



BRIEF COMMUNICATION

Mitochondrial DNA genome evidence for the existence of a third divergent lineage in the western Atlantic Ocean for the bull shark (*Carcharhinus leucas*)

Nadia Sandoval Laurrabaquio-Alvarado¹ | Píndaro Díaz-Jaimes²  |
 Silvia Hinojosa-Álvarez³ | Maria del Pilar Blanco-Parra^{4,5,6} | Douglas H. Adams⁷  |
 Juan Carlos Pérez-Jiménez⁸ | J. Leonardo Castillo-Géniz⁹

¹Posgrado en Ciencias del Mar y Limnología, UNAM, Mexico City, Mexico

²Unidad Académica de Ecología y Biodiversidad Acuática, Instituto de Ciencias del Mar y Limnología, UNAM, Mexico City, Mexico

³Escuela de Ingeniería y Ciencias, Centro de Biotecnología FEMSA, Tecnológico de Monterrey, Monterrey, Mexico

⁴Consejo Nacional de Ciencia y Tecnología, Mexico City, Mexico

⁵División de Ciencias e Ingeniería, Universidad de Quintana Roo, Chetumal, Mexico

⁶Fundación internacional para la naturaleza y la sustentabilidad, Chetumal, Mexico

⁷Florida Fish & Wildlife Conservation Commission, Fish & Wildlife Research Institute, Melbourne, Florida

⁸El Colegio de la Frontera Sur, Lerma, Mexico

⁹Instituto Nacional de Pesca y Acuicultura, Ensenada, Mexico

Correspondence

Píndaro Díaz-Jaimes, Unidad Académica de Ecología y Biodiversidad Acuática, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Apdo. Postal 70-305, México DF 04510, Mexico.
 Email: pindaro@cmar.unam.mx

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Abstract

We report for the first time a highly divergent lineage in the Caribbean Sea for the bull shark (*Carcharhinus leucas*) based on the analysis of 51 mitochondrial DNA genomes of individuals collected in the western North Atlantic. When comparing the mtDNA control region obtained from the mitogenomes to sequences reported previously for Brazil, the Caribbean lineage remained highly divergent. These results support the existence of a discrete population in Central America due to a phylogeographic break separating the Caribbean Sea from the western North Atlantic, Gulf of Mexico and South America.

KEYWORDS

bull sharks, genetic divergence, mitogenomes, phylogeography

Oceans cover a wide area of the earth's surface, with divergent oceanographic and ecological characteristics (e.g., temperature, salinity, endemism, species composition and abundance) creating smaller regions (Briggs & Bowen, 2012; Robertson & Cramer, 2014; Toonen *et al.*, 2016; Wilkinson *et al.*, 2009). The variety of physical conditions between regions is usually related to the distribution of genetic variants among populations or species and at different spatial scales (Bowen *et al.*, 2016). Some phylogeographic patterns due to genetic and taxonomic discontinuities have been reported for many

marine species (Briggs & Bowen, 2012), providing useful information for the delimitation of priority conservation areas or evolutionary significant units (ESUs) (Rocha *et al.*, 2007), which are units of conservation that result from independent evolutionary processes allowing the adaptive response to changes in the environment to be preserved. The genetic divergence for many shark species has been linked to gene flow barriers (Dudgeon *et al.*, 2012), but also to ecological (Dimens *et al.*, 2019) and/or reproductive traits (Chapman *et al.*, 2015). Mitochondrial DNA (mtDNA) is effective as a molecular

marker to define genetic divergence at the population or species level in sharks (Fields *et al.*, 2016; Greig *et al.*, 2001; Quattro *et al.*, 2006).

In the western Atlantic Ocean using the mtDNA-Control Region (mtDNA-CR) two divergent mtDNA lineages were reported between the Northern and Southern Hemisphere in several coastal shark species including the blacktip shark *Carcharhinus limbatus* Muller & Henle 1839 (Sodré *et al.*, 2012), the dusky shark *Carcharhinus obscurus* Lesueur 1818 (Benavides *et al.*, 2011), the night shark *Carcharhinus signatus* Poey 1868 (Domingues *et al.*, 2019), the bull shark, *Carcharhinus leucas* Müller & Henle 1839 (Karl *et al.*, 2011) and the tiger shark *Galeocerdo cuvier* Péron & Lesueur, 1822 (Carmo *et al.*, 2019). Similarly, for some species, genetic divergence has been found at a smaller scale among the waters of North and Central America. This has been the case for the blacktip shark (Gledhill *et al.*, 2015; Keeney *et al.*, 2005) and two hammerhead shark species, the bonnethead *Sphyrna tiburo* Linnaeus 1758 and the scalloped hammerhead *Sphyrna lewini* Griffith & Smith, 1834 (Chapman *et al.*, 2009; Fields *et al.*, 2016; Gonzalez *et al.*, 2019; Pinhal *et al.*, 2020), highlighting the existence of a phylogeographic break separating multiple shark populations in the western Atlantic Ocean.

The bull shark is an euryhaline species, with a cosmopolitan distribution in tropical and subtropical waters. It is also associated with coastal and estuarine habitats. Adult females use specific estuarine habitats for parturition. Neonate and juvenile individuals use these estuarine habitats as nurseries (Curtis *et al.*, 2011). Adults are found primarily in shallow ocean waters and tend to remain in the same broad areas over long periods, with limited migratory movements (Carlson *et al.*, 2010; Kohler & Turner, 2019), highlighting the importance of coastal habitats for this species. Records of movements of bull sharks

from the U.S. Atlantic coast to the Caribbean are scarce (Kohler & Turner, 2019). Of 2129 tagged bull shark individuals in the Gulf of Mexico and the Caribbean, only six sharks registered movements between the northern and southern Gulf of Mexico. Genetic analyses based on mtDNA sequences data detected two matrilineal lineages of bull sharks in North and South America (Karl *et al.*, 2011) that were attributed to philopatric behaviour. Philopatry was further confirmed by Sandoval Laurrabaquio-Alvarado *et al.* (2019) in the western North Atlantic Ocean using similar sampling locations (Texas, Louisiana and Florida). However, there is still insufficient information regarding the number and distribution of mitochondrial lineages related to the species' phylogeography in the entire western Atlantic Ocean.

To assess the number and distribution of lineages for bull shark in the western Atlantic Ocean, we analysed the complete mtDNA genome in 51 immature individuals evenly distributed from the northern and southern Gulf of Mexico, the Atlantic coast of Florida and the Caribbean Sea. Additionally, the mtDNA control region obtained from genome sequences was compared with previous mtDNA-CR sequences (810 pb) from Brazil used by Karl *et al.* (2011).

We analysed juvenile bull sharks (<190 cm total length) of six estuaries from the western Atlantic Ocean (Indian River Lagoon, Florida, IRL, $n = 12$), the northern Gulf of Mexico (Charlotte Harbor, Florida, CH, $n = 12$; Texas TEX, $n = 5$; Louisiana LOU, $n = 5$), the southern Gulf of Mexico (Tamiagua, Mexico TAM, $n = 11$) and the Caribbean Sea (Chetumal Bay, Mexico CAR, $n = 6$) (Figure 1). Tissue samples were collected from bull sharks across multiple years (1996–2018) during ongoing fisheries-independent monitoring surveys in U.S. waters and from local commercial fisheries in Mexico and preserved in nondenatured 95% ethanol.



FIGURE 1 Sampling sites and regions (in different colours) from which the sequences of the mtDNA genome were obtained for bull shark *Carcharhinus leucas* individuals. Sampling sites: Texas (TEX), Louisiana (LOU), Charlotte Harbor (CH), Indian River Lagoon (IRL), Tamiagua (TAM), Caribbean (CAR), Western north Atlantic (WNA), Northern Gulf of Mexico (NGM), Southern Gulf of Mexico (SGM), Caribbean (CAR). Numbers in parenthesis are the sample size for each location. Colours for locations represent the studied regions: western North Atlantic (orange), northern Gulf of Mexico (blue), southern Gulf of Mexico (green) and Caribbean (red)

Genomic DNA was obtained using the phenol-chloroform protocol (Sambrook *et al.*, 1989) and fragmented by sonication using a bio-disruptor. Fragmented DNA was cleaned using magnetic beads and libraries prepared using the KAPA HiFi HotStart PCR Kit, according to the manufacturer's instructions and sequenced using the Illumina sequencer MiSeq v3 600. The mtDNA genomes were assembled with Geneious v 10.2.3 (Kearse *et al.*, 2012) using as reference the bull shark mitochondrial genome of an individual collected from the Pacific Ocean in Taiwan Strait off China (GenBank accession number NC_023522; Chen *et al.*, 2014). The quality of sequences was measured on the basis of the deep sequencing, which was considered to be adequate at a minimum of 5× per lecture. The determination of mutations was assessed by checking each substitution against the mtDNA genome of the bull shark from China. Genetic diversity parameters were calculated with DnaSP v.6 (Rozas *et al.*, 2017), and genetic differentiation (based on Φ_{ST} Tamura and Nei distance with 20,000 permutations) estimated using Arlequin v.3.5.2.2 (Excoffier *et al.*, 2005). A phylogenetic analysis was conducted with BEAST v.1.10.14 (Suchard *et al.*, 2018) using the mitogenomes obtained for this research and other shark mitogenomes of the order Carcharhiniformes Compagno 1977 obtained from GenBank (accession numbers KC470543.1, KJ720818.1, KP091436.1, NC_023522.1, NC_024055.1, NC_024862.1, NC_025520.1, NC_026696.1, NC_027081.1, MN943498.1). Divergence times were estimated using three independent runs with 10,000, 100,000 and 1,000,000 generations, respectively, selecting the HKY model and a relaxed clock rate. To produce one single tree, we used LogCombiner and TreeAnnotator with a burn-in of 1,000,000 and edited with FigTree v.1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>). The Isolation by Distance model (Slatkin, 1993) was tested by evaluating the correlation between the logarithmic distance in kilometres, measured as the shortest coastal line separating localities, and the linearized Slatkin genetic distance based on pairwise Φ_{ST} estimates in ARLEQUIN.

A segment of the mtDNA control region (810 bp) was obtained from the 51 mitogenomes sequenced for comparisons to sequences

from Brazil ($n = 49$) used in Karl *et al.* (2011). Haplotype networks for the mtDNA genomes and the mtDNA-CR were obtained using PopART with the TCS algorithm (Clement *et al.*, 2002).

We obtained 51 mtDNA genomes (16,707–16,708 bp) of immature individuals that resulted in a total of 30 haplotypes with each locality displaying 3 to 10 haplotypes. A high haplotype diversity ($Hd = 0.730$ – 1.000) and low nucleotide diversity ($\pi = 0.00005$ – 0.0004) was estimated (Table 1). Pairwise-sample Φ_{ST} estimates resulted in high significant differences between CAR and the other locations ($\Phi_{ST} = 0.88$ – 0.96 ; $P = <0.00000$ – 0.0024 ; Table 2). The comparison between IRL against LOU was significant ($\Phi_{ST} = 0.14$; $P = 0.046$). When using the 810 bp fragment of the mtDNA-CR to assess divergence between western North Atlantic, the Gulf of Mexico and South America, the pairwise Φ_{ST} estimates resulted in highly significant differences among these three regions (Table 2); the Brazilian and the Caribbean locations showed significant differences between them, but also when compared to locations from the Gulf of Mexico and the western North Atlantic (IRL-Florida Atlantic) (range $\Phi_{ST} = 0.597$ – 1.000 , $P < 0.001$).

The phylogenetic tree (Figure 2a), using mtDNA genomes, indicates two divergent lineages separating the Gulf of Mexico/Atlantic and the Caribbean (CAR). This pattern was supported by the haplotype network. Furthermore, there was a second clade comprising haplotypes exclusively from the Caribbean Sea, which separated from those of the western North Atlantic and Gulf of Mexico for a high number of mutations (30–37) (Figure 2b). This pattern of genetic divergence was further confirmed in the haplotype network obtained from the 810 bp mtDNA-CR fragment which, in addition, showed a third mtDNA lineage comprising individuals from Brazil (Figure 2c). This evidence clearly confirms the existence of three mtDNA lineages in the western Atlantic Ocean.

