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Spatial Distribution and Abundance of Small Cetaceans in the Pacific Waters of Guatemala

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The establishment of marine protected areas (MPAs) requires a thorough assessment of the abundance, distribution, and habitat preferences of a variety of marine species. Small cetacean spatial distribution and abundance were examined in the Pacific waters of Guatemala to provide this information. Boat surveys were conducted for 38 months between January 2008 and June 2012. A total of 64,678 cetaceans in 505 sightings from nine Delphinidae species were recorded. Three species, referred to as common species, accounted for 90% (n = 456) of all sightings. They included *Tursiops truncatus* (56%, n = 278), *Stenella attenuata* (29%, n = 143), and *Stenella longirostris* (7%, n = 35). Group size was significantly different among the common species (p < 0.001). *S. longirostris* had the largest group size (444 ± 75 dolphins), followed by *S. attenuata* (28 ± 5 dolphins), and *T. truncatus* (15 ± 2 dolphins). *T. truncatus* was the most common in the study area (0.02 ± 0.002 sightings/km of survey effort), and *S. attenuata* (0.37 ± 0.16 dolphins/km) and *S. longirostris* (1.62 ± 0.41 dolphins/km) were the most abundant in the neritic (≤200 m depth) and oceanic zones (≥200 m depth), respectively. The wide-ranging distribution of *T. truncatus* overlapped with the distribution of *S. attenuata* in the neritic zone and *S. longirostris* in the oceanic zone. Little overlap was observed in the distribution of *S. attenuata* and *S. longirostris*. Most hot spots (∼66%) were in the oceanic zone and no hot spots were near or in the MPAs. Hot spots were identified along the 200 m isobath, the Middle America trench, and the San José Canyon. These could be areas of high productivity where dolphins concentrate to feed. To the north of the San José Canyon, five species of small cetaceans were observed in a stretch of the neritic zone including three MPAs. No other section of this zone had such high diversity. Results need to be taken with caution given the small sample size. Our results suggest that the protection of small cetaceans needs to consider the creation of oceanic MPAs that should be integrated into the existing network.

Keywords: odontocete, spatial analysis, boat surveys, eastern tropical Pacific, hot spots

INTRODUCTION

The effective management of wild animal populations depends on a strong foundation of knowledge regarding their distribution and abundance. A thorough understanding is necessary of the areas used by a population to enable effective prioritization of the conservation or management approaches to be used. In many Latin American countries, baseline information on cetaceans is sparse or absent. However, cetacean populations that inhabit the waters of those countries face extensive problems such as habitat degradation and bycatch from numerous types of fishing operations. According to the IUCN "Dolphins, Whales and Porpoises: 2002–2010 Conservation Action Plan for the World's Cetaceans" (Reeves et al., 2003), these problems pose serious threats to many dolphin populations. Populations of northeastern offshore spotted dolphins (*Stenella attenuata attenuata*) and eastern spinner dolphins (*Stenella longirostris orientalis*) have been reduced due to the dolphin bycatch of the purse-seine fishery for yellowfin tuna in the eastern tropical Pacific waters (Gerrodette and Forcada, 2005), although their populations were reported to be increasing in 2006 (Gerrodette et al., 2008). In countries such as Guatemala, Chile, Colombia, Panama, Peru, and Venezuela, dolphin meat has been used as bait for a range of fishing practices (Goodall et al., 1988; Vidal et al., 1994; Culik, 2004; Alfaro-Shigueto et al., 2008; Ávila et al., 2008; Loch et al., 2009; Mangel et al., 2010; Quintana-Rizzo, 2011a; Mel and Fisher, 2016; Mintzer et al., 2018; Campbell et al., 2020). Furthermore, in Guatemala, some fishermen harpoon dolphins because they consider them to be a threat and fishing competitor (Quintana-Rizzo, 2011a). Baseline information on population numbers and distribution could be extremely helpful for assessing the status of local populations and developing appropriate conservation and management decisions.

In Guatemala, baseline information on species abundance and distribution is particularly relevant as the government is currently in the process of expanding four existing coastal protected areas to include a marine zone and creating a new area that will include both terrestrial and marine zones in the Pacific Ocean. This initiative is part of the 2012–2022 Guatemalan National Strategy for Biological Diversity and Plan of Action that seeks to promote the sustainable use and conservation of at least 10% of local coastal–marine ecosystems (CONAP, 2013). Marine spatial planning efforts began in 2006 with the identification of gaps in the Guatemalan System for Protected Areas and the proposal of priority areas for marine conservation (CONAP and MARN, 2009). The proposals are currently being reviewed by the National Council of Protected Areas (in Spanish: Consejo Nacional de Áreas Protegidas, CONAP), the government agency whose mission is the conservation of biological diversity and sustainable use of protected areas of the country. Although this initiative is an encouraging step by the government toward the protection of marine resources, the effort needs to be supported by a solid foundation of scientific information that incorporates a wide range of marine megafauna species. The proposed network of coastal marine protected areas (MPAs) was based on characteristics such as substrate type, geology, topography, and depth; human pressures and threats to ecosystems; and biological elements including wetlands, mangroves, sea turtles, and birds (Hoyt, 2011). The presence of cetaceans was recognized in the review process but there were no assessments of the species abundance, distribution, habitat preferences, or identification of critical habitats. These aspects are critical in the early steps of establishing MPAs (Hoyt, 2011). More than 15 species of cetaceans have been identified in the Pacific waters of the country (Quintana-Rizzo and Gerrodette, 2009; Cabrera et al., 2014).

Various levels of information exist for the different cetacean species found off the Pacific coast of Guatemala. The lack of comprehensive data makes it impossible to determine the status of the different species or develop appropriate conservation and management strategies. Most studies have focused on particular species (e.g., *Megaptera novaeangliae*: Godoy Aguilar et al., 2009; Quintana-Rizzo, 2019. *Tursiops truncatus, S. longirostris,* and *Delphinus delphis*: Ortiz, 2011. *S. attenuata* and *S. longirostris*: Cabrera and Ortíz, 2012), and have been conducted in localized areas to different extents (Cabrera and Ortíz, 2010; Dávila, 2011; Cabrera et al., 2012; Quintana-Rizzo, 2019). However, one literature review identified 13 species of small cetaceans belonging to the Delphinidae and Kogiidae families (Cabrera et al., 2014). Information at a large scale is available from studies conducted in the 1990s in the eastern tropical Pacific (e.g., Wade and Gerrodette, 1993), which includes Guatemala, and describes species at the regional level (e.g., Reilly and Thayer, 1990; Escorza-Treviño et al., 2005; Chivers et al., 2007). Those studies reported two endemic subspecies of small cetaceans (*S. attenuata graffmani* and *S. longirostris centroamericana*) in the region (Dizon et al., 1994).

Many factors can influence the spatial and temporal distributions of cetaceans. They include physiographic characteristics such as water depth and seafloor slope (Cañadas et al., 2002; Baumgartner, 2006; Cubero-Pardo, 2007; Gómez de Segura et al., 2008; Azzellino et al., 2012), environmental factors such as sea surface temperature and salinity (Reilly, 1990), and biological factors such as prey distribution and breeding areas (Palacios et al., 2013). Important habitats require areas for feeding, breeding, socializing, and calving, as well as nursing and raising calves (Hoyt, 2011). Identifying areas essential for the day-to-day survival of species is a necessary component of an effectively designed spatial plan of prioritized conservation measures.

The effective protection of cetaceans could mean the protection of many marine organisms living in the ecosystem and of the ecosystem itself (Prideaux, 2003). This is because cetaceans typically live in large areas where, if effective protection measures are established, numerous other species could be conserved and protected, as well as their ecosystems and ecosystem processes. Isolated MPAs may serve to protect a certain species at a given time and place (Maxwell et al., 2014), but cetaceans are highly mobile. The protection of highly mobile species will necessitate the protection of areas that provide connectivity between critical habitats through a network of MPAs (Hyrenbach et al., 2000) and complementary management and mitigation measures.

Here we present an extensive analysis of the distribution and abundance of small cetaceans that have been observed in the Pacific waters of Guatemala. The analysis was based on data collected during boat surveys between 2008 and 2012. This is a unique dataset because of its sampling frequency and the spatial extent of the field effort within the Guatemalan Exclusive Economic Zone (EEZ). We have identified hot spot areas for all species of small cetaceans combined and for each of the most common species across the sampling area. The relationship between physiographic characteristics and social parameters such as group size was also examined. The results represent a vital contribution to marine spatial planning in Guatemala and fill a critical gap in knowledge to ensure that reserve designs are based primarily on the information obtained for species of interest (Hyrenbach et al., 2000).

