# UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
**FACULTAD DE CIENCIAS**

# Batoideos demersales del Golfo de Tehuantepec: nuevo registro, anomalías morfológicas, distribución de asociaciones y ecología reproductiva de *Zapteryx xyster* Jordan & Evermann, 1896

# TESIS

**QUE PARA OPTAR POR EL GRADO DE:**

DOCTORA EN CIENCIAS

**PRESENTA:**

M. en C. ANA MARÍA TORRES HUERTA

TUTOR PRINCIPAL DE TESIS: Dr. ADOLFO GRACIA GASCA
COMITÉ TUTOR: Dr. MARGARITO TAPIA GARCÍA
Departamento de Hidrobiología, U.A.M.
Dr. ISAIAS HAZARMABETH SALGADO UGARTE
FES Zaragoza

Ciudad Universitaria, CD. MX. Agosto 2020

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POSGRADO
CIENCIAS
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COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS
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OFICIO FCIE/DAIP/334/2020

ASUNTO: Oficio de Jurado

**M. en C. Ivonne Ramírez Wence**
**Directora General de Administración Escolar, UNAM**
**Presente.**

Me permito informar a usted que en la reunión ordinaria del Subcomité de Ecología, Manejo Integral de Ecosistemas, Biología Evolutiva y Sistemática del Posgrado en Ciencias Biológicas, celebrada el día **24 de febrero de 2020** se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** del estudiante **TORRES HUERTA ANA MARÍA** con número de cuenta **87019498** con la tesis titulada: **"Batoideos demersales del Golfo de Tehuantepec: nuevo registro, anomalías morfológicas, distribución de asociaciones y ecología reproductiva de *Zapteryx xyster* Jordan & Evermann, 1896",** realizada bajo la dirección del **DR. ADOLFO GRACIA GASCA:**

| | |
|---|---|
| Presidente: | **DR. RAMÓN ANDRÉS LÓPEZ PÉREZ** |
| Vocal: | **DRA. ALICIA CRUZ MARTINEZ** |
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| Suplente: | **DR. FELIPE GALVÁN MAGAÑA** |
| Suplente: | **DR. JAVIER TOVAR ÁVILA** |

Sin otro particular, me es grato enviarle un cordial saludo.

**ATENTAMENTE**
**"POR MI RAZA HABLARÁ EL ESPÍRITU"**
Cd. Universitaria, Cd. Mx., a 14 de agosto de 2020

**COORDINADOR DEL PROGRAMA**

**DR. ADOLFO GERARDO NAVARRO SIGÜENZA**

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***Dedicado a***

***María Guadalupe Torres Huerta y Carmen Huerta Torres***
*In memorian*

***Francisco Torres Martínez***

# ÍNDICE

# Resumen

Los batoideos son capturados como fauna de acompañamiento en la pesquería de camarón y descartados como especies sin valor comercial en el Golfo de Tehuantepec. De enero de 2008 a abril de 2014 se realizaron 538 arrastres de fondo entre Salina Cruz, Oaxaca y Puerto Madero, Chiapas; en un intervalo de profundidad de 16 a 62 m. Este documento está compuesto de cuatro artículos que detallan información sobre un nuevo registro de batoideo para la región, las anomalías morfológicas encontradas en diferentes especies de batoideos, la distribución de las asociaciones de batoideos y la ecología reproductiva de una especie de raya guitarra. El primer artículo caracteriza las asociaciones de los batoideos en las diferentes áreas de pesca del camarón y su relación con los factores ambientales; se capturó un total de 23,414 batoideos pertenecientes a 16 especies. Las especies *Urotrygon rogersi, U. chilensis* y *Narcine vermiculatus* representaron 70.1% de la abundancia y el 46.3% de la biomasa; se identificaron cinco asociaciones de batoideos mediante el análisis de clúster jerárquico y de perfiles de similitud; cuatro asociaciones se localizaron en profundidades <40 m y una asociación entre profundidades de 40 a 62 m; el principal grupo de batoideos (asociación de fondos arenosos de Oaxaca) se ubicó frente a los complejos lagunares más importantes; la comparación de la biomasa y la abundancia indicó que las especies pequeñas dominan en términos de abundancia en la mayoría de las asociaciones; finalmente, el conjunto de condiciones ambientales y características del hábitat (longitud geográfica, profundidad y temperatura de la superficie del mar) presentes en el Golfo de Tehuantepec explicó cambios importantes en la comunidad de

batoideos y como afectan su patrón de distribución espacio-temporal. El segundo artículo describe la ecología reproductiva de la guitarra bruja *Zapteryx xyster;* de un total de 451 especímenes se registró el peso total, la longitud total (LT), el sexo, el estado de madurez y la profundidad de captura; los datos indicaron que los adultos emigraron hacia aguas poco profundas (25-37 metros) para reproducirse a partir de febrero; los machos alcanzaron la madurez a 44 cm LT; mientras que las hembras a 48 cm LT; las hembras son síncronas; la ovulación y el apareamiento comienzan en marzo y el parto se lleva a cabo entre abril y mayo del año siguiente; las hembras mostraron un ciclo de 2 años con vitelogénesis y gestación consecutiva; la fecundidad fue de 5 a 8 embriones ($\overline{x} =$ 6) y la proporción de sexos de los embriones fue de 1:1; las crías nacen con una talla promedio de 17.3 cm LT; se observó dicromatismo sexual entre machos y hembras durante el período de reproducción, y polimorfismo sexual en hembras adultas; finalmente, la captura incidental de la guitarra bruja durante el cortejo y el apareamiento amenaza la supervivencia de esta especie. En el tercer artículo se describió la presencia de la raya redonda denticulada *Urotrygon cimar* (López y Bussing 1998) a partir de 101 especímenes, incluidos juveniles y adultos, con tallas entre 10.2 y 28.2 cm de ancho de disco. En el cuarto artículo se describieron las anomalías morfológicas encontradas en 15 ejemplares de vida libre y tres embriones del género *Urotrygon;* estas anomalías fueron: aletas pectorales con desarrollo incompleto o no fusionadas en la parte anterior, anoftalmia, agenesia de mixopterigio, desarrollo anormal y neoplasia en hígado.