The distribution and frequency of the mitochondrial DNA lineages are explained by the species evolutionary history, but also by reproductive and population dynamics. In the case of the bull shark, two matrilineal lineages have been reported in the western Atlantic

TABLE 1 Sampling locations and regions studied in the western north Atlantic and summary statistics per location

			Latitude–longitude	N	Nh	h	π	S
Western North Atlantic	IRL		28°03'19"N –80°34'34"W	12	4	0.803	0.00040	15
Northern Gulf of Mexico	TEX		29°34'11"N –94°56'12"W	5	5	1.000	0.00040	15
	LOU		25°51'19"N –91°12'92"W	5	5	1.000	0.00010	6
	CH		26°46'33"N –82°08'31"W	12	7	0.879	0.00030	18
Southern Gulf of Mexico	TAM		21°57'36"N –97°59'41"W	11	10	0.982	0.00030	24
Caribbean	CAR		18°20'0"N –88°5'0"W	6	3	0.733	0.00005	2

Note. π , nucleotide diversity; h, haplotype diversity; N, sample size, Nh, number of haplotypes; S, segregating sites.

	IRL (12)	CH (12)	TEX (5)	LOU (5)	TAM (11)	CAR (8)	BZ (49)
IRL (12)	–	0.159	0.008	0.526	0.080	0.862***	0.682***
CH (12)	0.001	–	0.006	0.000	0.000	0.741***	0.683***
TEX (5)	0.137*	0.016	–	0.160	0.122	1.000***	0.799***
LOU (5)	0.080	0.063	0.062	–	0.000	0.658***	0.597***
TAM (11)	0.011	0.000	0.005	0.015	–	0.826***	0.682***
CAR (6)	0.882***	0.904***	0.916**	0.961**	0.908***	–	0.679***

TABLE 2 Pairwise ϕ_{ST} estimates between locations for the whole mtDNA genomes (below diagonal) and for the 810 bp mtDNA-CR sequences (above diagonal)

Sample size for each locality is shown in parenthesis for the mtDNA genome (column) and mtDNA-CR (row). Estimates showing significant P values are in bold.

* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$.

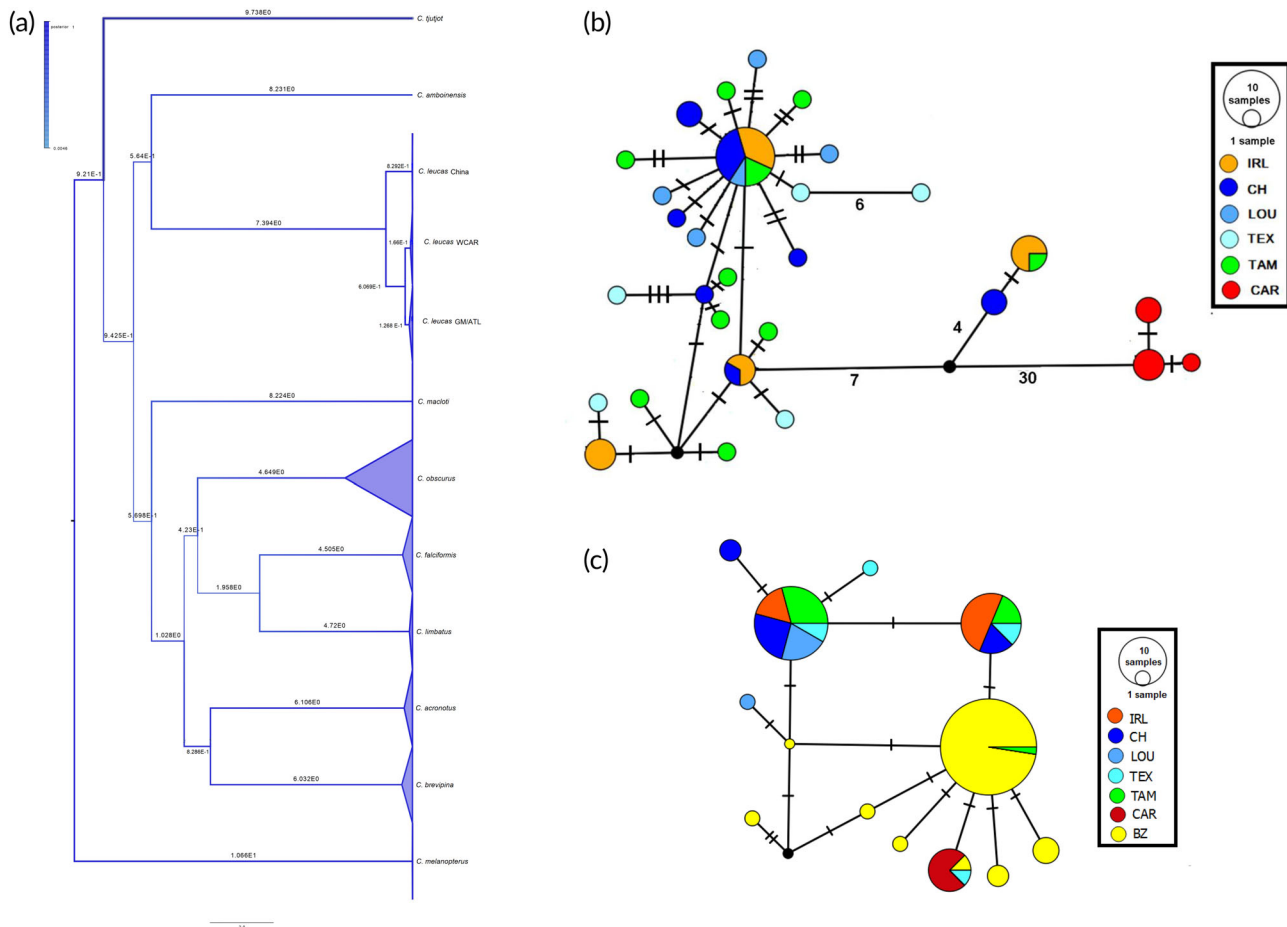


FIGURE 2 (a) Phylogenetic tree based on the mtDNA genome of bull shark *Carcharhinus leucas* against representative Carcharhinid species obtained with BEAST. Numbers in branches are estimates of divergence times in number of substitutions per site per million years. Posterior probabilities according to the Bayesian approximation are represented by the blue colour gradient. GM/ATL, Gulf of Mexico and Atlantic; CAR, Caribbean. Minimum spanning tree using the whole mtDNA genome sequences (b) and using the 810 bp mtDNA-CR fragment (c) Texas (TEX), Louisiana (LOU, Charlotte Harbor (CH), Indian River Lagoon (IRL), Tamiahua (TAM), Caribbean (CAR) and Brazil (BZ). Circle size is according to the haplotype abundance and intermediate lines/numbers in branches are the mutational steps between haplotypes

Ocean, corresponding to North America and South America (Karl *et al.*, 2011), but so far the limits of these possible populations and the genetic connection of these two broad regions with intermediate localities is unknown.

This study focused on immature individuals from the western North Atlantic, Gulf of Mexico and Caribbean Sea. This approach using juveniles aimed to identify the possible genetic signature in the area of origin, avoiding the potential bias from sampling adult

individuals which usually move to other areas. Neonates and juveniles typically remain closer to their natal site (Curtis *et al.*, 2011; Thorburn & Rowland, 2008), and contain the genetic signature of those specific locations.

The haplotypes using the complete mitogenome (16,707–16,708 pb) displayed a homogeneous distribution among areas of the Atlantic, and the northern and southern Gulf of Mexico, concordant with previous conventional tracking studies (Kohler & Turner, 2019). However, the Caribbean Sea had exclusive and highly divergent haplotypes. This is relevant because the tissue samples in this location were collected across multiple years (2013–2018), suggesting temporal stability of the genetic signature in this area, and not due to random events, including the close relationship of individuals.

The level of divergence based on the number of site differences among the most abundant haplotype from the Caribbean Sea and from North America (38 SNPs) is remarkable, and was higher than that reported between mitogenomes of *S. zygaena* Linnaeus 1758 from the East and West Atlantic (13 different SNPs; Guy *et al.*, 2017). Mitogenomes from the western North Atlantic and CAR diverged in 153–156 SNPs, a similar number of differences as compared to the bull shark mitogenome from China (156; Chen *et al.*, 2014), which is concordant with previous reports of differences between the Atlantic and Pacific lineages by Naylor *et al.* (2012) and Pirog *et al.* (2019).

The mitochondrial genome under neutral evolution under the effect of a phylogeographic break accumulates mutations at a constant rate that results in levels of divergence as observed here. As a contrast, the segregation of maternal lineages driven by female philopatry results in differences in haplotype frequencies based on a few nucleotide differences. Sex-biased dispersal usually has an effect on increasing haplotype frequencies of maternal lineages in a particular nursery area as has been reported for the bull shark (Sandoval Laurrabaquio-Alvarado *et al.*, 2019) and other shark species (Chapman *et al.*, 2015).

The high genetic divergence observed between mtDNA lineages may result from a phylogeographic or ecological break limiting gene flow between populations from the Gulf of Mexico and the Caribbean Sea. Similar divergence between the North Atlantic and the Gulf of Mexico compared to Central America has been reported based on mtDNA-CR sequences for the blacktip shark (Keeney *et al.*, 2005), the scalloped hammerhead (Chapman *et al.*, 2009; Pinhal *et al.*, 2020) and the bonnethead (Fields *et al.*, 2016), supporting the existence of limited gene flow between these two regions. Genetic divergence has been also reported for sharks among the waters of North and South America (Bernard *et al.*, 2017; Karl *et al.*, 2011), as we corroborated in this study in the comparisons of all our western North Atlantic and Brazilian mtDNA-CR sequences.

The magnitude of population differentiation reported for shark species in the western Atlantic Ocean seems to be proportional to the distance among localities. As an example, in the blacktip shark, significant differences were estimated between the western North Atlantic, the Gulf of Mexico (southern and northern) and Yucatan (Φ_{SC} estimated varied from 0.089 to 0.317). However, higher genetic differences were found when compared to Belize in the Caribbean Sea,

$\Phi_{SC} > 0.7$, $P < 0.00001$ (Gledhill *et al.*, 2015; Keeney *et al.*, 2005) and between the northern and southern locations in the western Atlantic Ocean, $\Phi_{SC} = 0.8$ (Sodré *et al.*, 2012). Nevertheless, there was no correlation between geographical and genetic distances for either the mtDNA genomes data set ($r^2 = 0.116$, $P > 0.05$) or the mtDNA-CR sequences ($r^2 = 0.371$, $P > 0.05$), supporting the existence of a phylogeographic break separating the Caribbean Sea from the other regions.

Similar levels of genetic differences based on mtDNA-CR sequences were also reported for bull sharks between samples from the US Atlantic and the northern Gulf of Mexico, $\Phi_{ST} = 0.097$ to 0.27 (Sandoval Laurrabaquio-Alvarado *et al.*, 2019) and between locations from the northern and southern western Atlantic, $\Phi_{ST} > 0.8$ (Karl *et al.*, 2011). In the present study, Φ_{ST} estimates coincide largely with these levels of divergence (western North Atlantic vs. Caribbean Sea, $\Phi_{ST} > 0.7$; Central America vs. South America, $\Phi_{ST} = 0.67$).

The haplotype network comparing the Brazilian, North American and Caribbean samples (Figure 2c) is similar to those reported for the blacktip shark and scalloped hammerhead (Gledhill *et al.*, 2015; Pinhal *et al.*, 2020). Within these three mitochondrial lineages of the bull shark in the western Atlantic (north, central and south), some haplotypes are shared among these areas. In all networks the genetic lineages are separated by one or two mutations using the mtDNA-CR. Our results show that a better resolution in the extent of genetic divergence is possible by using the complete mitochondrial genome. Future efforts should include mitogenomes from South America and also increase the number of mitogenomes from Central America.