MATERIALS AND METHODS

Study Area

The study area covers approximately 41,365 km^2 of the Pacific EEZ of Guatemala (**Figure 1**). It includes the continental shelf and oceanic plate. The Pacific continental shelf is an area of about 14,700 km^2, which extends from the coastline to 200 m depth and has an average width of 60 km (URL-IIA, 2004). The shelf edge is relatively straight, except for a major embayment on the east side, associated with the San José canyon (McMillen et al., 1982). This canyon is a major feature on the shelf and slope of the Guatemalan EEZ that drops from 200 to 2,000 m (Ladd and Schroder, 1985) and extends out into the Middle America Trench (von Huene et al., 1985). The Middle America trench is located within the oceanic plate at about 100 km from shore and reaches depths up to 6,400 m (Fisher, 1961).

The Guatemalan basin is part of the warm pool of the eastern tropical Pacific (>27.5°C), which results from a seasonally large net heat flux and weak wind mixing. The center of the warm pool is along the coast of southwestern Mexico and Guatemala (Fiedler and Talley, 2006). The area also includes the polygons of five proposed MPAs but the extent, size, and shape are under review (PNUD, 2018). From west to east, the MPAs are (**Figure 1**): (1) Manchón-Guamuchal (marine zone: 463.32 km^2), (2) Sipacate-Naranjo (marine zone: 543.90 km^2), (3) Monterrico (marine zone: 430.46 km^2), (4) Hawaii (marine zone: 239.76 km^2), and (5) Las Lisas (marine zone: 1018.48 km^2) (DIPESCA/MAGA/PNUD/TNC, 2018).

Field Effort and Cetacean Biodiversity

Boat surveys were conducted nearly every month from January 2008 to June 2012. Surveys were planned according to good weather conditions using two types of vessels: 6.7–7.62 m long fishing boats driving at 11–16 knots and the Guatemalan Coast Guard vessel (∼20 m long) driving at 7–8 knots. The latter towed a small vessel (∼7 m long) used to approach dolphin groups in which species confirmation was needed. All boat surveys were conducted under sea state conditions of Beaufort Sea State $\leq$ 3. Survey tracks were recorded in a Garmin GPSmap76, GPSmap 76S, or GPS Garmin Vista. Field time varied between 7 and 12 h/day.

Once a group of dolphins was spotted, the species identification, the number of individuals, and the presence or absence of calves were recorded, resuming sailing shortly after. Species identification with confidence levels of definite (high confidence in species identification) and probable (moderate confidence) were included in the analysis. A group was defined as all individuals displaying the same general activity within a 100 m distance (Wells et al., 1987), except in the case of groups of hundreds of individuals, which tended to spread over larger distances. A calf was defined as a dolphin up to about 75% of the presumed mother's length, which consistently traveled alongside the presumed mother, in baby position (Wells et al., 1987; Smolker et al., 1992; Urian and Wells, 1996). Each dolphin encountered was considered a sighting (Quintana-Rizzo and Wells, 2001). For each sighting, standard forms were completed with information about the time, geographical location, and environmental conditions.

Analysis

General Details

Statistical analyses were performed on the species that had at least 20 sightings to satisfy the minimum sample size of statistical comparisons (Ott, 1994). Thus, sightings from multiple years were pooled together. In the case of the bathymetric zone comparisons, statistical analyses only involved the species with at least 20 sightings in each zone (see below). An "all species" category was included in the abundance and spatial distribution analyses. Statistical tests were performed using the SPSS 26.0 package (2019) at a significance level of 0.05.

The study area was divided into the two marine zones based on bathymetry (Hedgpeth, 1957): neritic (<200 m depth) and oceanic (>200 m depth) to examine the relationship between cetacean abundance, distribution, and physiography (see below). Neritic and oceanic zones include ecosystems of the continental shelf and slope, respectively. Neritic waters lie over the continental shelf, beyond which the seafloor begins to descend more sharply. This zone division also allowed us to examine the significance of the current and planned protected areas since all of them are in the neritic zone. The study area included approximately 12,856 km of the neritic zone and 28,509 km of the oceanic zone.

Relative Abundance and Spatial Distribution

Cetacean sightings and track lines were plotted in ArcGIS Pro 2.7.0. The area for data analysis was divided into 10 km × 10 km grid cells resulting in 434 cells. For each species, three values were calculated within each grid cell: the total number of dolphins, the total number of sightings, and the total length of survey tracks. If no sightings occurred in a grid cell that was surveyed, the grid cell was attributed a value of zero but the cell was considered part of the survey effort. Two indices were calculated: (1) relative abundance of dolphins defined as individuals per unit effort (IPUE), and (2) sightings per unit effort (SPUE), where effort represents the distance surveyed in km. The latter was also a commonality index because a specie can be commonly sighted without being abundant or vice versa. IPUE and SPUE were calculated for all species combined and for each of the most common species in the neritic and oceanic zones. The two indices were compared between zones using a Mann–Whitney *U* test.

FIGURE 1 | Study area (light gray) inside the Guatemalan Pacific Economic Exclusive Zone including the neritic and oceanic zones, 200 m isobath, and coastal marine protected areas (medium gray color). Clear sections inside the study area represent sections that were not surveyed. The coastal protected areas from west to east are: (1) Manchon-Guamuchal, (2) Sipacate-Naranjo, (3) Monterrico, (4) Hawaii, and (5) Las Lisas.

A hot spot analysis was used to delineate the spatial occurrence or clustered distribution of dolphins (IPUE) and sightings (SPUE) of each of the most common species and all cetacean species combined. A hot spot analysis test for statistically significant spatial clustering of IPUE and SPUE using the Getis-Ord Gi* statistic (Getis and Ord, 1992), which determines the spatial clustering of grid cell values that are higher (hot spot) or lower (coldspot) than is expected by random distribution. It performs significant tests between nearby cells in the surrounding neighborhood area using a z-score (Getis and Ord, 1992). The recommended fixed distance band was used to ensure each feature has a neighbor within a specified distance that was objectively calculated within ArcGis Pro 2.7.1 (Queiroz et al., 2016; Yurkowski et al., 2019). Distributional maps were created at three levels of confidence (99, 95, and 90%), and all clusters that were within the 90% confidence level were considered hot spots. For the gap analysis, the spatial and percentage overlap (km^2 and % area, respectively) of species diversity hot spots of the study area and protected areas were calculated in ArcGis Pro 2.7.1.

Groups: Size, Calf Presence, and Sighting Relationship to Depth

Mean group size and the percentage of groups with calves were calculated for all the small cetacean species. Group size among the most common species was compared using a two-tailed Kruskal–Wallis test.

The analysis of group size and sighting relationship to depth included three components. First, the group size of the most common species was compared between the neritic and the oceanic zones using a two-tailed Mann–Whitney test. Since the zones are characterized by different bathymetry, they are a proxy to evaluate the relationship between group size and depth. Second, we examined if depth explained variation in group size by fitting a linear regression. The variables were log-transformed to ensure the data conformed to the assumptions of linear regression. Third, sighting depth among the most common species was compared using a two-tailed Kruskal–Wallis test. Depth was extracted using the bathymetry raster of the Guatemalan EEZ generated by DIPESCA/MAGA/PNUD/TNC (2018) in ArcGIS Pro 2.7.0.

RESULTS

Field Effort and Cetacean Biodiversity

A total of 171 surveys, covering 24,112 km, were conducted between January 2008 and June 2012 (**Table 1**). During the surveys, 64,678 cetaceans were sighted and 505 sightings were recorded. Species identification was confirmed in 98% (n = 495) of the cases. Nine species of small cetaceans, all belonging to the Delphinidae family, were identified. Three species accounted for 90% (n = 456) of all sightings (**Table 2**) and were referred to as the common species, which included: *T. truncatus* (56%, n = 278), *S. attenuata* (29%, n = 143), and *S. longirostris* (7%, n = 35). Two subspecies of *Stenella* were identified based on their morphological characteristics in some sightings. Of the 143 sightings of *S. attenuata*, 31 sightings (20%) were classified at the subspecies level. Of these 31 sightings, 26 were identified as *S. attenuata graffmani* and five were identified as *S. attenuata attenuata*. In the case of *S. longirostris*, eight (23%) out of the 35 sightings were classified at the subspecies level: four were identified as *S. longirostris centroamericana* and another four were identified as *S. longirostris orientalis*. Six species have the IUCN status of "Least Concern," two species have the status of "Data Deficient," and one species has the status of "Near Threatened" (**Table 2**). Sightings of seven species of small cetaceans included calves (**Table 2**).

