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Mendoza-Carranza, Manuel; Santiago-Alarcón, Diego; Pérez-Jiménez, Juan Carlos; Hernández-Lazo, Chrystian Carolina

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Research Article

Eyeless morphotype in the southern stingray (*Dasyatis americana*): a non-lethal and frequent abnormality from the southern Gulf of Mexico

Manuel Mendoza-Carranza[1], Diego Santiago-Alarcón[2]
Juan Carlos Pérez-Jiménez[3] & Chrystian Carolina Hernández-Lazo[1]
[1]El Colegio de la Frontera Sur, Manejo Sustentable de Cuencas y Zonas Costeras
Villahermosa, 86280, Tabasco, México
[2]Red de Biología y Conservación de Vertebrados, Instituto de Ecología, A.C. 91070, México
[3]El Colegio de la Frontera Sur, Adaptación humana y manejo de recursos en ecosistemas
Tropicales, Lerma Campeche, Campeche, México
Corresponding author: Manuel Mendoza-Carranza (mcarranza@ecosur.mx)

ABSTRACT. Elasmobranchs are active predators that depend on a highly developed visual system. The eyes of the southern stingray, *Dasyatis americana*, are adapted to a changing light environment in coastal zones. In this study we use morphological characters and molecular methods (mtDNA COI) to describe an eyeless morphotype of *D. americana* from six individuals collected from commercial small-scale fisheries on the Campeche Bank (southern Gulf of Mexico). Additionally to the eyeless characteristic, both regular (presence of eye) and eyeless (absence of eye) morphotypes have contrasting quantitative values and qualitative features for different phenotypic traits (color, teeth number, pelvic fin and spiracle form). Mature female and male eyeless morphotype had functional internal reproductive structures. Using the bar code gene, we found conclusive evidence that the eyeless morphotype belongs to the species *D. americana*. This is the first report on reproductively functional eyeless individuals of this species or close relatives elsewhere, which live sympatrically with regular *D. americana* individuals in the southern Gulf of Mexico.

Keywords: Dasyatidae, mutation, visual-sense, barcodingene, Campeche Bank, Gulf of Mexico.

Un morfotipo sin ojos de la raya látigo americana (*Dasyatis americana*): una anormalidad frecuente pero no letal en el sur del Golfo de México

RESUMEN. Los elasmobranquios son depredadores activos que dependen de un sistema visual bien desarrollado. Los ojos de la raya látigo americana, *Dasyatis americana*, están adaptados a intensidades de luz variables en zonas costeras. En este estudio se utilizan caracteres morfológicos y métodos moleculares (ADNmt COI) para describir el hallazgo de un morfotipo con ausencia de ojos en la raya *D. americana*, en un área costera marina tropical. La descripción está basada en seis ejemplares sin ojos colectados a partir de muestreos de flotas de pesca de pequeña escala que operan en el Banco de Campeche al sur del Golfo de México. Mediante comparación de las diferentes características fenotípicas (color, número de dientes, forma de la aleta pélvica y de los espiráculos) entre los morfotipos sin ojos y los morfotipos regulares, se encontraron diferencias contrastantes. Tanto los machos como hembras de los morfotipos sin ojos presentaron órganos reproductivos internos completos y funcionales. Utilizando los resultados obtenidos a través de análisis genéticos provenientes del código de barras genético, se confirma que los individuos sin ojos pertenecen a *D. americana*. Este es el primer reporte de individuos sin ojos de *D. americana* o de especies cercanas que son reproductivamente funcionales, y que viven simpátricamente con individuos de *D. americana* de morfotipo regular en el sur del Golfo de México.

Palabras clave: Dasyatidae, mutación, sentido de la vista, código de barras genético, Banco de Campeche, Golfo de México.