In the western Atlantic Ocean, several provinces and eco-regions have been documented based on differences in oceanographic features (Robertson & Cramer, 2014; Wilkinson *et al.*, 2009) generating a variety of habitats but also limitations to connectivity between areas for a variety of fish species (Carrillo *et al.*, 2015). The complex dynamics of the Caribbean Current generates three major regions: a northern region dominated by the strong northerly flow of this current, a southern region with weak southward or variable flow of the current, and an intermediate region between these two areas which acts as a boundary between the northern and southern circulation regimes (Carrillo *et al.*, 2015; 2017).

Differences in relevant reproductive characteristics for bull sharks, such as length at first maturity and potential reproductive asynchrony between North America and Central America, have been reported (Jenson, 1976; Castro, 2012), and may result in limited interactions between sharks of both regions representing potential reproductive barriers between populations. Tagging data suggest limited movement of bull sharks from North American waters (Carlson *et al.*, 2010; Kohler & Turner, 2019), similar to other shark species (e.g., scalloped hammerhead, and tiger shark; Rooker *et al.*, 2019).

The highly significant genetic differences between bull shark populations from North and Central America, the reported differences in reproductive parameters for the species among these areas, and the evidence of divergent lineages found for other related shark species among these areas suggests the existence of a divergent lineage of bull sharks in Central America, with a different evolutionary history

from those previously reported for North and South America. By using a mutational rate between 0.8% for scalloped hammerheads (Duncan *et al.*, 2006) and 0.4% for blacktip sharks (Keeney & Heist, 2006) and a generational time of 15 years for bull sharks (Natanson *et al.* 2014), the time for divergence between North and Central America was estimated between 68,000 and 126,700 years. Sea levels in the Caribbean Sea declined during glacial periods below -14.6 m on average that have been dated to occur 86,600 years ago (Moseley *et al.*, 2013). The decrease in sea level might have reduced access to estuaries, which are primary habitats for the species as nurseries creating a gap in the species distribution across the western Atlantic leading to the interruption of the gene flow between the Gulf of Mexico and Caribbean. However, since results in the present study are based on the single use of mitochondrial sequences, additional data would be required to clearly determine whether the divergence signal is driven entirely by philopatry or due to limited dispersion between areas separated by phylogeographic discontinuities.

Limitations to gene flow between populations from the above-mentioned biogeographical provinces requires evidence from nuclear DNA markers to confirm that the geographic break separating the western North Atlantic and the Caribbean plays a paramount role in isolating populations of both areas. In previous studies using microsatellite markers, significant genetic differences were reported between the western North Atlantic and South America, $\Phi_{ST} = 0.009$, $P < 0.05$ (Karl *et al.*, 2011). However, results were based on the use of only five microsatellite loci and reported differences require further confirmation because of the low number of markers used. Additional studies based on genomics would be useful in the definition of the bull shark population genetic structure in the western Atlantic Ocean.

In conclusion, this study provides consistent evidence for the existence of three independent evolutionary bull shark lineages in the entire western Atlantic Ocean: the first comprising the western North Atlantic and Gulf of Mexico, the second in Central America and the third in South America. These results add to previous genetic patterns reporting regional divergence and need to be considered for the implementation of management strategies for species conservation.

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CONTRIBUTIONS

P.D.J., N.S.L.A. and S.H.A. conceived and designed the study. N.S.L.A. and S.H.A. completed the laboratory work and completed writing. P.D.J., D.A. and N.S.L.A. drafted the manuscript with the

support of P.B.P., D.A., J.C.P.J. and L.C.G. P.B.P., D.A. and J.C.P.J. provided tissue samples.

ETHICS STATEMENT

All sharks were sampled by authorized staff under official permits or scientific exemptions of U.S. state government agencies whereas samples from Mexico were obtained from commercial catches.

ORCID

Pindaro Díaz-Jaimes  <https://orcid.org/0000-0002-3230-3538>

Douglas H. Adams  <https://orcid.org/0000-0002-3539-6629>

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Spatial patterns of shark-inflicted injuries on coastal bottlenose dolphins in the Mesoamerican Reef System

D. N. Castelblanco-Martínez ^{a,b,c}, E. A. Ramos ^{b,c,d}, J. J. Kiszka ^e, M. P. Blanco-Parra ^{a,b,c}, J. A. Padilla-Saldívar ^g, J. García ^{b,c} and C. A. Niño-Torres ^f

^aConsejo Nacional De Ciencia Y Tecnología, Ciudad de México, Mexico; ^bDivisión de Ciencias e Ingeniería, Universidad De Quintana Roo, Chetumal, Quintana Roo, Mexico; ^cFundación Internacional Para La Naturaleza Y La Sustentabilidad, Chetumal, Quintana Roo, Mexico; ^dThe Graduate Center, City University of New York, New York, NY, USA; ^eDepartment of Biological Sciences, Coastlines and Oceans Division, Institute of Environment, Florida International University, North Miami, FL, USA; ^fEl Colegio De La Frontera Sur, Chetumal, Quintana Roo, Mexico; ^gHalmos College of Natural Sciences and Oceanography, Nova Southeastern University, Fort Lauderdale, FL, USA

ABSTRACT

Understanding predator–prey relationships is critical in ecology, but relatively challenging when investigating elusive marine megafauna. In this study, we document the presence of shark-inflicted injuries on coastal bottlenose dolphins (*Tursiops truncatus*) in the Mesoamerican Reef System using photo-identification methods. We analyzed data from a total of 533 photo-identified bottlenose dolphins in Mexico (Ascención Bay, Espíritu Santo Bay, and Chetumal Bay), Belize (Turneffe Atoll, Drowned Cayes, Barrier Reef, and Placencia), and Honduras (Utila). We identified 16 individuals with shark-inflicted injury scars consistent with attacks by large sharks of the Family Carcharhinidae. Additionally, two bottlenose dolphins were encountered with round-shaped crater wounds, likely inflicted by a cookiecutter shark (*Isistius* spp.). The prevalence of shark-inflicted wounds in bottlenose dolphins varied markedly between sites, with the highest prevalence in Placencia and Ascención Bay (Mexico), and lowest in Turneffe Atoll and Drowned Cayes (Belize). Further research is required to evaluate how predation risk shapes the ecology of bottlenose dolphins in the Mesoamerican Reef region.

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Introduction

Understanding predation pressure on animal populations is critical in community and behavioral ecology. Predation risk can have a major role in shaping the population dynamics and behavior of animal species (Lima & Dill 1990; Magnhagen 1991; Lima & Bednekoff 1999; Creel et al. 2007). Although considered as high trophic level consumers, most small cetacean species are mesopredators and can experience varying levels of predation pressure from large apex marine predators, particularly killer whales (*Orcinus orca*) and sharks (Heithaus 2001a; Kiszka et al. 2015). Very little is known on the exposure of small cetaceans to predation risk for most coastal cetacean populations, and how predation risk can affect behavior, habitat use patterns, and fitness (Heithaus & Dill 2006; MacLeod et al. 2007; Kiszka et al. 2011). However, various studies have shown that small cetaceans exposed to predators and predation risk (particularly from large sharks and killer whales) include short to long-term responses. Short-term responses include fleeing or changes in group behavior (Connor & Heithaus 1996;

Ford & Ellis 1999), and longer-term responses can include changes in habitat use and grouping tactics (Heithaus & Dill 2002, Kiszka et al. 2011). Assessing relative predation risk is challenging since predation events on small cetaceans can be rare or difficult to observe. Several studies have suggested that predation attempts (e.g. scars and other injuries) could be used to gain insights into predation risk or pressure to a wide range of taxa, including coastal dolphins (Heithaus 2001b; Smith et al. 2018).

The Mesoamerican Reef System (MARS) is the largest continuous reef in the Western Hemisphere (16.48–21.5° N, 85.77–86.8° W). It stretches over 1,000 km from the Bay Islands (Utila, Cayos Cochinos, Roatan, and Guajana) north of Honduras through Guatemala and Belize to the tip of Mexico's Yucatan peninsula (Paris & Chérubin 2008). Many productive ecosystems are part of the MARS including coral reefs, seagrass beds, and mangrove areas, which provide critical habitats for many species and coastal fisheries. At least 19 species of marine mammals have been reported in the Exclusive Economic Zones (EEZ) of the Mexican Caribbean and Belize (Niño-Torres

et al. 2015; Ramos et al. 2016; García-Rivas et al. 2019). Throughout these regions, the bottlenose dolphin (*Tursiops truncatus*) is recognized as the best-studied and most common and abundant species in bays, rivers, and lagoons along the coast, in shallow lagoons of some offshore atolls (Grigg & Markowitz 1997; Campbell et al. 2002; Dick & Hines 2011), and in the deep waters east of the MARS. Despite their abundance, relatively few populations or communities of dolphins have been studied in Belize and far less in the Mexican Caribbean (Niño-Torres et al. 2015; Ramos et al. 2016). Current information on their distribution suggests they overlap extensively in coastal and deep waters with a variety of species of sharks; however, interactions between these species have not been investigated. Shark populations are relatively poorly known in the MARS, but around 40 species including large-bodied predatory species such as bull (*Carcharhinus leucas*) and tiger sharks (*Galeocerdo cuvier*) have been recorded in the region (Pikitch et al. 2005; Bond et al. 2012; Blanco-Parra et al. 2016). Here we investigate the prevalence of sublethal shark attacks on common bottlenose dolphins (*Tursiops truncatus*) in the MARS along the coasts of Mexico, Belize, and Honduras using photo-identification methods.

Methods

Evidence of predator–prey interactions between sharks and bottlenose dolphins was obtained through the image-based detection of scarring patterns and wounds on dolphins. Following Heithaus (2001a), we only considered attempted predation events if the wounds or scarring were found in living animals photographed *in situ*. Images were collected during systematic and opportunistic boat-based photo-identification surveys conducted between 1992 and 2019, primarily for monitoring the distribution, habitat use, health status, and behavior of marine mammals in several locations of the MARS of Mexico (Ascención Bay, Espíritu Santo Bay, and Chetumal Bay), Belize (Turneffe Atoll, Barrier reef, Drowned Cayes, Placencia), and Honduras (Utila; Figure 1).

External diagnostic patterns were used to distinguish the offshore from the coastal ecotype (see Carwardine 2020, for a review). Offshore bottlenose dolphins are described to be longer, heavier, darker, and show a more falcate dorsal fin shape than the coastal ecotype (Simões-Lopes et al. 2019). Additionally, the coastal ecotype uses shallow, coastal waters (<18 m deep, <3 km from the shore), while the offshore ecotype shows a wider distribution and inhabits deep waters far from the coast (>200 km) (Simões-Lopes et al. 2019). For each obtained photograph, we examined

the visible areas of the animals for scarring and/or injuries likely resulting from shark bites, primarily the dorsal surface of the dolphin from its blowhole to caudal peduncle. A shark-related injury was identified by their crescent-shaped wound pattern, consisting of deep and widely spaced teeth rakes (different from those caused by a conspecific, for example) (Heithaus 2001b) or small round or oval scooped-out wounds consistent with injuries caused by cookiecutter sharks (Dwyer & Visser 2011). Injuries or scarring was described in terms of location on the body and healing state. The healing state included three categories: fresh (with a clear differentiation between skin, blubber, and muscle tissues), partially healed (the differentiation between tissues is no longer evident, partially repigmented), and fully healed (completely repigmented). The placement of each wound or scar on the body of the dolphins was recorded according to Smith et al. (2018): the left and right anterior, dorsal fin, mid-flank, anterior peduncle, and posterior peduncle. Two experienced shark experts (MPBP and JK) analyzed the images to confirm that the identified wound was a shark-inflicted injury and to attempt to identify the shark group or species likely to have inflicted the bite.