TABLE 1 | Survey effort including the number of days, sightings, species, and kilometers surveyed in the Pacific Ocean of Guatemala.

Year	Month	# of days	# Sightings	# Species	Km surveyed
2008	January	1	4	2	232.29
	April	2	7	3	307.45
	May	1	6	4	213.32
	June	2	5	2	432.94
	August	6	7	3	614.35
	September	2	3	2	195.39
	October	9	14	2	1,016.21
	November	6	8	2	628.65
	December	8	14	4	824.05
2009	January	7	13	2	1,046.13
	February	7	10	2	834.47
	March	8	12	3	1,175.56
	April	7	16	3	776.44
	May	8	15	2	1,368.07
	June	5	4	2	662.12
	July	5	18	4	635.42
	August	2	14	2	320.86
	September	3	16	3	496.64
	October	2	5	2	239.26
	November	5	28	5	757.81
	December	8	25	4	1,418.59
2010	January	5	19	4	760.14
	February	7	22	5	1,009.77
	March	5	2	1	698.27
	April	2	2	2	301.54
	December	1	3	2	139.76
2011	January	2	14	5	293.89
	March	6	32	5	995.03
	April	5	14	5	652.07
	May	5	27	4	751.29
	June	5	31	5	711.46
	July	4	8	3	435.03
	September	4	24	4	680.00
	October	3	6	1	423.86
	December	2	5	3	334.84
2012	February	3	18	5	502.98
	March	4	8	3	590.13
	June	4	26	2	635.87

Spatial Distribution and Relative Abundance

Small cetaceans were sighted throughout the study area including the neritic and oceanic zones (**Figure 2**). However, the proportion of sightings in each zone varied among them. Ninety percent of the sightings of *S. attenuata* occurred in the neritic zone while 97 and 62% of the sightings of *S. longirostris* and *T. truncatus*, respectively, occurred in the oceanic zone (**Table 2**). The sighting frequency for the least common species was *Grampus griseus* (4%), *D. delphis* (2%), *Pseudorca crassidens* (1%), *Feresa attenuata* (0.40%), *Orcinus orca* (0.20%), and *Steno bredanensis* (0.20%). *G. griseus* and *P. crassidens* were sighted in the two zones, *O. orca* and *S. bredanensis* were only sighted in the neritic zone, while *D. delphis* and *F. attenuata* were only sighted in the oceanic zone (**Table 2**).

Relative abundance (IPUE and SPUE) was estimated for the entire sampling area, as well as for the neritic and oceanic zones. For the entire sampling area, mean IPUE was calculated at 2.14 dolphins/km, and mean SPUE was calculated at 0.04 sightings/km. No statistically significant difference was found between the IPUE and SPUE of all

TABLE 2 | Summary of small cetacean species sighted of the Pacific waters of Guatemala including the number of sightings, mean and range of group size, percentage of groups with calves, and Mann–Whitney *U* test (*U*) results of group size comparisons between the neritic (<200 m depth) and oceanic (>200 m depth) zones.

		Neritic				Oceanic				
	IUCN status	Sightings	GS ± SE	Range	% of groups with calves	Sightings	GS ± SE	Range	% of groups with calves	*U*, *p*-value
Common species										
Stenella attenuata	LC	129	20 ± 3	1–300	51	14	105 ± 42	1–550	50	594, 0.04
Stenella longirostris	DD	1	175	–	100	34	427 ± 76	1–2,050	62	NA
Tursiops truncatus	LC	106	11 ± 3	1–225	11	172	17 ± 3	1–225	20	7,578, 0.02
Least common species										
Delphinus delphis	LC	–	–	–	–	10	133 ± 32	60–275	50	NA
Feresa attenuata	LC	–	–	–	–	2	22 ± 6	15–27	0	NA
Grampus griseus	LC	1	1	–	0	17	11 ± 4	1–55	6	NA
Orcinus orca	DD	1	4	–	100	–	–	–	–	NA
Pseudorca crassidens	NT	5	12 ± 3	3–20	40	2	103 ± 98	5–200	0	NA
Steno bredanensis	LC	1	3	–	0	–	–	–	–	NA

SE, standard error. IUCN (www.iucnredlist.org) status: DD, data deficient; LC, least concern; NT, near threatened.

species combined between zones ($p > 0.05$, **Table 3**). However, higher numbers of individuals and sightings were detected in the individual grid cells in the oceanic zone than in the neritic zone.

The distribution of small cetaceans was more fragmented in the oceanic zone than in the neritic zone (**Figures 3**, **4**). A hot spot analysis showed eight IPUE clusters throughout the oceanic zone, particularly near the 200 m bathymetry line, the San José Canyon, and the Middle America Trench. In contrast, only one IPUE cluster of small cetaceans was found in the neritic zone, which was located on the northwestern side and near the 200 m bathymetry line (**Figure 5**). There were more SPUE than IPUE clusters in the oceanic ($n > 10$) and neritic ($n = 4$), including three large SPUE clusters (≥300 km each) in the San José canyon (**Figures 5**, **6**).

The mean IPUE of *T. truncatus* was calculated at 0.50 dolphin/km during the study. Total SPUE was 0.02 sightings/km (**Table 3**). No statistically significant difference was found in the IPUE and SPUE of this species between zones (**Table 3**). In the neritic zone, the sightings were concentrated on the eastern part of the zone, but in the oceanic zone they were more evenly distributed. Similar to the pattern observed in the "all cetacean species" category, the individual grid cells with sighting data of *T. truncatus* had a slightly higher abundance in the oceanic zone than in the neritic zone. However, when the overall area of the surveys was taken into account, the relative abundance of the IPUE and SPUE indexes in these two zones was not statistically different (**Table 3**). Mean SPUE was ≤0.03 sightings/km in both zones. Expectedly, IPUE showed more variation with a mean value of 0.29 dolphins/km in the neritic zone and 0.66 dolphins/km in the oceanic zone (**Table 3**). Based on the hot spot analysis, two IPUE clusters were identified: one small cluster extended from the neritic to the oceanic zone and a second large cluster in the oceanic zone. Most of the SPUE clusters were in the oceanic zone where six clusters were identified near the 200 m bathymetry line and the San José canyon (**Figure 6B**).

IPUE of *S. attenuata* was calculated at 0.004 dolphin/km and SPUE was determined to be 0.01 sightings/km (**Table 3**). IPUE and SPUE between zones were statistically different, but SPUE were higher in the neritic zone while IPUE were higher in the oceanic zone (**Table 3**). This means that a higher number of sightings/km of *S. attenuata* was recorded in the neritic zone while a higher number of dolphins/km was recorded in the oceanic zone (**Table 3**). A higher sighting density of *S. attenuata* was detected on the eastern side of the coast, which encompasses three of the MPAs. Based on the hot spot analysis, significant clusters of SPUE were identified in deeper waters, near the 200 m isobath (**Figure 6C**). In the oceanic zone, three IPUE clusters were identified, two of which were along the Middle America Trench and the other farther offshore at nearly 200 km from the coast (**Figure 5C**).

Stenella longirostris had a mean IPUE of 1.07 dolphins/km. Except for one sighting, all sightings of *S. longirostris* occurred within the oceanic zone where the mean IPUE was 1.62 dolphins/km and the mean SPUE was 0.004 sightings/km (**Table 3**). Three general areas were identified by the hot spot analyses for *S. longirostris*, the San José Canyon, the central region of the continental slope, and the central region of the Middle America Trench. The hot spots identified were consistent between IPUE and SPEU (**Figures 5D**, **6D**).