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INTRODUCTION

The ecological role of elasmobranchs as top predators depends on some relevant adaptations to environments in which they occur (Jordan *et al.*, 2013). Since elasmobranchs are active predators, most of them depend on a highly developed visual system (Creel & Christianson, 2008; Heithaus *et al.*, 2008). Furthermore, their electroreception and chemoreception systems are fundamental to locate and capture prey. For benthic rays these senses are also used to avoid being predated (Hueter *et al.*, 2004). Elasmobranchs have adapted to live in a variety of marine and freshwater habitats (*e.g.*, estuaries and rivers (from cold temperate to tropical waters), coral reefs and mesopelagic (200-1000 m) and bathypelagic (1000-4000 m) zones, (Compagno, 1984, 1990). Given their ecological diversity, the eyes of cartilaginous fishes show particular adaptations to the light environment in which they live, as well as to their preferred feeding strategies and predator avoidance behaviors (Hueter *et al.*, 2004; Lisney & Collin, 2007; Lisney *et al.*, 2012).

Habitat use has been associated to variable eye size and type (Lisney & Collin, 2007; Lisney *et al.*, 2012). In comparison to the large eyes of oceanic and deep-sea elasmobranchs, eyes of those elasmobranchs inhabiting coastal benthic environments are commonly small or medium-size in relation to body size (Lisney & Collin, 2007). The high concentration of plankton and suspended organic and inorganic matter in shallow coastal environments can obscure visual stimuli (Kirk, 1979; Bowmaker, 1995), and so coastal species may rely more heavily on their non-visual senses (*e.g.*, electroreception) (Raschi *et al.*, 2001).

The eyes of the southern stingray *Dasyatis americana* Hildebrand & Schroeder, 1928 (dorsally positioned) are adapted to a changing light environment in coastal zones, where seasonal changes in water transparency are common due to seasonal variations in nutrient and sediment input from rivers (Hueter *et al.*, 2004; Litherland *et al.*, 2009; Lisney *et al.*, 2012). Additionally, vision and eye position of *D. sabina* (Lesueur, 1824), a species related to *D. americana*, has been shown to be beneficial in turbid shallow coastal waters to avoid predation (McComb & Kajiura, 2008). Moreover, this advantage is complemented with some other behavioral strategies such as vigilance groups; in *Pastinachus sephen* vigilance groups of three stingrays are formed arranged in a rosette form increasing the predator detection capabilities (Semeniuk & Dill, 2005). Elasmobranchs with small-eyes or eyeless are very uncommon in nature and they have been reported in only two deep-sea genera worldwide: *Benthobatis* and *Typhlonarke*, both having degenerated eyes covered by skin (Gruber, 1977; Locket, 1977) or "almost non-existent" eyes (De Carvalho *et al.*, 2003; Lisney & Collin, 2007).

Here, we present a description of an eyeless morphotype of the southern stingray based on six specimens caught by the coastal small-scale fishery of the southern Gulf of Mexico, collected during sampling surveys at the San Pedro and Chiltepec ports in Tabasco, Mexico (Fig. 1). Since eyeless organisms presented several morphological differences, we studied the possibility of a new species. In order to test this hypothesis, we then used a fragment of the mtDNA COI gene to explore the genetic similarity of the referred eyeless morphotype with that of the regular morphotype of the southern stingray.

MATERIALS AND METHODS

Sampling process

Eyeless and regular southern stingrays were obtained from commercial catches of the small-scale fleet from San Pedro and Chiltepec ports, Tabasco (Fig. 1). The fishing area of San Pedro and Chiltepec ports small-scale fleets are located on the Campeche Bank (18º40'38"-19º05'25"N and 92º27'07"-92º05'11"W) covering an area of 532 km^2 (Fig. 1). Stingrays were captured with bottom long-lines with tuna circle hooks of 60 mm shank length. Catch depth ranged from 10 to 40 m. The southern stingray occurrence in this multispecies fishery at Campeche Bank is common throughout the year (Ramírez-Mosqueda *et al.*, 2012).

All the stingrays used were not killed specifically for this study; specimens are part of the commercial catch of the artisanal anglers of San Pedro Port, Tabasco, Mexico. Specimen and tissue collections were under the consideration and approval of the commercial exploitation union of San Pedro and Chiltepec ports. Furthermore, eyeless individuals were deposited in the ECOSUR scientific fish collection of San Cristóbal de las Casas, Chiapas (ECOSC), under collection permit number DGOPA.04543.060711.1761 issued by SAGARPA (The Secretariat of Agriculture, Livestock, Rural Development, Fisheries and Food of the Mexican Government).