Results

We analyzed a total of 519 photo-identified individuals of coastal bottlenose dolphins from Ascención Bay ($n = 72$), Espíritu Santo Bay ($n = 19$), Chetumal Bay ($n = 57$), Barrier reef ($n = 12$), Drowned Cayes ($n = 146$), Turneffe Atoll ($n = 180$), Placencia ($n = 7$), and Port of Honduras ($n = 26$). Additionally, we analyzed 14 photo-identified offshore bottlenose dolphins from the east of Turneffe Atoll. We identified 18 bottlenose dolphins with scarring consistent with shark-inflicted injuries (Table 1, Figure 1). Among them, two bottlenose dolphins of the offshore ecotype were encountered with rounded wounds, one completely healed and one fresh (Figure 2). The prevalence of shark bites in bottlenose dolphin communities varied markedly between sites, with the highest rates in Placencia, Belize (14.3%), and Ascención Bay, Mexico (8.3%) (Table 2). The majority of shark injuries were completely healed (88.8%). The wounds were observed on the anterior and posterior peduncle (77.7%), on the anterior region of the body (16.6%), and on the mid-flank (5.6%).

Most of the observed scars (88.8%, $n = 16$) were crescent-shaped and jagged, suggesting that large sharks from the family Carcharhinidae have been involved in attacks. Two large bites on coastal bottlenose dolphins in Ascención Bay (Mexico) were attributed to a tiger shark (Figure 2(a, b)). Also, two offshore

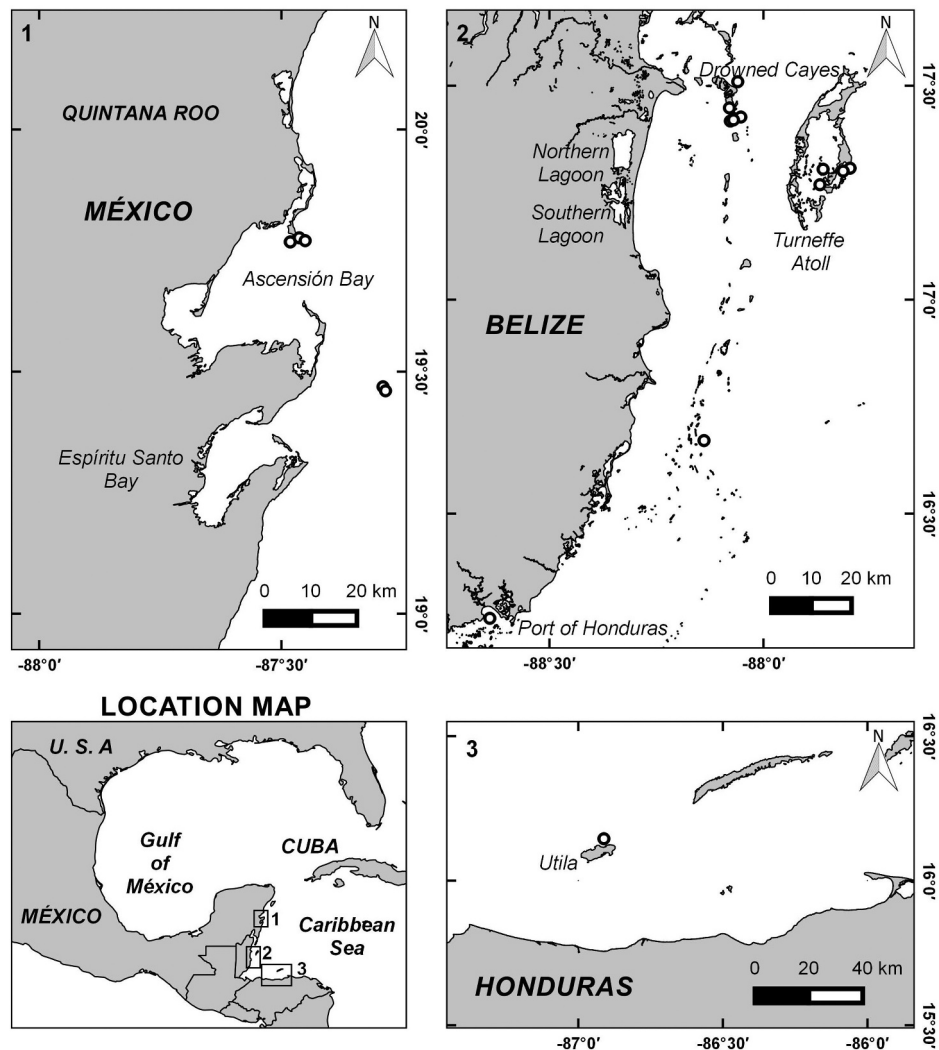


Figure 1. Mesoamerican Reef System and the locations of sightings of bottlenose dolphins with shark-inflicted wounds (open circles), in Mexico (1), Belize (2) and Honduras (3).

bottlenose dolphins exhibited rounded crater wounds, with broken skin and visible muscle tissue characteristics of the bite of cookiecutter sharks (*Isistius* spp.), one dolphin east of Turneffe Atoll, Belize, and a second one of off Utila, Honduras.

Discussion

The analysis of external injuries provides valuable information on the risks of predation to dolphins from sharks in the MARS region. We found differences in the rates of shark-inflicted injuries throughout our study area. For example, Turneffe Atoll (Belize) had the lowest proportion of shark injuries (2.6%) despite having the largest catalog of identified animals ($n = 194$ dolphins) photographed intermittently in studies from 1992 to 2018. In contrast, dolphins in Ascención Bay

(Mexico) had a relatively higher proportion (8.3%) despite research efforts beginning in 2018. These differences could indicate a higher predation risk experienced by bottlenose dolphins in some populations, possibly due to reduced fishing pressure for large sharks or habitat of higher suitability for sharks. However, our data were potentially biased by disparate research efforts in different locations and more research is needed to determine this. Similarly, we were unable to characterize the risk of shark injury to the offshore ecotype of bottlenose dolphins in deep waters due to a lack of information on dolphin populations in these habitats.

The overall prevalence of shark-inflicted injuries was relatively low, although variable across our study area (0–14.3%). The sample size in Placencia (Belize) was too small to be compared to other locations. Overall,

Table 1. Cases of predation attempts of sharks on *Tursiops truncatus* in the Mesoamerican Reef, inferred by scarring pattern. F: Female, M: Male, U: Unknown. Cl: *Carcharhinus leucas*, Gc: *Galeocerdo cuvier*.

Case No.	Date	Location	Country	Ecotype	Depth (m)	Sex	Location of bite	Healing state	Shark species
1	1992-03-30	Turneffe Atoll	Belize	Coastal	< 5	F	Anterior peduncle	Fully healed	Cl or Gc
2	1992-07-10	Turneffe Atoll	Belize	Coastal	< 5	M	Anterior peduncle	Fully healed	Cl or Gc
3	1997-03-11	Drowned Cayes	Belize	Coastal	< 5	U	Anterior peduncle	Fully healed	Cl or Gc
4	1997-10-24	Drowned Cayes	Belize	Coastal	< 5	U	Anterior peduncle	Fully healed	Cl or Gc
5	2005-08-30	Drowned Cayes	Belize	Coastal	< 5	U	Anterior peduncle	Fully healed	Small Carcharhinid
6	2012-02-08	Turneffe Atoll	Belize	Offshore	< 50	U	Anterior L	Fresh	Cookiecuter shark (<i>Isistius</i> spp.)
7	2013-06-27	Port of Honduras	Belize	Coastal	< 5	U	Anterior peduncle	Fully healed	Cl or Gc
8	2016-05-01	Placencia	Belize	Coastal	< 5	U	Anterior peduncle	Fully healed	Cl or Gc
9	2017-07-30	Turneffe Atoll	Belize	Coastal	< 5	U	Anterior R	Fully healed	Cl or Gc
10	2018-07-15	Drowned Cayes	Belize	Coastal	< 5	U	Posterior peduncle	Fully healed	Small Carcharhinid
11	2018-09-18	Ascención Bay	Mexico	Coastal	4.16	U	Anterior peduncle	Fully healed	Gc
12	2018-09-18	Ascención Bay	Mexico	Coastal	4.16	U	Anterior and posterior peduncle	Fully healed	Cl or Gc
13	2018-09-20	Ascención Bay	Mexico	Coastal	4	U	Anterior	Fully healed	Cl or Gc
14	2018-10-09	Ascención Bay	Mexico	Coastal	2.3	F	Anterior peduncle	Fully healed	Undetermined
15	2018-10-12	Ascención Bay	Mexico	Coastal	< 5	U	Anterior peduncle	Fully healed	Gc
16	2018-12-19	Utilia	Honduras	Offshore	U	U	Anterior peduncle R	Fully healed	Cookiecuter shark (<i>Isistius</i> spp.)
17	2019-10-10	Ascención Bay	Mexico	Coastal	3.5	U	Anterior peduncle	Fully healed	Small Carcharhinid

the prevalence of shark bite scars in the MARS region is similar to other areas of the tropical and subtropical Atlantic Ocean, such as the southern Caribbean and the Florida coastal Everglades (e.g. Luksenburg 2014; Sarabia et al. 2018). However, rates observed in Ascención Bay (8.3%, Mexico) are higher than in several other coastal locations of the southern Caribbean (Luksenburg 2014), South Florida (Sarabia et al. 2018), and several locations along the east coast of Africa (Heithaus et al. 2017).

We observed that all the scars inflicted by sharks were located on the body trunk area (anterior peduncle, flank), while no bites were found in tail/peduncle, dorsal fin, and head zones. These findings are similar to previous reports for bottlenose dolphins in several regions (Heithaus 2001b; Luksenburg 2014; Smith et al. 2018). However, the calculated proportions are based on relatively small sample sizes across our sampled site and most photos of dolphins cover the dorsal surface of the animal and rarely the tail or ventrum. Most importantly, they should be considered as minimal estimates because of our inability to collect photographs on all parts of the body and due to the likelihood that old and healed injuries were missed (Heithaus 2001a; Heithaus et al. 2017).

The identification of the shark species based on the wounds inflicted on their prey is difficult but according to their shape and size, some scars can more reliably be assigned to a particular shark species or family (Cockcroft et al. 1989). There are 18 shark species documented as predators of dolphins but only five species are considered regular predators (Heithaus 2001a), from which two species regularly occur in the MARS (Blanco-Parra et al. 2016): tiger (*Galeocerdo cuvier*) and bull sharks (*Carcharhinus leucas*). Bull sharks have seasonal aggregations in the Mexican Caribbean and are considered top predators of the coral reefs consuming large preys including other sharks, mammals, sea turtles, and a variety of cephalopods and teleosts (Roff et al. 2016). Other large shark species such as the reef shark (*Carcharhinus perezii*) and dusky sharks (*C. obscurus*) occur in the MARS but are considered only occasional predators to cetaceans (Heithaus 2001a), mainly feeding on large teleosts (Roff et al. 2016). Most of the observed injuries were crescent-shaped and jagged wounds characteristic of large shark bites (Heithaus 2001b), suggesting that the most frequent cause of attacks was encounters with large sharks of the Family Carcharhinidae.