Groups: Size, Calf Presence, and Sighting Relationship to Depth

Group size was variable among small cetacean species (**Supplementary Figure 1**), although general conclusions were difficult to make for species with a small number of observations ($n < 5$). In the case of the two least common species with greater than five sightings, the mean group size was 133 for *D. delphis* and 11 for *G. griseus*. Among the most three common species, group size was significantly different

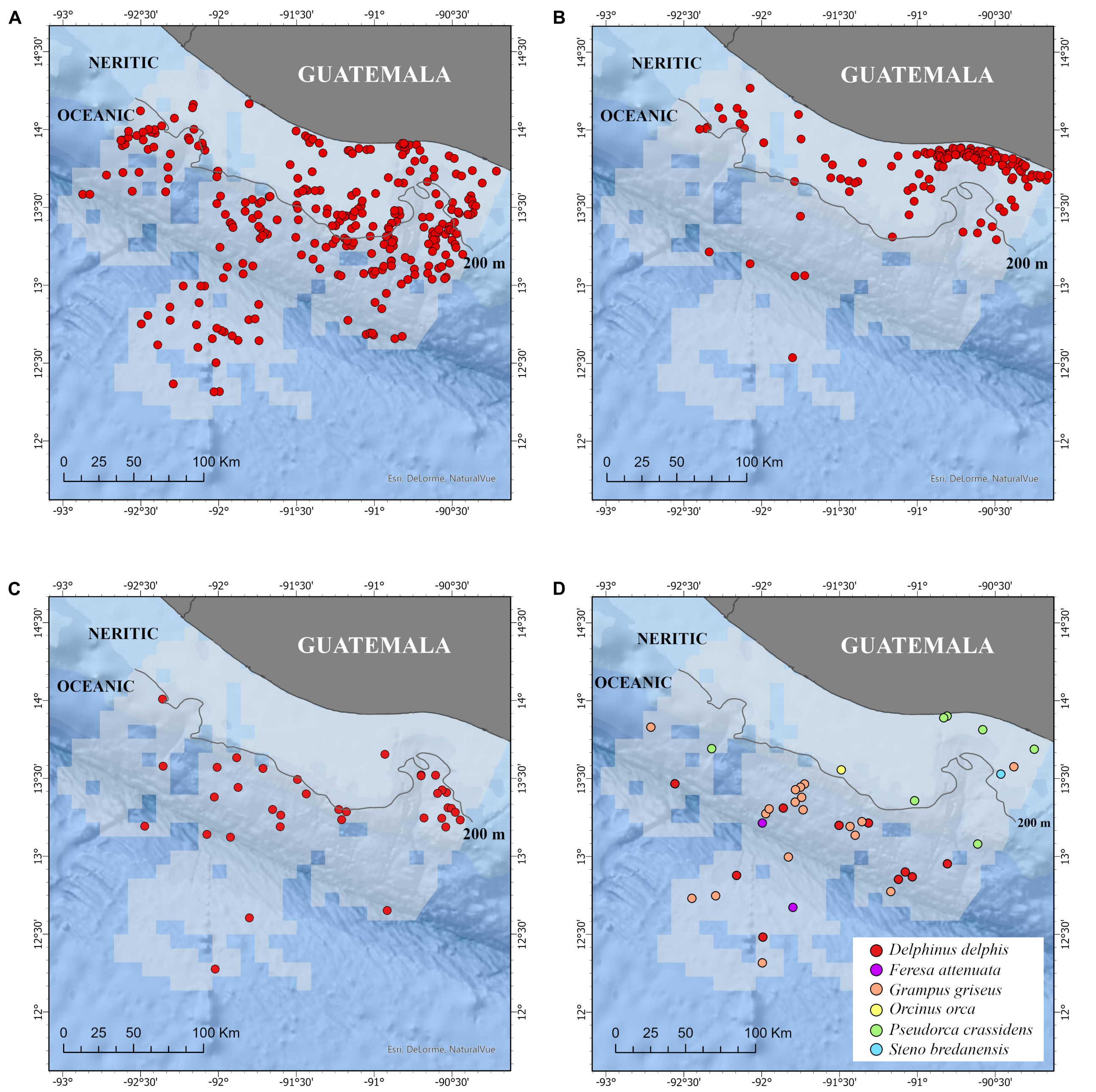

FIGURE 2 | Sightings of the three most common species: **(A)** *Tursiops truncatus*, **(B)** *Stenella attenuata*, and **(C)** *Stenella longirostris,* and **(D)** of the least common species in the study area (light gray) in the Pacific waters of Guatemala. Neritic and oceanic zones, 200 m isobath, and coastal marine protected areas (medium gray color) are also included. Additional details of the study area are shown in **Figure 1**.

(Kruskal–Wallis test = 96.03, df = 2, $p < 0.001$). Group size was the largest in *S. longirostris* with a mean of 444 dolphins, followed by *S. attenuata* with a mean of 28 dolphins, and *T. truncatus* with a mean of 15 dolphins (*S. longirostris* vs. *S. attenuata* $U = 637.50$, $p < 0.001$; *S. longirostris* vs. *T. truncatus* $U = 924.00$, $p < 0.001$; *S. attenuata* vs. *T. truncatus* $U = 12343.50$, $p < 0.001$).

The percentage of groups with calves was also variable. In the case of the most common species, *S. attenuata* and *S. longirostris* had the highest proportion of groups with calves, which corresponded to at least 50% and 60% of the groups, respectively (**Table 2**). Groups with calves of *S. attenuata* were sighted in the two bathymetric zones. The percentage of groups of *T. truncatus* with calves was less than ≤20% regardless of zone type (**Table 2**). Groups with calves were also detected in *D. delphis*, *G. griseus*, *O. orca*, and *P. crassidens*. In the case of *P. crassidens*, groups with calves were only seen in the neritic zone,

TABLE 3 | Sightings per unit effort (SPUE) and dolphins per unit effort (IPUE) for all small cetacean species and the most common species sighted of the Pacific waters of Guatemala.

		Neritic zone		Oceanic zone		
	Total	**Total**	**Mean ± SE**	**Total**	**Mean**	***U*, *p*-value**
SPUE						
All species	16.36	4.65	0.030 ± 0.03	11.71	0.040 ± 0.004	25,049.00, 0.68
Stenella attenuata	2.40	1.52	0.010 ± 0.002	0.88	0.003 ± 0.001	18,902.00, 0.00*
Stenella longirostris	1.49	0.27	0.001 ± 0.001	1.22	0.004 ± 0.001	NA
Tursiops truncatus	10.54	2.68	0.020 ± 0.002	7.86	0.030 ± 0.003	24,870.00, 0.51
IPUE						
All species	1,131.24	227.38	1.39 ± 0.42	903.86	2.89 ± 0.57	24,014, 0.24
Stenella attenuata	208.14	61.75	0.37 ± 0.16	146.39	0.50 ± 0.25	18,549.00, 0.00*
Stenella longirostris	508.83	3.02	NA	505.81	1.62 ± 0.41	NA
Tursiops truncatus	253.77	46.96	0.29 ± 0.13	206.81	0.66 ± 0.29	25,398.00, 0.88

Effort is defined as the number of sightings (in the case of SPUE) or individuals (in the case of IPUE) 1,000 km surveyed. Mann–Whitney U test (U) results comparisons between the neritic (<200 m depth) and oceanic (>200 m depth) zones are also included.
**Significant differences at p < 0.05. Total = sum of all the grid cell values calculated for a given index (SPUE or IPUE) during the entire study period.*

even though two groups were sighted overall in the oceanic zone (**Table 2**).

Group size varied between bathymetric zones (see **Table 2**). Depth did not always explain the variation in group size, although it accounted for a very small percentage of the variance in some cases. Groups were larger in the oceanic zone than in the neritic zone for *S. attenuata* and *T. truncatus*. In the case of *S. attenuata*, groups varied between 1 and 550 dolphins ($\bar{x} = 105$) in the oceanic zone and between 1 and 300 dolphins ($\bar{x} = 20$) in the neritic zone (**Table 2**). Further, there was a significant linear relationship, though weak positive relationship, between the logarithm of group size of *S. attenuata* and the logarithm of depth ($F_{1,141} = 13.82$, $p < 0.001$; $R^2 = 0.09$). In the case of *T. truncatus*, groups varied between 1 and 225 dolphins in both zones, however, the mean group size was only 17 in the oceanic zone and 11 in the neritic zone (**Table 2**). For this species, a significant linear and weak positive relationship was also found between the logarithm of group size and the logarithm of depth ($F_{1,276} = 4.88$, $p = 0.03$; $R^2 = 0.02$). A zone comparison was not possible for *S. longirostris* because all but one of the sightings occurred in the oceanic zone. The largest group of *S. longirostris* had 2,050 dolphins (**Table 2**). For this species, no significant linear relationship between the logarithm of group size and the logarithm of depth was identified ($F_{1,33} = 1.14$, $p = 0.29$).

Dolphin sightings occurred at a wide range of depths. Sighting depth was significantly different among the three most common species (Kruskal–Wallis test = 142.53, df = 2, $p < 0.001$). Sightings of *S. longirostris* and *T. truncatus* occurred in deeper waters than those of *S. attenuata* (*S. longirostris* vs. *S. attenuata* $U = 260.00$, $p < 0.001$; *S. longirostris* vs. *T. truncatus* $U = 3666.50$, $p = 0.02$; *S. attenuata* vs. *T. truncatus* $U = 6838.50$, $p < 0.001$). Mean depth of all the sightings of *T. truncatus* was 1,346 m (range = 5–6,031 m), of *S. longirostris* was 1,773.74 (range = 78–6,002 m), and of *S. attenuata* was 269 m (range = 18–5,988 m) (**Figure 7**).