Morphology

Morphometric and morphological description of eyeless stingrays were based on six specimens. The first eyeless individual observed, but not collected, was a mature male coming from catches of the small-scale fishery fleet of Chiltepec Port, Paraíso, Tabasco on April 2008. Subsequently, three females and two males (one mature and one immature) were collected at San

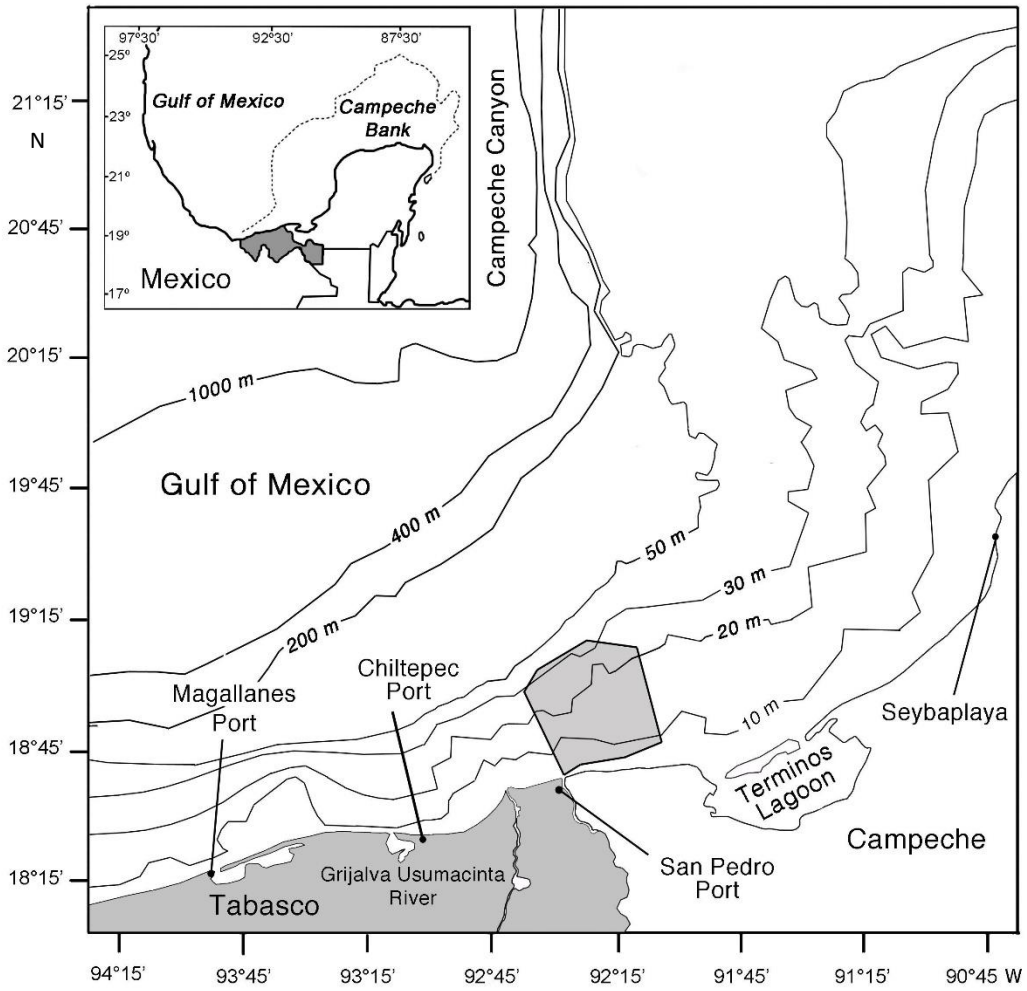

Figure 1. Fishing area on the Campeche Bank (the southern Gulf of Mexico) where eyeless specimens of the southern stingray *Dasyatis americana* were caught. Light-grey polygon indicates fishing area of the small-scale fleet from San Pedro Port. The inset indicates the location of Tabasco State in Mexico, and the limit (dashed line) of the Campeche Bank.