The shark wounds we identified on dolphins in Belize and Honduras were characteristic of cookiecutter sharks (*Isistius* spp.). These species have been suggested as the cause of crater wounds on large pelagic fishes and cetaceans (Jones 1971). Wounds left by *I. plutodus* have

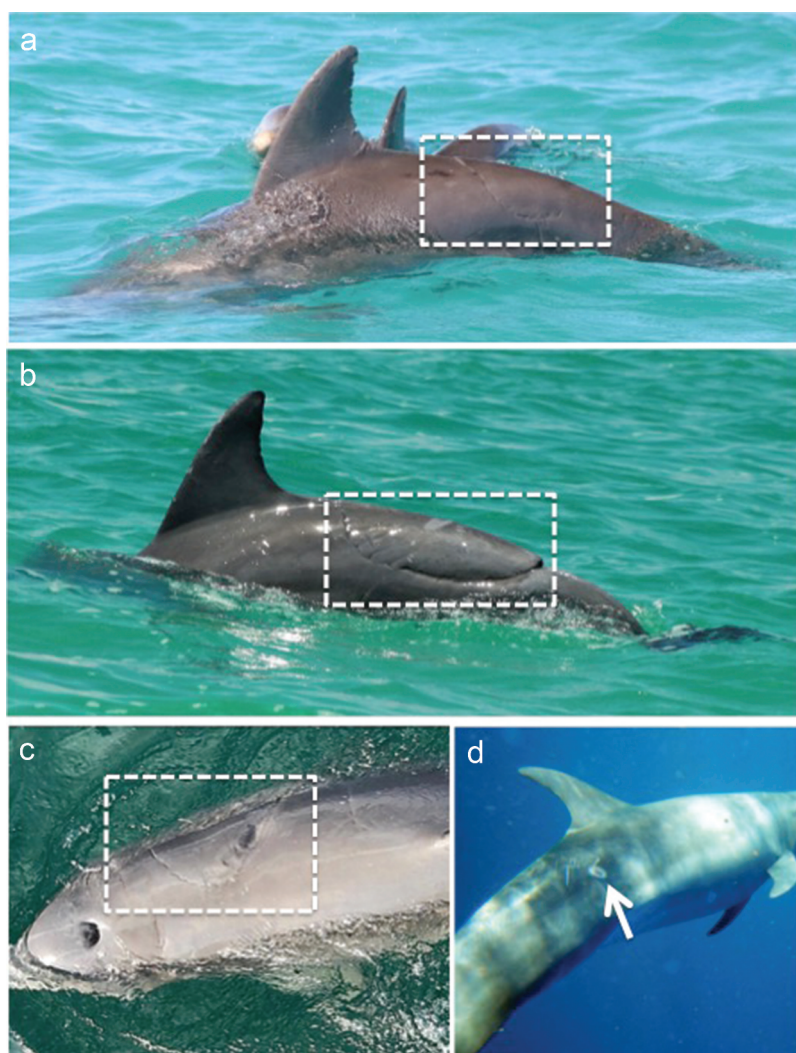


Figure 2. Examples of injuries inflicted by sharks to bottlenose dolphins in the Mesoamerican Reef system: Ascención Bay, Mexico (A and B); Turneffe Atoll, Belize (C); and Utila, Honduras (D). The injuries were likely caused by tiger shark (A and B), a large Carcharhinid (C), and cookiecutter shark *Isistius brasiliensis* (D).

Table 2. Prevalence of shark injuries on bottlenose dolphins *Tursiops truncatus* in different locations throughout the Mesoamerican reef region. All corresponded to coastal ecotype except for the offshore dolphins sighted east of Turneffe Atoll. The case from Utila was not included since photo-identification data of this region are not available.

Study period	Country	Location	No. dolphins identified	No. dolphins with wounds	Prevalence of wounds
2018–2019	Mexico	Ascención Bay	72	6	8.3%
2018–2019	Mexico	Espíritu Santo Bay	19	0	0.0%
2012–2019	Mexico	Chetumal Bay	57	0	0.0%
2014–2018	Belize	Barrier reef	12	0	0.0%
1997–1999 2005–2018	Belize	Drowned Cayes	146	4	2.7%
1992–1996; 2001–2002; 2005–2018	Belize	Turneffe Atoll	194	5	2.6%
2016	Belize	Placencia	7	1	14.3%
2013	Belize	Port of Honduras	26	1	3.8%
			533	17	3.2%

been described as oval and elongated in shape and those inflicted by *I. brasiliensis* as round-shaped and leaving a crater wound (Compagno 1984; Pérez-Zayas et al. 2002). The cookiecutter shark (*I. brasiliensis*) is the most common squaloid shark reported to inflict crater

rounded wounds on cetaceans (Jones 1971; Reddcliff 1988), but in the Caribbean, there are only reports of wounds caused by the largetooth cookiecutter shark (*I. plutodus*) in cetaceans (Pérez-Zayas et al. 2002). Based on the rounded shape of the wounds observed

in this study, these wounds could have been inflicted by *I. brasiliensis* or a small *I. plutodus*. These wounds were found on an offshore bottlenose dolphin in the deep waters of Belize and another in the deep waters off Utila, Honduras.

The influence of predation risk and pressure on small cetaceans in the MARS region is still poorly understood. The decline of large sharks in most coastal ecosystems particularly in coral reefs in the Caribbean region (Stallings 2009; Ward-Paige et al. 2010) might have reduced their impact on coastal dolphins (Roff et al. 2016) which could potentially include their habitat use patterns and survival. Future studies should invest in an understanding of the overlap of dolphin and shark distributions through a systematic study of both groups.

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ORCID

D. N. Castelblanco-Martínez  <http://orcid.org/0000-0003-3229-8406>

E. A. Ramos  <http://orcid.org/0000-0003-4803-3170>

J. J. Kiszka  <http://orcid.org/0000-0003-1095-8979>

M. P. Blanco-Parra  <http://orcid.org/0000-0003-2492-2168>

J. A. Padilla-Saldívar  <http://orcid.org/0000-0001-8966-453X>

J. García  <http://orcid.org/0000-0002-3626-4302>

C. A. Niño-Torres  <http://orcid.org/0000-0002-3626-4302>

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VI. Tiburones y rayas

Autores

SUSANA PERERA-VALDERRAMA, MARÍA DEL PILAR BLANCO-PARRA,
FRIDA LARA-LIZARDI, SERGIO CERDEIRA-ESTRADA,
RAÚL MARTELL-DUBOIS, LAURA OLIVIA ROSIQUE-DE LA CRUZ,
HANSEL CABALLERO-ARAGÓN, JORGE CHRISTIAN ALVA-BASURTO,
VANESSA FRANCISCO-RAMOS, RAINER RESSL

Colaboradores

DORKA COBIÁN ROJAS, MARÍA DEL CARMEN GARCÍA-RIVAS,
EDGAR MAURICIO HOYOS-PADILLA, DR. JAMES KETCHUM

Los tiburones y las rayas tienen un papel esencial como depredadores tope, en los ecosistemas marinos que habitan, y ocupan los últimos eslabones de la cadena trófica (Heithaus *et al.*, 2008); desempeñan funciones de control sobre poblaciones de numerosas especies marinas (Myers *et al.*, 2007), con lo que contribuyen a mantener el equilibrio con sus competidores, garantizando así la diversidad de especies (Myers y Worm, 2005). Su presencia mantiene el equilibrio de las cadenas tróficas en los principales ecosistemas que habitan (Terborgh y Estes, 2010); por ejemplo, su eliminación en el arrecife desencadenaría el conocido efecto en cascada, pues dispararía la proliferación de sus competidores carnívoros, lo cual incidiría negativamente en las poblaciones de herbívoros (Brunnschweiler, 2010). La ausencia de herbívoros, a su vez, conduciría a una proliferación de algas que compiten por el espacio con los corales. Esto podría contribuir a un cambio de fase en el ecosistema hacia un estado dominado por algas (Dulvy *et al.*, 2004).

La pesca de tiburones en México es una actividad importante desde el punto de vista económico y social: más de 90% de la producción es destinada al consumo nacional (DOF, 2007). Los tiburones, sin embargo, son un recurso pesquero vulne-

rable y susceptible a la sobrepesca, con un bajo potencial reproductivo, un reducido número de crías, largos periodos de gestación, crecimiento lento y una madurez sexual tardía (Castro, 1993). Por estos motivos, en México, numerosas especies han visto sus poblaciones disminuidas significativamente. A la vez, estas especies son utilizadas como atractivo turístico en varias zonas costeras de México, y su presencia ha sido motivo de creación de ANP en diferentes regiones del país (Hoyos *et al.*, 2014).

En el Caribe mexicano, los tiburones ocupan el cuarto lugar en la producción pesquera (Blanco-Parra *et al.*, 2016). En el estado de Quintana Roo, en 2013, los elasmobranquios representaron 6.5% de la captura total del estado en peso desembarcado (Blanco-Parra *et al.*, 2016). Los tiburones toro (*Carcharhinus leucas*), tigre (*Galeocerdo Cuvier*) y martillo (*Sphyrna mokarran*) son tres de las siete especies más capturadas en el Caribe mexicano (Blanco-Parra *et al.*, 2016).

El conocimiento de los patrones de movimiento de los tiburones en el Caribe mexicano permanece incompleto debido a que la gran mayoría de las especies son difíciles de estudiar en su medio (Hoyos *et al.*, 2014). Aún se desconocen varios aspectos biológicos, el uso de hábitat y ecología trófica de estas especies.

El conocimiento de los factores biológicos, geográficos y ambientales responsables de los patrones de distribución, la diversidad y el uso del hábitat de los tiburones puede ayudar a informar a los tomadores de decisiones acerca de las estrategias de manejo ((Barker y Schluessel, 2005). En este sentido, es necesario mantener acciones de monitoreo efectivas para estas especies, tanto en su hábitat natural como en sus áreas de reproducción y crianza, que constituyen hábitats críticos para mantener la continuidad del reclutamiento (Heupel *et al.*, 2007).

6.1 INDICADORES BIOLÓGICOS PARA EL MONITOREO DE TIBURONES Y RAYAS Y SUS PROTOCOLOS

6.1.1 Indicador IB1-OC5. Diversidad de especies

En la actualidad, los elasmobranquios (tiburones y rayas) son uno de los grupos de animales marinos más amenazados a nivel mundial (Lucifora *et al.*, 2011). Por esta razón, resulta de vital importancia el conocimiento adecuado de su diversidad (Camhi *et al.*, 2007). El diseño de estrategias de conservación para tiburones y rayas depende del conocimiento básico de la distribución y diversidad de las especies (Barker y Schluessel, 2005). Además, evaluar las poblaciones de tiburones y rayas nos ayuda a determinar qué sitios presentan una mayor complejidad ecológica (Heithaus *et al.*, 2008). Áreas con una riqueza moderada de especies de elasmobranquios han mostrado tener una alta riqueza funcional, lo cual indica que hay especies que tienen funciones únicas dentro de los ecosistemas y, por tanto, tienen una baja redundancia funcional (ecológica) (Hussey *et al.*, 2015). De esta forma, la presencia de varias especies que cumplen un mismo rol ecológico pueden ser indicadoras de una mayor resiliencia del ecosistema (Palumbi *et al.*, 2009).

6.1.2 Indicador IB2-OC5. Abundancia relativa por especie

La abundancia poblacional es un indicador básico para el manejo de un recurso. En el estudio de tiburones y rayas se han desarrollado técnicas que calculan la abundancia relativa por especie, la cual representa la probabilidad de observación e indica su importancia como regulador del ecosistema (Santana-Garcon *et al.*, 2014). La abundancia relativa se calcula a partir de la relación que hay entre el número de individuos observados de una especie y un referente en tiempo, área, arte de pesca o esfuerzo pesquero (Brooks *et al.*, 2011) y es calculada con el fin de conocer el estado de las poblacio-

nes de tiburones y rayas en una región determinada (Bond *et al.*, 2012). El número de individuos de una población es un indicador del estado de salud de esta y representa un indicador del estado de los ecosistemas debido a las interacciones tróficas que se presentan (Kacev *et al.*, 2017). Cuando disminuye el tamaño de una población de tiburones y rayas esto implica un efecto cascada en la cadena trófica y, por tanto, un cambio en la estructura de los ecosistemas con implicaciones para la conservación de la biodiversidad de estos (Myers *et al.*, 2007). Estudios en rayas han demostrado que después de una explotación prolongada, se evidencian cambios en la abundancia y en la composición de especies, favoreciendo la desaparición de especies de tallas grandes y el aumento en la abundancia de especies pequeñas (Dulvy *et al.*, 2000).