DISCUSSION

Cetacean Biodiversity, Abundance, and Spatial Distribution

Nine species of small cetaceans all belonging to the Delphinidae family were identified during the study. Those species corresponded to nine out of 13 species of small cetaceans confirmed for the Guatemalan Pacific EEZ during the most extensive survey effort conducted by the National Oceanic and Atmospheric Administration, Southwest Fisheries Science Center surveys (NOAA-SWFSC; Quintana-Rizzo and Gerrodette, 2009). Differences between the two studies are related to differences in the number of pelagic species that were identified. The NOAA-SWFSC surveys covered the entire Guatemalan oceanic zone where those species are typically found, while this study sampled only about a third of the same zone; thus, reducing the probability of encountering pelagic species. Also, some species are gregarious by nature and might be more difficult to spot and identify (Sahri et al., 2020). The total number of small cetacean species identified in this study was smaller than that reported for the neighboring country of Mexico (15 species; Rosales-Nanduca et al., 2011), and other countries of the eastern tropical Pacific including Costa Rica (12 species; May-Collado et al., 2005) and Colombia (12 species; Palacios et al., 2012). Those studies included data collected by the NOAA-SWFSC surveys in their corresponding EEZ.

Tursiops truncatus was the most commonly sighted species in the entire study area as indicated by the high SPUE estimates. However, the species was not often sighted inside of 10 km along most of the coastline (**Figure 2A**). This was surprising considering that *T. truncatus* is usually a coastal species in many parts of the world (Würsig, 1978; Wells et al., 1980; Irvine et al., 1981; Quintana-Rizzo and Wells, 2001; Oviedo et al., 2005; Gamboa-Poveda and May-Collado, 2006) and it can

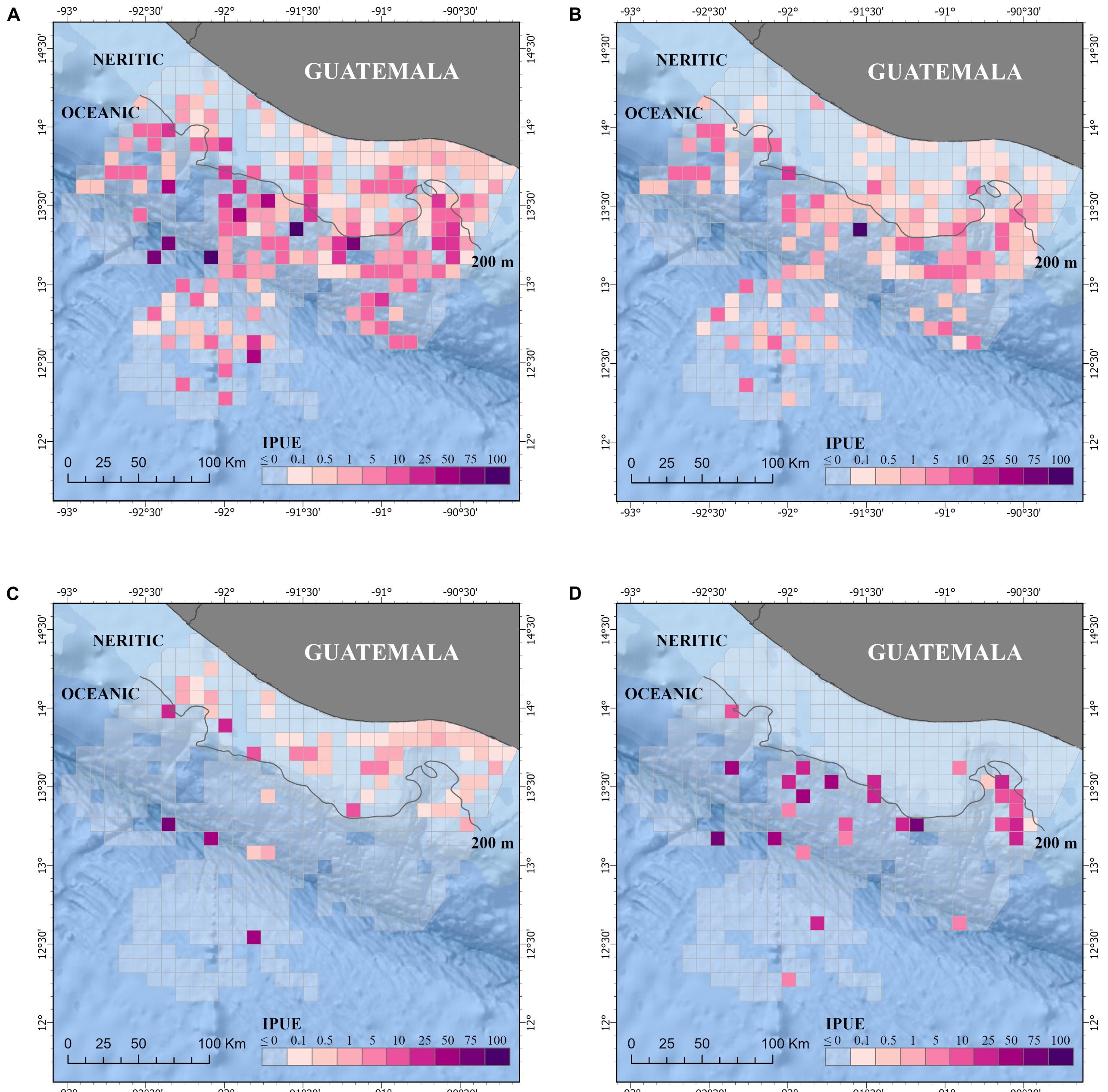

FIGURE 3 | Relative abundance is defined as individuals per survey effort (IPUE) of all small cetacean species **(A)** and the three most common species: **(B)** *Tursiops truncatus*, **(C)** *Stenella attenuata*, and **(D)** *Stenella longirostris* in the Pacific waters of Guatemala. Effort is km of survey summarized by 10 km × 10 km grid cells. Neritic (<200 m depth) and ocean (>200 m depth) zones are also included. Additional details of the study area are shown in **Figure 1**.

typically be found within 1 km from shore in coastal communities (Wells et al., 1980, 1987; Wells, 2003), some of which are in the Pacific Ocean (Defran et al., 1999). In Guatemala, the behavior of *T. truncatus* suggests that more research is needed to understand its habitat use. Along the eastern half of the coast, the species displayed a characteristic avoidance behavior toward the artisanal fishing boats used for the surveys (EQR unpublished data). When the survey boat tried to approach the dolphins during a sighting, they typically fled the area at a high speed. Although it is natural for some dolphins to avoid being followed during a sighting, this repeated and widespread reaction might not be. The behavior could be a response to the uncontrolled dolphin-watching activities of the area, although those activities tend to use a different type of vessel and they do not occur in half of this area. This reactive behavior could also be a learned behavior related to previous experiences that dolphins have had with artisanal fishing vessels (Wells et al., 1980, 1987; Wells, 2003). Habitat differences including the lack of protected