Pedro Port, Centla, Tabasco on March 2012 and October 2012. Characteristics of regular individuals were based on the description of McEachran & de Carvalho (2002). Additionally, we used morphometric characteristics of 76 regular *D. americana* (*i.e.*, with eyes) individuals (24 females, 44 males) captured during fishery sampling surveys from 2008 to 2012. Disc width (DW), snout length (SL), pelvic fin length (PL), mouth width (MW), spiracle diameter (SD) and, in the case of males, the clasper length (CL) was obtained; all measurements are reported in centimeters. The number of rows of the upper jaw of four eyeless individuals and 16 regular individuals of similar sizes were counted (McEachran & de Carvalho, 2002). Additionally, the morphological features (form and size) of the pelvic fin, nasal curtain, spiracles form, and the color of the ventral and dorsal sides of the body were recorded. The morphometric data of eyeless and regular individuals were compared using the DW/SL, DW/PL, and DW/MW ratios. The non-parametric Mann-Whitney U test (Zar, 2010) was used for comparisons between morphotypes.

Molecular laboratory methods

Small pieces (5-10 g) of muscle tissue from three eyeless female rays and two regular males and two regular females of *D. americana* individuals were collected. Samples were placed in 100% ethanol. To avoid DNA contamination, all tools were flame-sterilized before sampling each specimen. Each eyeless stingray was collected as a reference voucher specimen and deposited in the Fish Collection of El Colegio de la Frontera Sur, San Cristóbal de las Casas (ECOSC 7411, 7412, 7413).

Sequence analysis was carried out at the Canadian Centre for DNA Barcoding by using standard protocols (Hajibabaei *et al.*, 2005). DNA was extracted from 1 mm^3 tissue plugs that were placed in vertebrate lysis buffer with proteinase K and digested overnight at 56ºC. Genomic DNA was subsequently extracted using a membrane-based approach on the Biomek FX (Biomek FX, Brea, California, USA) liquid handling station and AcroPrep 96 (AcroPrep 96, Pall Co., Port Washington, New York, USA) filter plates with 1.0 mM PALL glass-fibre media (Ivanova *et al.*, 2006). A 652-658bp segment of COI was amplified with different fish primers, including FishF1, FishR1, FishF2, FishR2 (Ward *et al.*, 2009) or an M13-tailed fish-primer cocktail (Ivanova *et al.*, 2007).

PCR reaction mixes of 12.5 µL, which included: 6.25 µL of 10 percent trehalose, 2 µL of ultrapure water, 1.25 µL of 10 PCR buffer, 0.625 µL of MgCl2 (50 mM), 0.125 µL of each primer (0.01 mM), 0.0625 µL of dNTP mix (10 mM), 0.625 µL of *Taq* polymerase (New England Biolabs, Ipswich, Massachusetts, USA or Invitrogen, Carlsbad, California, USA), and 2.0 µL of DNA template. Amplification protocols followed those described in Hajibabaei *et al.* (2005). PCR products were visualized on agarose gels (Invitrogen) and positive samples were selected for sequencing. Products were labeled by using the Big Dye Terminator v.3.1 cycle sequencing kit (Applied Biosystems, Carlsbad, USA) as described in Hajibabaei *et al.* (2005). Forward and reverse strands were sequenced with an ABI 3730 capillary sequencer (ABI, Carlsbad, USA), following manufacturers protocol. Sequences were aligned using SEQSCAPE v.2.1.1 software (Applied Biosystems). Sequence data, electropherograms, trace files, primer details, photographs, and collection localities for specimens are available from http:// www.barcodinglife.org. Sequence accession numbers from bold systems v3 are eyeless (MXV517-12, MXV518-12, MXV519-12) and regular (MXV513-12, MXV514-12, MXV515-12, MXV520-12).