6.1.3 Indicador IB3-OC5.

Proporción de sexos y madurez sexual

En la historia de vida de los tiburones y las rayas, estas características determinan la resiliencia de sus poblaciones ante las amenazas antropogénicas y sirven como indicadores del riesgo que tienen las especies a la extinción o a la disminución drástica de sus poblaciones (Carrier *et al.*, 2012). La proporción de sexos permite conocer la capacidad de incremento de su población o potencial reproductivo (Smith *et al.*, 1998). Una proporción 1:1 entre machos y hembras adultas en determinado sitio puede indicar que se trata de una zona de apareamiento o un área de crianza (Salomón-Aguilar *et al.*, 2009). Además, es importante conocer si existe segregación por sexo, puesto que se ha comprobado que machos y hembras pueden presentar una función trófica distinta en cada ecosistema (Mucientes *et al.*, 2009). Junto con la proporción de sexos, la madurez sexual ayuda a conocer el potencial reproductivo de las especies (Stehmann, 2002); brinda información sobre potenciales áreas de crianza y zonas de reproducción (Heupel *et al.*, 2007);

es un índice básico para manejar las poblaciones de tiburones y rayas en áreas prioritarias o vulnerables, y permite generar modelos poblacionales, que permitan predecir el futuro de las especies (Stehmann, 2002).

6.1.4 Indicador IB4-OC5.

Estructura de tallas de la población

La composición de tallas de una población es de vital importancia para predecir el efecto de actividades antropogénicas en estos organismos, fundamentalmente la sobrepesca (Stevens *et al.*, 2000). Los tiburones y las rayas se caracterizan por tener un crecimiento lento, por lo que la pérdida de organismos de tallas grandes implica un riesgo elevado para la población (Kacev *et al.*, 2017). La estructura de tallas permite conocer las características estructurales de la población, en cuanto a grupos de edades, identificar zonas de distribución de neonatos, juveniles y adultos, e identificar zonas de crianza que requieren una protección especial (Cailliet *et al.*, 2006).

6.1.5 Indicador IB5-OC5.

Composición específica de la dieta

Los elasmobranquios son frecuentes depredadores tope de los ecosistemas en que habitan (Myers *et al.*, 2007). La posición de los tiburones en la parte superior de muchas redes alimentarias marinas juega un papel importante en la regulación (Baum y Worm, 2009). La información sobre la composición de sus dietas es esencial para entender las relaciones tróficas y los flujos de energía dentro de los ecosistemas (Wetherbee *et al.*, 2004). Asimismo, esta información sirve para entender la historia natural, la función en el ecosistema marino y el impacto en la depredación de una especie en particular (Kacev *et al.*, 2017). Un nicho trófico más amplio sugiere que la especie tiene la capacidad de buscar sus alimentos en un espacio geográfico más amplio y de fuentes distintas; por el contrario, un nicho trófico más restringido indica que la especie es más vulnerable (Sunday *et al.*, 2015).

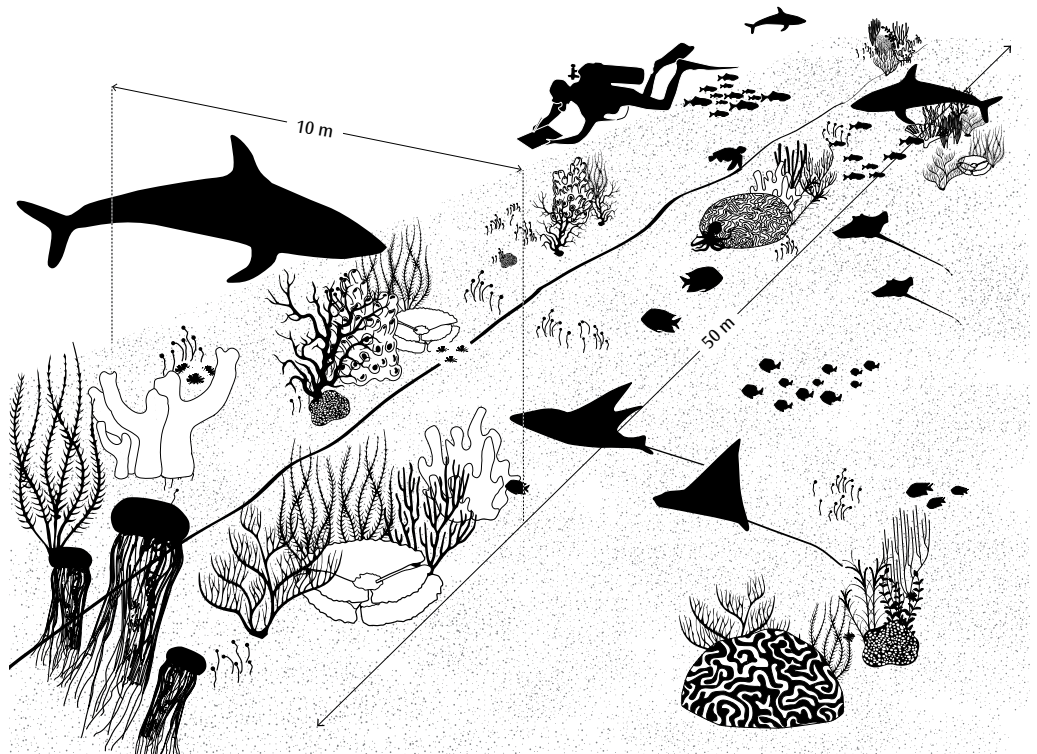


Figura 61. Transectos en banda de 50 metros para el monitoreo de tiburones.

6.1.6 Protocolos para la medición de los indicadores del IB1-OC5 al IB5-OC5

6.1.6.1 Monitoreo de recorrido (submarino y aéreo)

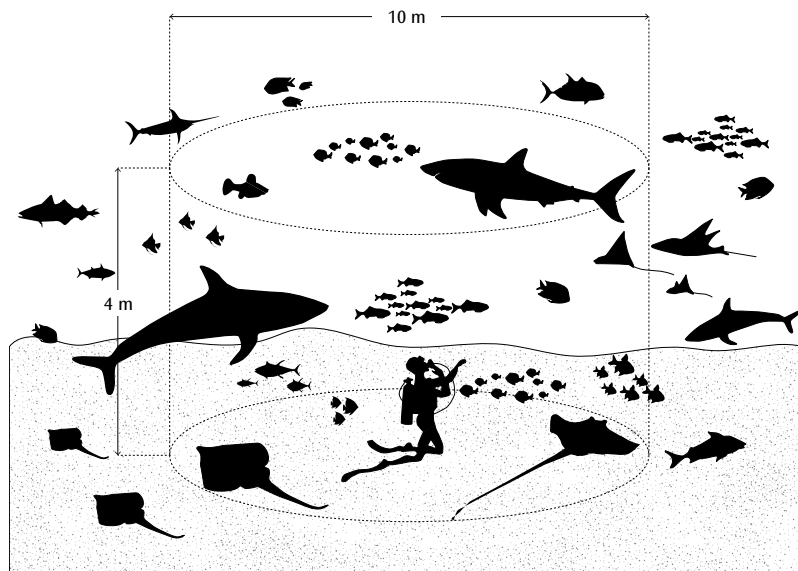


Figura 62. Censos de barrido para el monitoreo de tiburones.

1. Realizar, al menos, una vez al año en cada sitio. Utilizar cuatro observadores con equipo de buceo autónomo.
2. Realizar seis transectos en banda de 50 m de largo en línea recta por 10 m de ancho (figura 61).
3. Realizar además dos censos en punto fijo (figura 62), los cuales consisten en registrar todos los tiburones y las rayas que están presentes dentro de un cilindro de 10 m de diámetro y 4 m de altura, durante un tiempo determinado, que puede variar entre 40 y 60 minutos y que se debe determinar por el investigador principal. De esa forma se estimará la diversidad, abundancia y densidad de tiburones para cada sitio.
4. Si se puede realizar el censo aéreo, utilizar un vehículo no tripulado o dron en transectos de 15 minutos en la misma

Cuadro 16. Planilla de registro de datos de tiburones y rayas.
Censos submarinos

INFORMACIÓN DEL OBSERVADOR	
Nombre: _____	E-mail (opcional): _____
País: _____	Institución / Organización (opcional): _____

INFORMACIÓN DEL SITIO OBSERVADO	
Fecha (dd/mm/aa): ____/____/____	Nombre del sitio: _____
Coordenadas GPS: (Inicio) Latitud (N/+): _____	Longitud (W/-): _____
(Fin) Latitud (N/+): _____	Longitud (W/-): _____
Profundidad (m ___ / ft ___): _____	Prof. medida con: Computador buceo ___ Sonar ___ Cuerda ___ Visual ___
Visibilidad / transparencia - Vertical (m ___ / ft ___): _____	Método de medición: Disco Secchi ___ Visual ___
Región marina: Gran Caribe: ___ Pacífico Nororiental tropical: ___	
País: _____	Estado / Provincia: _____
Población cercana: _____	Área natural protegida (ANP): Si ___ No ___
Nombre del ANP: _____	
Temperatura del agua (°C ___ / °F ___): _____	Temperatura del agua medida en: Superficie ___ Fondo ___
Temperatura del agua medida con: Computadora de buceo ___	Termómetro ___
Tipo de fondo: Arrecife ___ Pastos marinos ___ Algas ___ Arena ___	
Fuerza de la corriente: Fuerte ___ Media ___ Regular ___	

Especie	Sexo	Madurez	Talla estimada	Posición respecto al observador	Distancia respecto al observador	Número foto

área donde se realicen los censos submarinos. Con una ruta definida será posible determinar la abundancia y densidad de tiburones en cada sitio.

5. En cada recorrido anotar la siguiente información (cuadro 16):

- Fecha del recorrido.
- Hora del recorrido.
- Coordenadas iniciales del sitio de monitoreo.
- Temperatura superficial del mar.
- Fuerza de corriente.
- Visibilidad estimada en metros.
- Tiempo de vuelo y distancia recorrida (para recorrido aéreo).

6. Registrar para cada individuo (tiburones y rayas) (cuadro 16):

- Especie. Debe contar con una guía de campo para la identificación de las especies. Se deberán tomar fotografías

para apoyar la identificación.

- Sexo. De acuerdo con la presencia de gonopterigios en machos (figura 63).
- Madurez. De acuerdo con la talla y marcas de reproducción.
- Talla estimada. La talla furcal, es decir, del morro a la base de la aleta caudal. Se utilizarán dos láser para calcular la talla mediante fotometría.
- Posición y distancia del individuo con respecto al observador.
- Fotografía del individuo.

6.1.6.2 Monitoreo mediante análisis de capturas

Este monitoreo se puede realizar de dos maneras: acompañando cuando sea posible a los pescadores en las jornadas de pesca o en los sitios de desembarco de las pesquerías costeras.

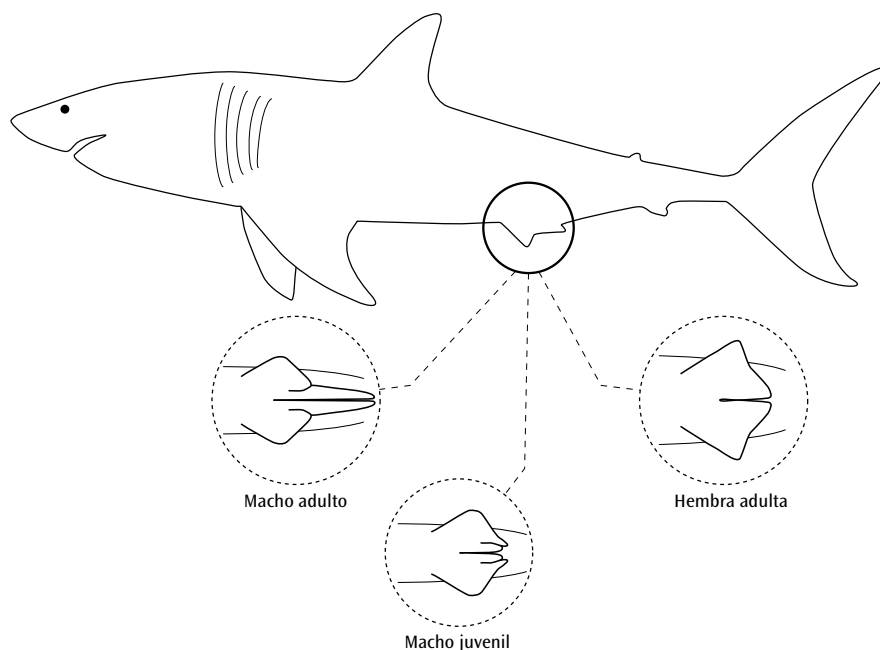


Figura 63. Dimorfismo sexual en tiburones y rayas.