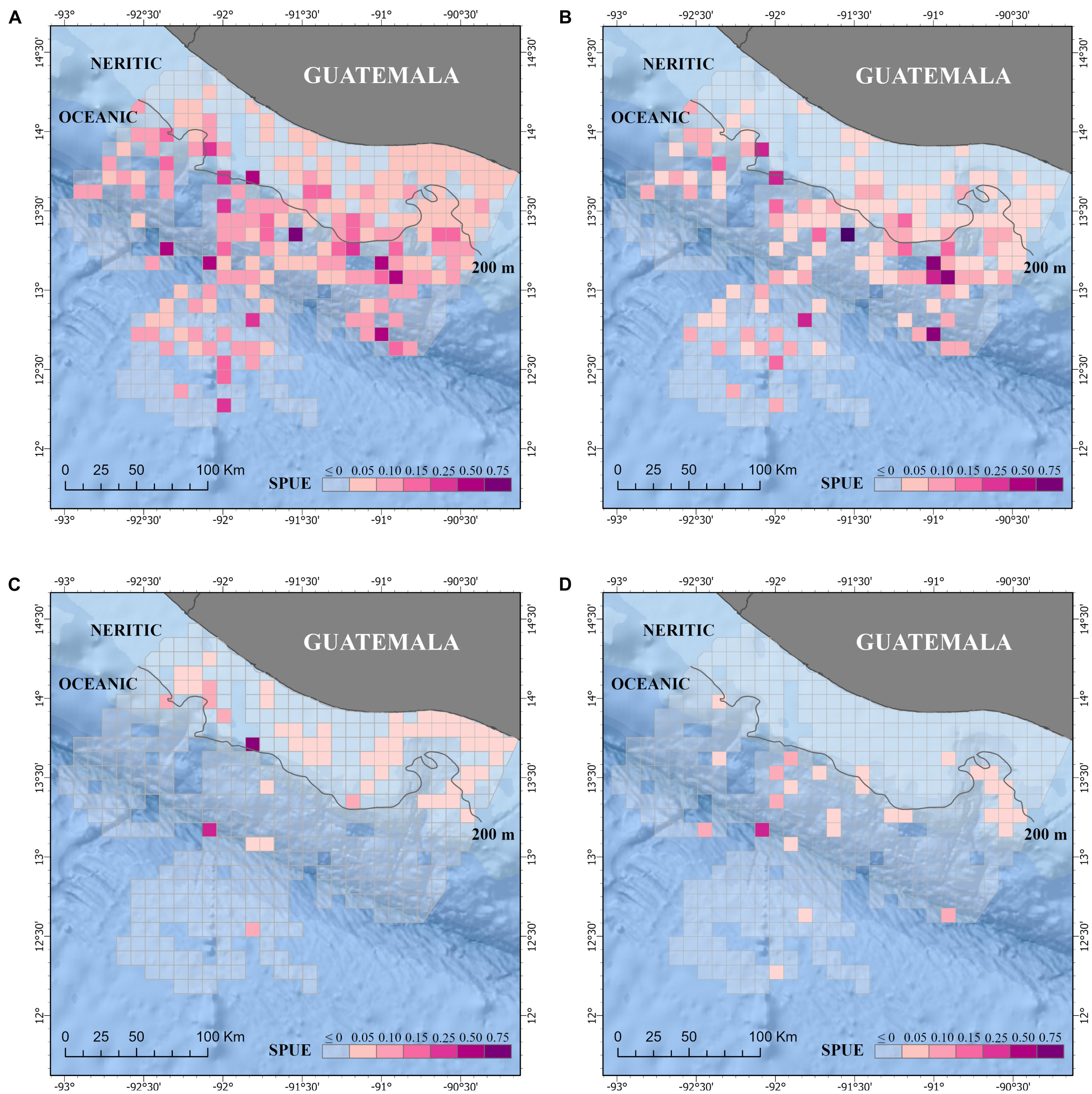

FIGURE 4 | Sightings per unit effort (SPUE) of all cetacean species **(A)** and the three most common species: **(B)** *Tursiops truncatus*, **(C)** *Stenella attenuata*, and **(D)** *Stenella longirostris* in the Pacific waters of Guatemala. Effort is km of survey summarized by 10 km × 10 km grid cells. Neritic (<200 m depth) and ocean (>200 m depth) zones are also included. Additional details of the study area are shown in **Figure 1**.

areas such as bays and rivers; prey availability and abundance, intraspecific competition, among others, could also play a role on its distribution. Quintana-Rizzo (2011a,b) documented that some fishermen in this region of the coast harpoon the species to use its meat as shark bait, but it is unclear how common the practice continues to be.

In addition to *T. truncatus*, *S. attenuata* and *S. longirostris* were the other most common species detected during this study. *S. attenuata* had the highest IPUE estimate in the neritic zone while *S. longirostris* had the highest IPUE estimate in the oceanic zone. *S. attenuata* and *S. longirostris* also had the highest proportion of groups with calves. Previous studies reported the same three species as common in Guatemala (Quintana-Rizzo and Gerrodette, 2009; Cabrera, 2011; Cabrera et al., 2014; Ortiz, 2019) and the Pacific coast of Central America (e.g., Costa Rica; Rodríguez and Rodríguez-Fonseca, 2004). Each of these three species showed a distinctive spatial distribution indicating that they have different habitat preferences. *T. truncatus* was found

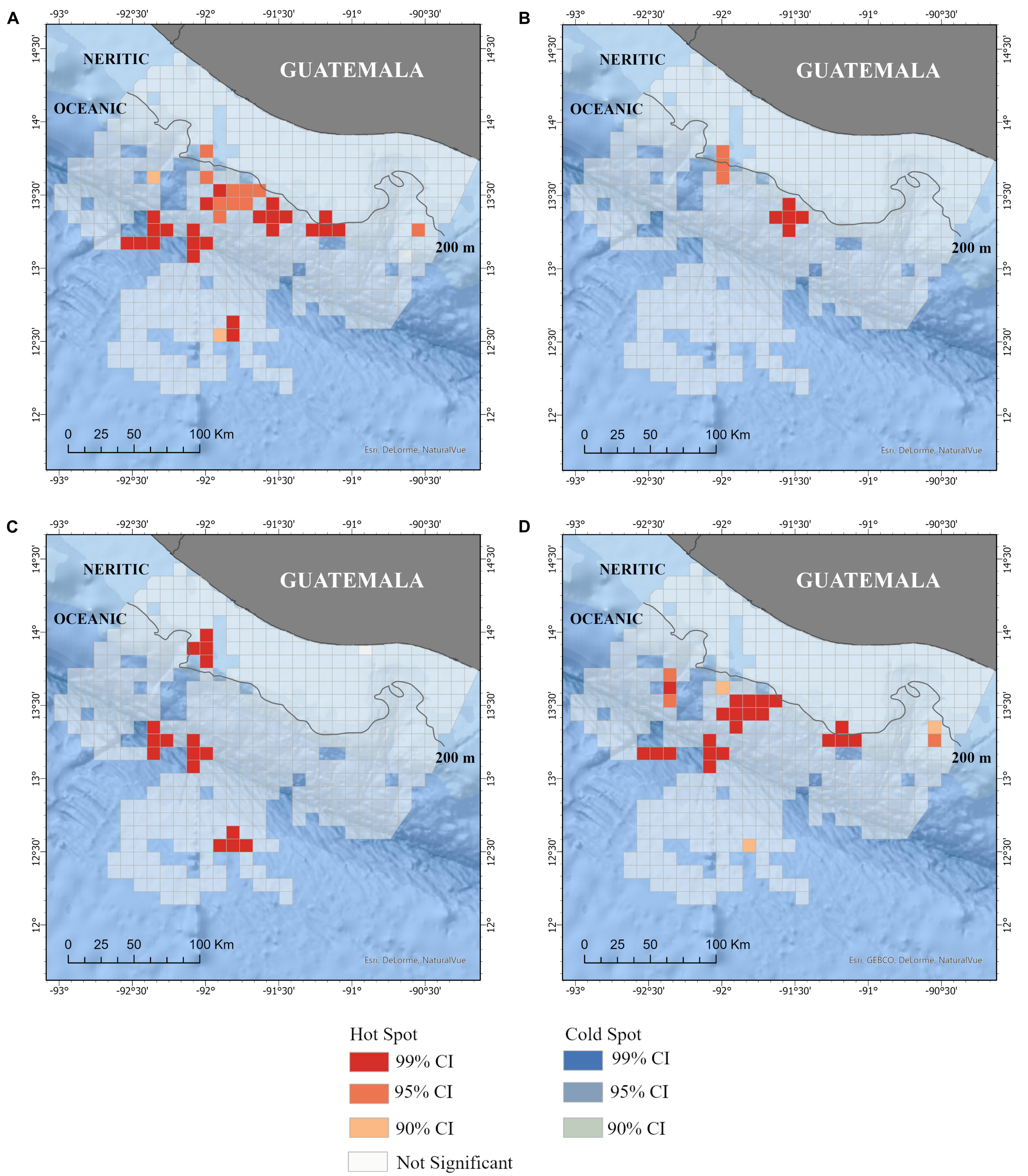

FIGURE 5 | Hot spots of distribution of all cetacean species **(A)** and the three most common species: **(B)** *Tursiops truncatus*, **(C)** *Stenella attenuata*, and **(D)** *Stenella longirostris* in the Pacific waters of Guatemala. No cold spots were identified. Neritic (<200 m depth) and ocean (>200 m depth) zones are also included. Additional details of the study area are shown in **Figure 1**.

throughout most of the study area, whereas 90% of the sightings of *S. attenuata* were recorded in the neritic zone, and all but one sighting of *S. longirostris* were recorded in the oceanic zone.