Phylogenetic analysis

Phylogenetic hypotheses were constructed using the program Mr. Bayes v3.1.2 (Huelsenbeck & Ronquist, 2001). Two independent runs were conducted, with 4 chains in each run for a total of 2.5 million generations, sampling every 100 generations. The first 12,500 trees (50%) were discarded as the 'burn-in'. In total, 12,500 trees from each run were used to build our majority-rule consensus tree. For the analyses, a TPM2uf+I+G model of molecular evolution was used as suggested by jModelTest2.1.2 (Guindon & Gascuel, 2003; Darriba *et al.*, 2012) with shape parameter $\alpha = 2.176$ and proportion of invariable sites Pinvar = 0.625 as calculated with the j-Model Test. To implement the TPM2uf model in Mr. Bayes, the next more complex available mode (GTR) was used as recommended in the user´s manual. The different parameters (gamma shape parameter, proportion of invariable sites, nucleotide frequencies, and nucleotide substitution rates) were fixed according to the values calculated with the j-Model Test. Sequence divergence between the different haplotypes was calculated using both the Jukes-Cantor (substitutions weighed equally) and the Tamura-3 parameter (substitutions, shape parameter, and proportion of invariable sites as calculated with j-Model Test) models of substitution that were implemented in the program MEGA v5.1 (Tamura *et al.*, 2011).

RESULTS

Morphology

The morphological traits between the regular and eyeless morphotypes of southern stingrays were different (Table 1). Besides the absence of eyes (Table 1, Figs. 2a-2b), other differences that existed between these two morphotypes were the spiracle form and size, in eyeless individuals spiracle is rounded and slightly dorsoventrally depressed, whereas in the regular individuals spiracle is like a rectangle and relatively bigger than in eyeless morphotypes (Figs. 2a-2b). The body color, in eyeless stingrays is spotted grey-black on the ventral edge and the dorsal color is darker [brown, green, olive] compared to the regular morphotype (Table 1, Figs. 2c-2f). Nasal curtain of eyeless specimens is short, not fleshy and limited to the upper border of the mouth (Figs. 2c-2d). Pelvic fin shape in eyeless female is rounded, small, and oriented to the sides of the body, whereas in regular female stingrays, the pelvic fin is trapezoid, larger, and oriented towards the anteroposterior axis (Table 1, Figs. 2e-2h). There are no marked differences between regular and eyeless male individuals in the form of the pelvic fin.

The sizes of eyeless females were 57, 58, and 73 cm DW, respectively, the sizes of eyeless mature males were 64 and 73 cm DW, respectively, and the size of the eyeless immature male was 63 cm DW. No significant morphometric differences were observed between regular and eyeless stingrays (Table 1). To avoid damage to all collected specimens, we dissected only the biggest male (73 cm DW) and female (73 cm DW) of eyeless specimens to examine the internal reproductive organs. Both mature eyeless male and female had functional internal reproductive structures. In the mature male, a pair of well-developed testis was observed. Uterine trophonemata in the female were abundant and long (approx. 1 cm) indicating a possible

Table 1. Morphological traits for both *Dasyatis americana* regular and eyeless morphotypes. Size of proportions is cm. *Data based on McEachran & de Carvalho (2002) description.

Trait	*Dasyatis americana* (n = 68)	Eyeless *Dasyatis americana* (n = 6)
Eyes	Present, prominent	Absent
Dorsal color	Light brown, olive and grey*(Our data)	Dark green, brown and olive
Ventral color	Completely white, occasionally with light-grey margins	White with gray-black band and spots at the borders, except in the posterior side of disc
Snout	Barely projecting* (Our data)	Not projecting
Nasal curtain	Fleshy, covering the upper jaw, sometimes all the mouth	Not fleshy, not reaching the upper border of the upper jaw
Pelvic fin females	Trapezoid, anteroposterior orientation	Rounded, lateral orientation
Pelvic fin males	Trapezoid, anteroposterior orientation	Trapezoid, anteroposterior orientation
Size range	46-97	57-73
Pelvic fin length/disc width (%)	10.00-20.91	13.70-20.79
Mouth width/disc width (%)	5.67-10.53	8.77-9.59
Preoral length/disc width (%)	15.28-23.52	18.13-20.34
Snout angle	135º* 120º-146º	118º-130º
Rows number in upper jaw	39-48	45-53