Cuadro 17. Planilla de registro de datos de tiburones y rayas. Capturas por pescadores

INFORMACIÓN DEL OBSERVADOR
 Nombre: _____ E-mail (opcional): _____
 País: _____ Institución / Organización (opcional): _____

INFORMACIÓN DEL SITIO OBSERVADO
 Fecha (dd/mm/aa): ___/___/___ Nombre del sitio: _____
 Coordenadas GPS: (Inicio) Latitud (N/+): _____ Longitud (W/-): _____
 (Fin) Latitud (N/+): _____ Longitud (W/-): _____
 Profundidad (m ___ / ft ___): _____ Profundidad medida con: Computador buceo ___ Sonar ___ Cuerda ___ Visual ___
 Visibilidad / transparencia - Vertical (m ___ / ft ___): _____ Método de medición: Disco Secchi ___ Visual ___
 Región marina: Gran Caribe: ___ Pacífico Nororiental tropical: ___
 País: _____ Estado / Provincia: _____
 Población cercana: _____ Área natural protegida (ANP): Sí ___ No ___
 Nombre del ANP: _____
 Temperatura del agua (°C ___ / °F ___): _____ Temperatura del agua medida en: Superficie ___ Fondo ___
 Temperatura del agua medida con: Computadora de buceo ___ Termómetro ___
 Tipo de fondo: Arrecife ___ Pastos marinos ___ Algas ___ Arena ___
 Volumen de captura: ___ Esfuerzo de pesca: ___

Especie	Sexo	Peso	Tiburones				Rayas			Posición resp. obs.	Distancia resp. obs.	Núm. foto	Long. clasper	Estado clasper	Ovoc. fec.	Tam. ovoc. >	Núm. embr.	Sex. embr.
			L	L	L	L	L	A	L									
			T	F	P	I	D	D	T									

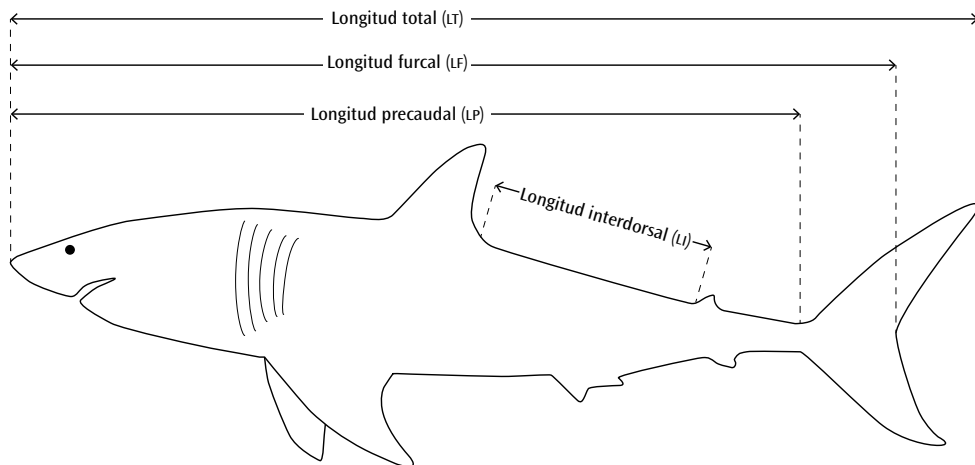


Figura 64. Mediciones morfológicas a tiburones. Longitud total (LT), longitud furcal (LF), longitud precaudal (LP), longitud interdorsal (LI).

1. De cada viaje de pesca anotar (**cuadro 17**):

- Volumen de captura (kg).
- Fauna acompañante de la captura
- Esfuerzo de pesca (tamaño del arte, número de anzuelos, tiempo de calado).

2. Durante el levante del arte (palangre o red de enmalle) o en los desembarcos, registrar para cada individuo (tiburones y rayas) (**cuadro 17**):

- Fecha de la captura.
- Hora de la captura.
- Especie.
- Fotografía de la especie.
- Peso.
- Morfometría (tiburones) (**figura 64**).
 - Longitud total (LT).
 - Longitud furcal (LF).
 - Longitud precaudal (LP).
 - Longitud interdorsal (LI).
- Morfometría (rayas) (**figura 65**).
 - Longitud del disco (LD).
 - Ancho del disco (AD).
 - Longitud total (LT) en el caso de especies con pedúnculo caudal.
- Peso.
- Sexo (**figura 63**).
- Longitud del clasper (para machos) desde el punto de inserción en la aleta o cloaca hasta la punta (**figura 66**).
- Grado de calcificación del clasper (para machos).

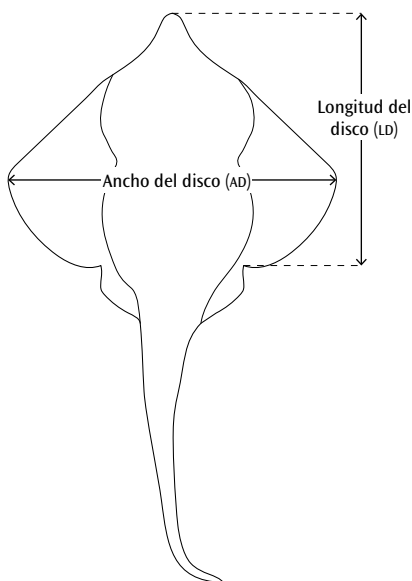


Figura 65. Mediciones morfológicas a rayas. longitud del disco (LD), ancho del disco (AD).

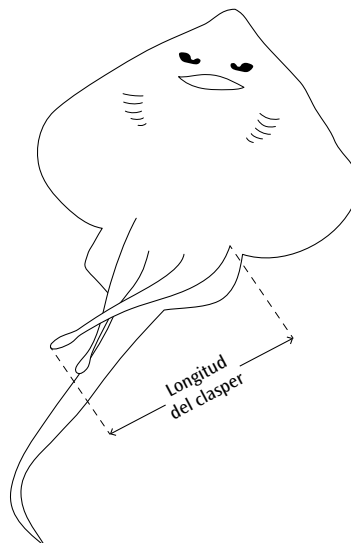


Figura 66. Longitud del clasper.

Figura 67. Presencia de ovocitos maduros en los tiburones y rayas capturados (para hembras). FOTO: ALEXEI RUIZ ABIERNO



Figura 68. Presencia de embriones en hembras de tiburones capturados. FOTOS: ALEXEI RUIZ ABIERNO

- Presencia de ovocitos fecundados (para hembras) (figura 67).
- Tamaño de ovocito más grande (para hembras).
- Número de embriones (para hembras) (figura 68).
- Sexo de los embriones (para hembras)
- Tamaño de los embriones y del saco vitelino si esta presente.

6.1.6.3 Monitoreo utilizando dispositivos remotos de video con carnada (BRUVS)

Con el fin de evaluar la presencia de los tiburones en diferentes ambientes, se utilizarán dos tipos de dispositivos: 1) bentónicos y 2) pelágicos a la deriva.

Los BRUVS bentónicos se ubicarán en sitios de monitoreo que incluyan diferen-

tes hábitats, desde lagunas arrecifales hasta pendientes arrecifales. Se pueden colocar sobre el fondo marino o a un metro de este. Consisten en una estructura que sirve de base para el sistema de grabación de video (por lo general, cámara GoPro), una pesa de plomo, un contenedor con carnada para atraer a las especies de peces, tiburones y rayas (ej. tiburón toro, gata, gris de arrecife, raya blanca, etc.) y un sistema de líneas y boyas que mantiene el dispositivo a la vista desde la superficie (Shortis *et al.*, 2007; figura 69).

Los BRUVS pelágicos (en inglés, mid-water BRUVS), a diferencia de los BRUVS bentónicos, se colocan en la columna de agua y se desplazan en dirección de la corriente (figura 70). Consisten en sistemas de esta-



Figura 69. Dispositivos remotos (BRUVs) bentónicos: a) dispositivo, b) colocación de un dispositivo desde la embarcación y c) imágenes obtenidas del dispositivo colocado en el fondo de un arrecife. FOTOS: DORKA COBIÁN ROJAS/PNG

bilización, flotación, grabación de video y un contenedor de carnada. La estabilización es proporcionada por las boyas superficiales, unidas mediante una línea madre y pesos en el extremo de la base, los cuales mantienen estables los equipos a una profundidad de 10 m, dependiendo de la velocidad de la corriente. De una a tres boyas mantienen las plataformas a flote, y están conectadas a la base. El sistema de video consiste en una cámara de video GoPro con dos láser paralelos a una distancia de 50 cm, para la obtención de tallas en un posterior análisis (figura 70). Este tipo de BRUVs permite evaluar ambientes completamente pelágicos y registrar especies como el tiburón zorro, tiburón piloto, marlín rayado, pez vela.

- Temperatura.
- Hábitat.
- Profundidad.
- Fuerza de corriente.
- Visibilidad.
- Oxígeno disuelto.
- Salinidad.
- Durante el análisis de los videos que se hace cuadro a cuadro, anotar (cuadro 18):
 - Número de individuos por especie.

A partir de los videos obtenidos se calcula la abundancia máxima relativa, dada por el número máximo de individuos de cada especie que aparecen juntos al mismo tiempo en una toma (o cuadro; MaxN).

Una vez obtenida la abundancia relativa (MaxN) en cada video, es posible realizar una estimación de la diversidad de especies, considerando el número total de tiburones y rayas por especie y total, registrados en cada sitio.

- Durante la ubicación de los dispositivos, anotar (cuadro 18):