The wide-ranging distribution of *T. truncatus* across zones overlapped with the distribution of *S. attenuata* in the neritic zone and *S. longirostris* in the oceanic zone. However, there was

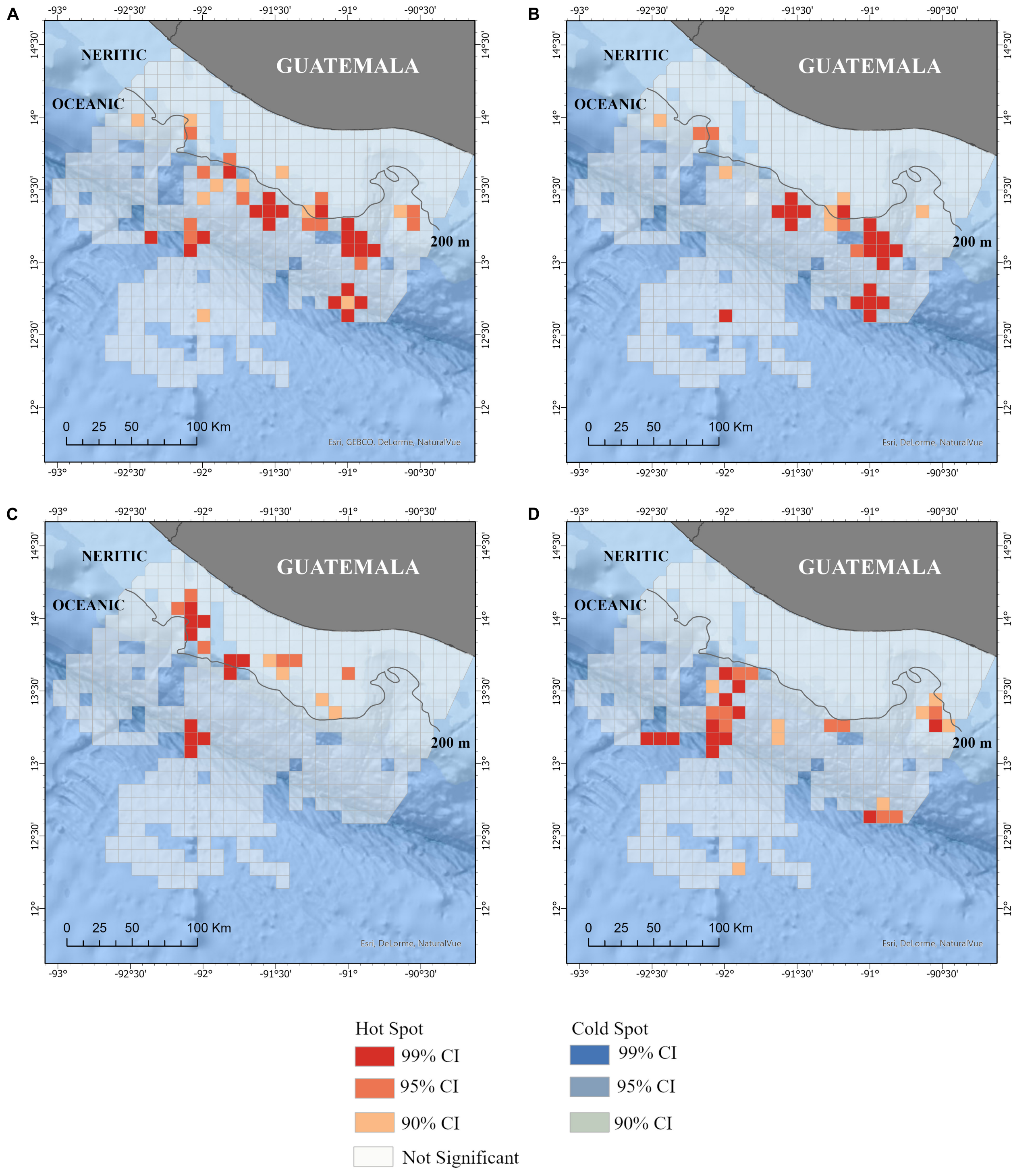

FIGURE 6 | Hot spots of sightings of all cetacean species **(A)** and the three most common species: **(B)** *Tursiops truncatus*, **(C)** *Stenella attenuata*, and **(D)** *Stenella longirostris* in the Pacific waters of Guatemala. No cold spots were identified. Neritic (<200 m depth) and ocean (>200 m depth) zones are also included. Additional details of the study area are shown in **Figure 1**.

little overlap in the distribution of *S. attenuata* and *S. longirostris* in the study area. This latter pattern is inconsistent with the observations of Au and Perryman (1985), who stated that the Central American Bight, which includes the coastal waters from Guatemala to Ecuador, is the most important area of overlap for *S. attenuata* and *S. longirostris*. Their study was based on data

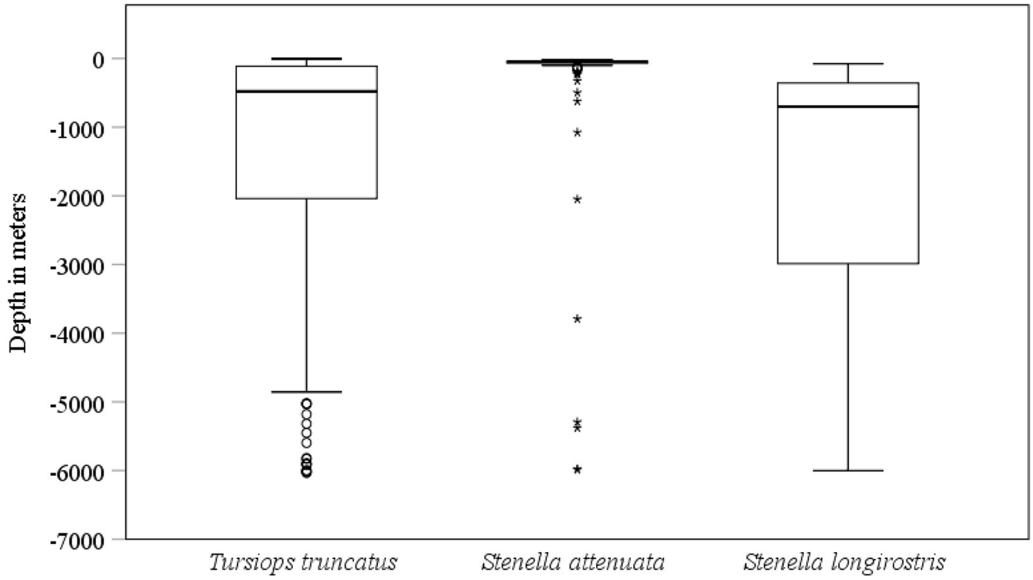

FIGURE 7 | Central tendency and variability of group size of the most common species of small cetaceans identified in the Pacific waters of Guatemala. The solid line drawn across each box represents the median group size. The lower boundary is the 25th percentile and the upper boundary is the 75th percentile of a box. The lines on top and bottom of each box represent the largest and smallest group size, respectively, excluding outliers (o) and extreme values (*).

collected during the NOAA-SWFSC surveys which, as previously mentioned, were more spatially comprehensive and oceanic-focused. They did not report any sightings in the neritic zone of Guatemala, but in the oceanic zone of the eastern tropical Pacific they reported the offshore forms of the two species (*S. attenuata attenuata*, *S. longirostris orientalis*), which use tropical surface waters with temperatures over 25°C and a shallow mixed layer, shoal, and sharp thermocline at 50 m. In the same area, it was reported that *S. attenuata attenuata* commonly occurred in large mixed groups with *S. longirostris* and yellowfin tuna (*Thunnus albacares*) (Au and Perryman, 1985; Perrin and Hohn, 1994; Ballance et al., 2006). On the other hand, in the present study, the most sighted form of *S. attenuata* was probably the coastal form, *S. attenuata graffmani,* since those sightings occurred in the neritic zone and this subspecies does not overlap with *S. longirostris orientalis*. *S. attenuata graffmani* occurs in a narrow coastal band along the Pacific coasts of southern Mexico to south Peru (Perrin, 2009).