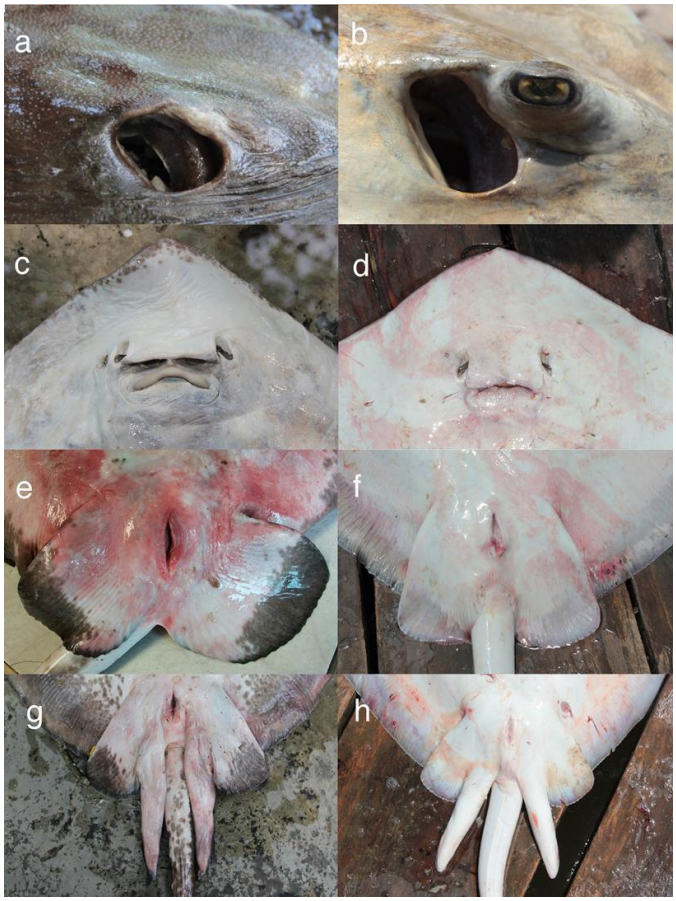

Figure 2. Morphological characteristic of eyeless and regular (normal) southern stingrays, *Dasyatis americana,* caught on the Campeche Bank (southern Gulf of Mexico). a) eyeless, and b) eye detail of a normal individual; nasal curtain of c) eyeless, and d) normal individual, pelvic fins of e) eyeless, and f) normal female; pelvic fins and claspers of g) eyeless, and h) normal males.

previous gestation cycle. The largest oocyte was 19 cm in diameter. No embryos were observed.

Phylogenetic analysis

Based on phylogenetic analysis, sequences from the eyeless morphotype (Fig. 3) are nested within the same clade as those sequences deriving from the regular morphotype, indicating that they belong to the same species (*D. americana*). There is a small genetic divergence, however, between the two morphotypes that ranges from 0.3 to 0.5 percent based on both Jukes-Cantor and Tamura-3-parameter models. The Bayesian majority-rule consensus phylogram indicates that COI sequences from *D. americana* form a monophyletic clade (Fig. 3).

DISCUSSION

In this study, we identified two genetic haplotypes belonging to the species *D. americana* based on the bar code gene COI. These two haplotypes correspond to morphologically different specimens of the southern stingray, one haplotype has functional eyes and the other is eyeless. Eyeless specimens had fully functional internal and external reproductive organs, indicating that they can reproduce in nature; lack of eyes should be rather an adaptation to low light environments (see below). Minor abnormalities apparently do not affect biological functions of individuals compared to major changes commonly found in embryos, which possibly may not survive once they are born (Devadoss, 1983; Mnasri *et al.*, 2010; Mejía-Falla *et al.*, 2011). In reference to ecologically functional "minor" changes for *D. americana*, a higher teeth number and a darker dorsal color in eyeless specimens compared to regular individuals were recorded. During a period of six years, the eyeless morphotype of *D. americana* was more frequent than other abnormalities recorded for this species. In our study area, only one other minor abnormality was recorded, an albino female of *D. americana* (82 cm DW) on November 2012 (Fig. 4); two occurrence of albinism of this same species have been reported in Palmico Sound, North Carolina (Schwartz & Safrit, 1977) and in Tabasco, Mexico coast (Wakida-Kusunoki, 2015).

