for the species on the continental shelf of California (USA), Baja California (Mexico), and the GoC (Hansen, 1990; Defran and Weller, 1999; Morteo *et al.*, 2004; Bearzi, 2005). Coastal bottlenose dolphin aggregations are generally less than 30 individuals, and typically range between two and 15 individuals (Shane *et al.*, 1986). The maximum group size observed in this study (300 individuals) could be attributed to the mixing of several primary groups (smaller units strongly associated with each other; Morteo *et al.*, 2014), or to the presence of groups from the oceanic ecotype, which typically form aggregations ranging from 50 to 100 individuals (Scott and Chivers, 1990; Bearzi, 2005). Thus, a hypothesis for the temporal differences observed in group size and correlations to fluctuations in RAs across years (low in 2007 and 2008, high in 2011 and 2012), is that environmental conditions may influence the presence of groups of both coastal and oceanic ecotypes in the study area. Additionally, La Niña and El Niño events could influence behavioral and social responses to changes in biological productivity. Future research should include systematic surveys in adjacent offshore waters to better understand these complex environmental dynamics.

The frequency of feeding behavior increased during the upwelling season (January to June), and the second most frequent behavior, transit, increased during the rainy season (July to December). The shifting in observed behaviors may be explained by the availability of prey in response to environmental conditions (Jáuregui-Ostos, 2003; Rubio-Rocha and Beltrán-Magallanes, 2003). Additional research is needed to assess the fitness of this population due to extreme climatic events as noted in other coastal cetacean populations throughout the world (*e.g.* Sprogis *et al.* 2018).

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