Group Size

Ecological factors play a role in determining group size (Gomez-Salazar et al., 2012; Markham et al., 2015; Casari and Tagliapietra, 2018; Moura et al., 2019). This was evident in the group size differences between zones. In the shallow waters of the neritic zone, large numbers of small groups of the common species were observed, while in the deep waters of the oceanic zone large groups of the same species were more frequently sighted. Group size differences between habitats are an ecological strategy to avoid predation and a foraging strategy to adapt to diverse prey items (Connor, 2000; Krause and Ruxton, 2002; Markham et al., 2015). Specifically, small offshore cetaceans tend to form large groups as a social mechanism to minimize the risk of predation by individual dolphins (dilution effect) and to deal with larger and more irregular patches of prey availability (Connor, 2000; Bearzi, 2005; Silva et al., 2008). For example, *S. longirostris longirostris* forms large groups that prey on unpredictable mesopelagic fishes and squids in the eastern and western Pacific (Perrin and Gilpatrick, 1994; Dolar et al., 2003). In contrast, coastal cetacean species tend to form smaller groups as the predation risk is comparatively small and prey resources are generally more predictable (Moors-Murphy, 2014; Acevedo-Gutiérrez, 2018).

In the neritic zone of Guatemala, *S. attenuata* was the most commonly detected species. The mean group size (20 ± 3 dolphins) was comparable to that of the neritic zones of the Pacific near Costa Rica (mean = 10, range = 1–50 dolphins; May-Collado and Forcada, 2012) and Panama (mean = 23, range = 1–50 dolphins; Garcia and Dawson, 2003). Oceanic groups were slightly smaller in Guatemala (105 dolphins) than in the rest of eastern tropical Pacific (mean = 120; Ferguson et al., 2006) but larger than in the Philippines (mean = 84, range = 1–540 dolphins; Dolar et al., 2006).

Hot Spots and Related Habitats

Other habitat differences included the number of hot spots. Less than five SPUE and IPUE hot spots were identified for all species combined in the neritic zone, and no hot spots were identified near or within the MPAs. The low number could be because the analysis identifies areas of high spatial clustering, which were uncommon in this zone. In the neritic zone, several hot spots (≥10) were identified, but the results need to be taken with caution given the small sample size. However, some general patterns were observed. The hot spots were located along the 200 m isobath (near the continental shelf edge), the Middle America trench, and the San José Canyon. These are likely areas of high productivity where dolphins concentrate to feed. The offshore waters of Guatemala are characterized by seasonal eddies that act as retention mechanisms for planktonic organisms, which serve as food sources for first-order consumers and consequently generate food for higher trophic predators (Ehrhardt and Fitchett, 2006; Acosta-Pachón et al., 2017). The accumulation of members of the pelagic food web near the continental shelf edge and over the shelf break is a recognized phenomenon throughout the world ocean. Marine mammals, birds (Certain et al., 2007), fish (e.g., Uriarte and Lucio, 2001), and phytoplankton (Lampert et al., 2002) benefit from inorganic nutrients supplied by physical forcing (New and Pingree, 1990). Submarine canyons, such as the San José Canyon, serve as conduits for the transport of deep, nutrient-rich waters to the continental shelf waters of coastal ecosystems (Fernandez-Arcaya et al., 2017; Santora et al., 2018). Canyons support high levels of biodiversity and serve as feeding grounds for many species (De Leo et al., 2014; Moors-Murphy, 2014; Santora et al., 2018). In the San José Canyon, swordfish (Carey and Robinson, 1981; Carey, 1983) and hundreds of sea turtles (Brittain, 2016) have been sighted, and several hot spots of *S. longirostris* and *T. truncatus* were identified in this study.

Five species of small cetaceans (*S. attenuata, T. truncatus, P. crassidens, G. griseus,* and *Steno bredanensis*) were sighted to the north of the San José Canyon, in a stretch of approximately 30 km of the neritic zone that includes three of the MPAs (Monterrico, Hawaii, and Las Lisas) and waters off Puerto (port) Quetzal (**Figure 1**). *S. attenuata* was particularly common in this section as indicated by IPUE and SPUE estimates. Additionally, some of these dolphins exhibited a degree of residency to the area (Quintana-Rizzo, 2011b); thus, suggesting that the habitat provided resources needed for their survival. No other section of the Guatemalan neritic zone had such high diversity or such a continuous presence of small cetaceans.

In the Puerto Quetzal-Monterrico-Las Lisas section, the all species IPUE estimate varied from 0.1 to 1 dolphin/km whereas the SPUE estimate was more consistent at 0.05 sightings/km. Other sections of the coast had either zero sightings or sightings of either *T. truncatus* or *S. attenuata*. The frequent presence of small cetaceans in the Puerto Quetzal-Monterrico-Las Lisas section could be due to a "spillover effect" from the San José canyon, where currents bring nutrient-rich waters to the nearby coastal areas; thus, attracting several cetacean species. It could also be an effect of sampling effort but a similar pattern has been observed in recent surveys (EQR unpublished data).

Implications and Future Perspectives for Conservation

Our results suggest that the protection of small cetaceans needs to consider the creation of oceanic MPAs. Those areas should be integrated into the current network of MPAs to ensure habitat connectivity because protected areas in coastal habitats alone might provide little safety to highly mobile cetaceans (Dinis et al., 2016). A highly mobile species is *O. orca*, and a group of this species that was sighted in Guatemala was confirmed through photographic identification to have been seen in Cabo Corriente, Mexico, 11 years earlier (Cabrera et al., 2012). This shows that some species move across hundreds of miles in the eastern tropical Pacific and MPAs can serve as a tool to provide connectivity among habitats. Other offshore species deserve close attention because millions of dolphins died since the 1960's as bycatch in tuna nets in the eastern tropical Pacific Ocean (Gerrodette and Forcada, 2005; Wade et al., 2007). The management of oceanic MPAs could be challenging due to the financial burden required to patrol offshore sites and/or maintain the proper law enforcement presence in a vast area. It is already difficult for the country to manage its local coastal marine resources, which in theory are easier to protect due to their proximity to shore. Still, there are important international tools that could be used such as the Convention on the Conservation of Migratory Species of Wild Animals and the United Nations Convention on the Law of the Sea for increased offshore habitat protection (Hoyt, 2011).

Other conservation actions are greatly needed for the protection of small cetaceans. Dolphin-watching activities need to be managed, especially as they are becoming more popular along the Puerto Quetzal-Monterrico-Las Lisas section. The guidelines for those activities have been effective for some years but their control is non-existent. This is worrisome because the local activities seem to affect the behavior of large cetaceans such as humpback whales (Quintana-Rizzo, 2019), and it is unclear how they could impact small cetaceans. Research is needed to study their potential effects on dolphins. Additionally, the bycatch of small cetaceans in commercial fishing operations needs to be investigated. This is a common threat in Latin America (Van Waerebeek and Reyes, 1994; Palacios and Gerrodette, 1996; Reeves et al., 2003; Ávila et al., 2008) and other parts of the world (Palacios and Gerrodette, 1996). Further, boat collisions and the effects of commercial shipping need to be examined. Puerto Quetzal is one of the main commercial ports of Guatemala and due to its proximity to the MPAs, ship traffic, noise, and pollution near the port need to be evaluated and proper management and conservation measurements need to be established. This port moved nearly a quarter of a million cargo tons in 2018 (UN-ECLAC, 2018), and is one of the top 30 busiest ports of 118 ports in Latin America and the Caribbean according to the United Nations Economic Commission for Latin American and the Caribbean (UN-ECLAC, 2018).

Conservation is a complex task. It requires an integrated ecosystem approach to be successful, and our research has shown that oceanographic features, and not the political boundaries, are most likely to affect the distribution of small cetaceans. Conservation management should also focus on protecting wildlife habitat linked to important activities such as feeding, resting, breeding, and caring for young (Smith et al., 2016). They should also take into consideration the presence of different subspecies since they will probably require different measures of management (e.g., *S. attenuata*: coastal subspecies forms small groups in the neritic zone, and the offshore subspecies forms groups of hundreds of individuals in the oceanic zone). Biological, ecological, and oceanographic information should be used to identify MPAs that reflect the needs of mobile marine species in order to be relevant to those species that they intend to protect.

DATA AVAILABILITY STATEMENT

The full raw datasets used for this study are available on request to the corresponding author. Data collected by AAC, J-OW, and VD are available as **Supplementary Table 1**.

ETHICS STATEMENT

During this study the following research permits were obtained: Guatemalan Government National Council for Protected Areas (CONAP) 053/2009 and 007/2011.

AUTHOR CONTRIBUTIONS

EQ-R conceived the original idea for this manuscript. EQ-R, AAC, JO-W, and VD expanded and agreed on the details of the publication. EQ-R (lead), VD, and AAC analyzed the data. JO-W reviewed the format of the bibliography. EQ-R led the writing with contributions from all authors who discussed the results and commented on the manuscript. All authors conducted fieldwork and collected data.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.674134/full#supplementary-material

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