Implications of abnormalities for the individuals and populations are poorly understood (Capapé *et al.*, 2012). Origin and frequency of such abnormalities have been attributed to several factors, including genetic alterations, parasitic infection, tumors, predation, or water pollution (Orlov, 2011; Rubio-Rodríguez *et al.*, 2011). Pollution in the Campeche back is due to crude oil extraction (García-Cuéllar *et al.*, 2004; Wakida-Kusunoki & Caballero-Chávez, 2009). One of the world's most intense and biggest oil spills occurred in this area, the 1979 Ixtoc oil spill. It produced a strong and longtime environmental impact in a wide area of the coastal marine environments of the Mexican Gulf of Mexico (Jernelöv & Lindén, 1981), in particular the benthic environment (Teal & Howarth, 1984), to which *D. americana* is strongly associated. Despite the acute toxicity of these events to aquatic life, the effects may be related to multigenerational toxicant-induced heritable mutations as presented in this research (Cronin & Bickham, 1998). However, other possibility is a mutation in some regulatory gene that produces eyeless individuals in *D. americana* of the Campeche Bank (Ravi & Venkatesh, 2008). We suggest that such a mutation has no deleterious effect on these individuals because the high turbidity of the water makes vision a less important sense; in addition, the well developed and functional reproductive organs reported in this study indicate successful offspring production.

It is important to highlight that almost all reports on abnormalities in rays and sharks derive from one or maximum two individuals, and usually such abnormalities are fatal to the carriers, for example in *Amblyraja doellojuradoi* (Pozzi & Bordalé, 1935), *Urotrygon rogersi* (Jordan & Starks, 1895) and *Dasyatis guttata* (Bloch & Schneider, 1801) (Mejía-Falla *et al.*, 2011; Ramirez-Hernandez *et al.*, 2011; Delpiani *et al.*, 2012). This indicates that abnormalities in the studied population of southern stingrays have a higher prevalence compared to other elasmobranch populations and apparently do not have detrimental effects on fitness.

The study area has waters with low transparency due to the high productivity levels of this region generated by the strong seasonal freshwater runoff from the Grijalva-Usumacinta basin (Monreal-Gómez *et al.*, 2004; Lara-Lara *et al.*, 2008) and due to the proximity to the Campeche canyon and the Campeche Bank, where the influence of an important upwelling has been observed (Zavala-Hidalgo *et al.*, 2006). Despite the well-adapted eyes of *D. americana* (dorsally positioned) to low light level environments (Hueter *et al.*, 2004; Litherland *et al.*, 2009; Lisney *et al.*, 2012), it is known that the visual sense in elasmobranchs is complemented by other senses such as electroreception and chemoreception (Kotrschal *et al.*, 1998; Lisney & Collin, 2007). Hence, because vision may not play an important role in prey detection by benthic elasmobranchs (Warrant & Locket, 2004; McComb & Kajiura, 2008), we can hypothesize that in an environment with low levels of light as the southern Campeche Bank, eyeless do not constitute a disadvantage because southern stingrays can use multiple sensory strategies (Raschi, 1986).