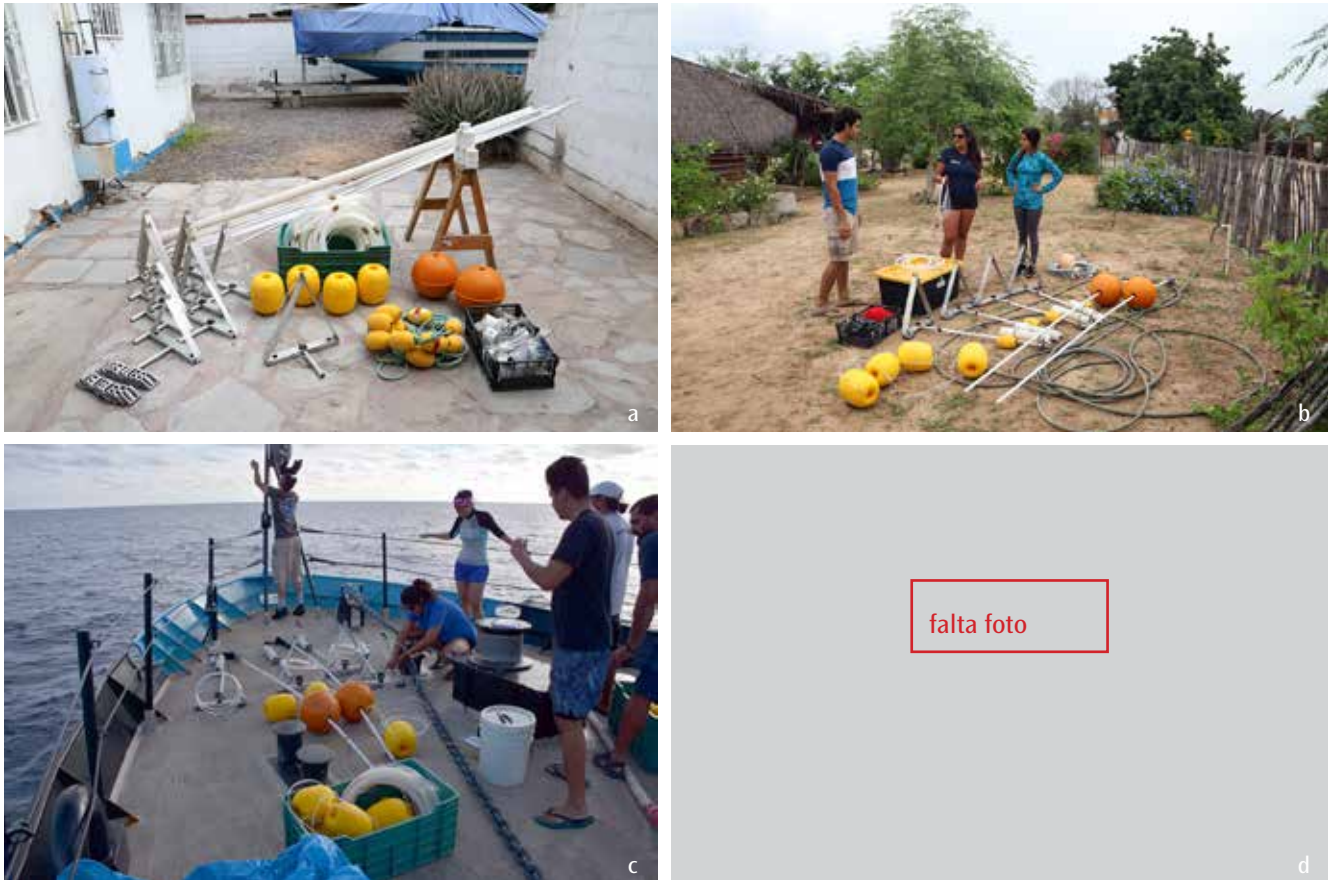


Figura 70. Dispositivos remotos (BRUVS) pelágicos a) Materiales necesarios para armar el dispositivo; b) dispositivo armado, c) dispositivo listo para ser colocado desde la embarcación y d) tipo de resultado en video. FOTOS: MIGUEL GRAU

Con base en los individuos en los que es posible determinar el sexo, se calculará una proporción entre machos y hembras.

De acuerdo con la talla, las marcas de apareamiento y la presencia de gonoptergios desarrollados (en el caso de los machos), será posible establecer la proporción de individuos adultos y juveniles para cada sitio.

Utilizando los datos de los censos submarinos y las estimaciones mediante BRUVS, será posible realizar una estimación general de la estructura de tallas de la población.

****La robustez** de los indicadores dependerá de cuántos individuos son registrados para cada especie y cuántos pudieron ser medidos de manera precisa.

6.1.6.4 Monitoreo ciudadano (guías de buceo o pescadores)

1. Para realizar este monitoreo se solicita a guías de buceo o pescadores con experiencia en el área de estudio que, en caso de avistar individuos de tiburones o rayas durante su salida de buceo o de pesca, reporten la siguiente información (**cuadro 19**):
 - Fecha del avistamiento o de la captura.
 - Hora del avistamiento o de la captura.
 - Nombre del sitio de avistamiento.
 - Coordenadas del sitio de captura.
 - Especie.
 - Número de individuos.
 - Fotografía de la especie.
 - Morfometría.
 - Longitud total (LT).

Cuadro 18. Planilla de registro de datos de tiburones y rayas. BRUVS

INFORMACIÓN DEL OBSERVADOR
 Nombre: _____ E-mail (opcional): _____
 País: _____ Institución / Organización (opcional): _____

INFORMACIÓN DEL SITIO OBSERVADO
 Fecha (dd/mm/aa): ___/___/___ Nombre del sitio: _____
 Coordenadas GPS: (Inicio) Latitud (N/+): _____ Longitud (W/-): _____
 (Fin) Latitud (N/+): _____ Longitud (W/-): _____
 Hora lance: _____ Hora recogida: _____
 Profundidad (m ___ / ft ___): _____ Profundidad medida con: Computador buceo ___ Sonar ___ Cuerda ___ Visual ___
 Visibilidad / transparencia - Vertical (m ___ / ft ___): _____ Método de medición: Disco Secchi ___ Visual ___
 Región marina: Gran Caribe: ___ Pacífico Nororiental tropical: ___
 País: _____ Estado / Provincia: _____
 Población cercana: _____ Área natural protegida (ANP): Sí ___ No ___
 Nombre del ANP: _____
 Temperatura del agua (°C ___ / °F ___): _____ Temperatura del agua medida en: Superficie ___ Fondo ___
 Temperatura del agua medida con: Computadora de buceo ___ Termómetro ___
 Tipo de fondo: Arrecife ___ Pastos marinos ___ Algas ___ Arena ___
 Fuerza corriente: _____ Oxígeno disuelto: _____ Salinidad: _____

<i>Especie</i>	<i>Número de individuos</i>	<i>Minuto del video</i>

6.2 MATERIALES Y EQUIPO NECESARIOS

- Equipo de buceo libre o autónomo
- Cinta métrica
- Tabla de anotar
- Pesas de plomo (2 libras cada una)
- Línea cúbica de plástico tipo palangre
- Cabos para los BRUVS
- Tubos de PVC
- GPS
- Sonda de conductividad, temperatura y profundidad (CTD)
- Boyas
- Anzuelos
- Cámaras (GoPro)
- Armazón de acero inoxidable para cámaras remotas
- Carnada (*Sardina Sardinops sagax*)
- Cemento

**Cuadro 19. Planilla de registro de datos de tiburones y rayas.
Monitoreo ciudadano (buzos)**

INFORMACIÓN DEL OBSERVADOR	
Nombre: _____	E-mail (opcional): _____
País: _____	Institución / Organización (opcional): _____

INFORMACIÓN DEL SITIO OBSERVADO	
Fecha (dd/mm/aa): ____/____/____	Nombre del sitio: _____
Coordenadas GPS: (Inicio) Latitud (N/+): _____	Longitud (W/-): _____
(Fin) Latitud (N/+): _____	Longitud (W/-): _____
Profundidad (m __ / ft __): _____	Profundidad medida con: Computador buceo __ Sonar __ Cuerda __ Visual __
Visibilidad / transparencia - Vertical (m __ / ft __): _____	Método de medición: Disco Secchi __ Visual __
Región marina: Gran Caribe: __ Pacífico Nororiental tropical: __	
País: _____	Estado / Provincia: _____
Población cercana: _____	Área natural protegida (ANP): Si __ No __
Nombre del ANP: _____	
Temperatura del agua (°C __ / °F __): _____	Temperatura del agua medida en: Superficie __ Fondo __
Temperatura del agua medida con: Computadora de buceo __ Termómetro __	
Tipo de fondo: Arrecife __ Pastos marinos __ Algas __ Arena __	

<i>Especie</i>	<i>Longitud total estimada</i>

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Autores

Álvarez-Filip, Lorenzo

Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos

Blanco-Parra, María del Pilar

Universidad de Quintana Roo

Caballero-Aragón, Hansel

Comisión Nacional para el Conocimiento y Uso de la Biodiversidad

Cerdeira-Estrada, Sergio

Comisión Nacional para el Conocimiento y Uso de la Biodiversidad

Christian Alva-Basurto, Jorge

Programa de las Naciones Unidas para el Desarrollo – Comisión Nacional de Áreas Naturales Protegidas

Francisco-Ramos, Vanessa

Programa de las Naciones Unidas para el Desarrollo – Comisión Nacional de Áreas Naturales Protegidas

Herrera-Pavón, Roberto

El Colegio de la Frontera Sur

Herrera-Silveira, Jorge

Centro de Investigación y de Estudios Avanzados

Lara-Lizardi, Frida

Pelagios Kajunjá

Martell-Dubois, Raúl

Comisión Nacional para el Conocimiento y Uso de la Biodiversidad

Perera-Valderrama, Susana

Comisión Nacional para el Conocimiento y Uso de la Biodiversidad

Ressl, Rainer

Comisión Nacional para el Conocimiento y Uso de la Biodiversidad

Reyes-Bonilla, Héctor

Universidad Autónoma de Baja California Sur, La Paz

Rodríguez-Zúñiga, María Teresa

Comisión Nacional para el Conocimiento y Uso de la Biodiversidad

Rosique-de la Cruz, Laura Olivia

Comisión Nacional para el Conocimiento y Uso de la Biodiversidad

Santamaría-del Ángel, Eduardo

Universidad Autónoma de Baja California, Ensenada

van Tussenbroeck, Brigitta I.

Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos

Villeda-Chávez, Edgar

Comisión Nacional para el Conocimiento y Uso de la Biodiversidad

Zamora-Vilchis, Itzel

Universidad de Quintana Roo

Colaboradores

Acosta-González, Gilberto

Centro de Investigación Científica de Yucatán

Banaszak, Anastazia

Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos

Bejarano, Marylin

Pronatura Sur, A.C.

Brito-Bermúdez, Abelardo

Comisión Nacional de Áreas Naturales Protegidas

Caballero-Vázquez, José Adán

Centro de Investigación Científica de Yucatán

Cabanillas-Terán, Nancy

El Colegio de la Frontera Sur – Chetumal

Carrillo, Laura

El Colegio de la Frontera Sur – Chetumal

Cobián Rojas, Dorka

Parque Nacional Guanahacabibes, Cuba

Connor, Sarah

Iniciativa de Turismo del Arrecife Mesoamericano

Fulton, Stuart

Comunidad y Biodiversidad, A.C.

García-Rivas, María del Carmen	<i>Comisión Nacional de Áreas Naturales Protegidas</i>
Garza-Pérez, Rodrigo	<i>Universidad Nacional Autónoma de México</i>
Gómez-Hernández, Yadira	<i>Comisión Nacional de Áreas Naturales Protegidas</i>
Gómez-Lozano, Ricardo	<i>Comisión Nacional de Áreas Naturales Protegidas</i>
González-Baca, Arturo	<i>Comisión Nacional de Áreas Naturales Protegidas</i>
González-González, Arturo	<i>Comisión Nacional de Áreas Naturales Protegidas</i>
González-Posada, Alba	<i>Comisión Nacional para el Conocimiento y Uso de la Biodiversidad</i>
Hernández-Arana, Héctor	<i>El Colegio de la Frontera Sur -Chetumal</i>
Hernández-Palacio, Nayeli	<i>Comisión Nacional de Áreas Naturales Protegidas</i>
Hernández-Terrones, Laura	<i>Centro de Investigación Científica de Yucatán</i>
Herrera-Silveira, Jorge	<i>Centro de Investigación y de Estudios Avanzados</i>
Hoyos-Padilla, Edgar Mauricio	<i>Pelagios Kajunjá</i>
Ibarra-Navarro, Roberto	<i>Comisión Nacional de Áreas Naturales Protegidas</i>
Ketchum, James	<i>Pelagios Kajunjá</i>
López-Alcaide, Saúl	<i>Comisión Nacional para el Conocimiento y Uso de la Biodiversidad</i>
Loreto, Rosa María	<i>Amigos de Sian Ka'an</i>
Maldonado, Gisela	<i>Grupo Tortuguero del Caribe</i>
Marcos-Benítez, Hunahpú	<i>Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos</i>
Mariño-Tapia, Ismael	<i>Universidad Nacional Autónoma de México</i>
Omar Ortiz-Moreno, Felipe Ángel	<i>Comisión Nacional de Áreas Naturales Protegidas</i>
Padilla, Claudia	<i>Instituto Nacional de Pesca</i>
Rojas-Montiel, Bárbara	<i>Comisión Nacional para el Conocimiento y Uso de la Biodiversidad</i>
Rueda-Flores, Marisol	<i>Iniciativa Arrecifes Saludables</i>
Santos-González, Teresa Patricia	<i>Comisión Nacional de Áreas Naturales Protegidas</i>
Soto, Mélina	<i>Iniciativa Arrecifes Saludables</i>
van Tussenbroeck, Brigitta I.	<i>Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos</i>
Vega-Zepeda, Alejandro	<i>El Colegio de la Frontera Sur – Chetumal</i>
Vera-Vázquez, Elisa	<i>Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos</i>