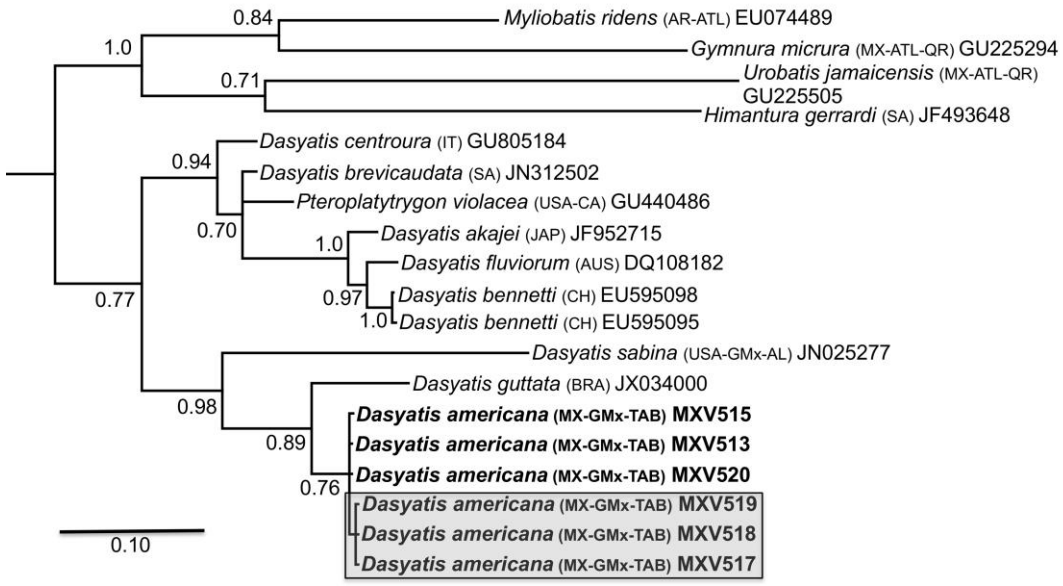

Figure 3. Bayesian majority-rule consensus phylogram of mitochondrial DNA Cytochrome Oxydase I (mt DNA COI) bar code gene of stingrays (Rajiformes). 650 bp of the mtDNA COI bar code gene were used. Support values on branches are Bayesian posterior probabilities. Sequences include species name from which it derives, followed by its geographic location and GenBank™ accession number. Sequences from *Dasyatis americana* are in bold font and sequences from eyeless *D. americana* are highlighted in the gray-shaded square. Sequences from *Myliobatis ridens* Ruocco, Lucifora, Díaz de Astarloa, Mabragaña & Delpiani, 2012 (Myliobatidae), *Gymnura mycrura* (Bloch & Schneider, 1801) (Gymnuridae), *Himantura gerrardi* (Gray, 1851) and *Urobatis jamaicensis* (Cuvier, 1816) (Urotrygonidae) were used as outgroups to root the phylogeny. AR: Argentina, MX: Mexico, SA: South Africa, IT: Italy, USA: United States of America, JAP: Japan, AUS: Australia, CH: China, BRA: Brazil, QR: Quintana Roo, CA: California, AL: Alabama, TAB: Tabasco, ATL: Atlantic Ocean, GMx: Gulf of Mexico. Scale indicates percentage sequence divergence among haplotypes.

Figure 4. Albino female of the southern stingray *Dasyatis americana* (82 cm disc width).

We performed informal interviews with fishermen of adjacent fishery areas of Seybaplaya, Campeche and Magallanes ports in Tabasco (at the northeast and west of our study area respectively) to know about possible occurrences of eyeless stingrays. Fishermen at these locations affirm that eyeless stingrays have not been observed. In fact, the higher capture volumes of this species are concentrated in the San Pedro and Frontera ports (Ramírez-Mosqueda *et al.*, 2012). Additionally, no reports about eyeless individuals of this species or close relatives have been published elsewhere. Thus, we suggest that the distribution of eyeless southern stingrays is restricted to a small area comprising the southern Campeche Bank that might be also associated with the deep waters of the Campeche Canyon (1000-3200 m depth). The isolated distribution of eyeless southern stingray could be related with a philopatric behavior observed in elasmobranchs (Hueter *et al.*, 2005), such behavior has been suggested for *D. brevicaudata* (Hutton, 1875) (Le Port & Lavery, 2012) and *D. akajei* (Müller & Henle, 1841) (Li *et al.*, 2013). Moreover, this potential philopatric behavior in eyeless individuals could be related to the genetic divergence observed between eyeless and regular individuals of the southern stingray (Duncan *et al.*, 2006). Thus, we suggest that a combination of environmental (*e.g.*, low transparency waters) and genetic factors (*e.g.*, genes controlling philopatric behavior) is responsible for the evolution of an eyeless population of *D. americana* in the southern Gulf of Mexico.

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