# Abstract

The batoids are captured as bycatch in the shrimp fishery and discarded as non-commercial value species in the Gulf of Tehuantepec. A total of 538 bottom trawls were carried out between January 2008 and April 2014, at depths of 11 to 62 m off Salina Cruz, Oaxaca, and Puerto Madero, Chiapas. This document consists of four papers detailing information on a new batoid record for the region, the morphological abnormalities found in the *Urotrygon* genus, distribution of batoid demersal assemblages, and the reproductive ecology of a species of guitarfish. The first paper characterizes the batoid assemblages in the different shrimp fishing areas and their relationship with the environmental factors; we captured a total of 23,414 batoids belonging to 16 species; the species *Urotrygon rogersi*, *U. chilensis* and *Narcine vermiculatus* represented 70.1% of the abundance and 46.3% of the biomass; five batoid assemblages were identified using hierarchical cluster and similarity profile analyses; four assemblages were located at depths less than 40 m and one assemblage was located at depths between 40 and 62 m; the main batoid group (sandy bottom off Oaxaca assemblage) was located in front of the most important lagoon complexes; the abundance biomass comparison method indicated that small species were dominant in terms of abundance in most assemblages; finally the set of environmental conditions and habitat characteristics (longitude, depth and sea surface temperature) present in the Gulf of Tehuantepec predicted important changes in the batoid community and affected its spatiotemporal distribution pattern. The second paper describes the reproductive ecology of the witch guitarfish *Zapteryx exasperata*; a total of 451 specimens, total weight, total length (TL), sex, maturity stage, and catch depth of each organism were recorded; data indicated that adults migrated towards shallow waters (25-37

meters) to reproduce beginning in February; males reached maturity at 44 cm TL whereas females reached maturity at 48 cm TL; witch guitarfish females are synchronous, therefore, ovulation and mating begin in March and parturition begins in April; females showed a 2-year cycle with consecutive vitellogenesis and gestation; fecundity was 5 to 8 embryos ($\bar{x} = 6$) and the sex ratio of embryos was 1:1; birth size was observed with an average size at parturition of 17.3 cm TL; there was sexual dichromatism between males and females during the breeding period, and sexual polymorphism in adult females; finally the incidental catch of the witch guitarfish during courtship and mating threatens the survival of this species. The third paper describes the presence of the denticled roundray *Urotrygon cimar* (López y Bussing, 1998) from 101 specimens, including juveniles and adults; sizes ranged from 10.2 to 28.2 cm total length. The fourth paper describes the morphological abnormalities found in 15 free-ranging specimens and three embryos of the genus *Urotrygon*; abnormalities consisted of developed pectoral fins that were not fused interiorly, pectoral fins that were not completely developed, anophthalmia, absence of a clasper, an abnormally developed liver, and neoplasia of the liver.

# I. Introducción general

El Golfo de Tehuantepec es considerado una de las tres zonas centroamericanas del Pacífico Tropical Oriental con altos niveles de productividad (Ortega-García *et al.* 2000). Esta productividad es el resultado de la combinación de condiciones físicas y dinámicas de las aguas, donde el factor más importante es el efecto de los vientos que soplan con gran fuerza de noviembre a febrero. Debido a estos vientos existe una estacionalidad muy marcada (Lluch-Cota *et al.* 1997; Tapia-García *et al.* 2007; Barton *et al.* 2009), que influye en la composición y distribución del fitoplancton (Robles-Jarero y Lara-Lara 1993; Lluch-Cota *et al.* 1997; Lara-Lara *et al.* 1998; Meave-del-Castillo y Hernández-Becerril 1998), zooplancton (Ayala-Duval *et al.* 1996), invertebrados bentónicos (Gamboa-Contreras y Tapia-García 1998) e ictiofauna demersal (Tapia-García 1998).

Los peces son el recurso pesquero más importante en el Golfo de Tehuantepec. Se estima una biomasa total de 457,679 toneladas, la cual esta principalmente sub aprovechada o no explotada (Acal y Arias 1990; CONAPESCA 2017). El mayor volumen de captura comercial de peces se obtiene en la pesquería de túnidos con 15,950 toneladas promedio anuales y de la pesquería de tiburón con 4,392 toneladas promedio anuales (CONAPESCA 2017). Sin embargo, el mayor volumen de peces es capturado incidentalmente mediante arrastres de fondo en la pesquería de camarón. La pesquería de camarón captura ~4,000 toneladas anuales, comparada con 118,624 toneladas de peces (Tapia-García y García-Abad 1998; CONAPESCA 2017). Los teleósteos representan el 87% y los elasmobranquios el 13% del peso de la captura incidental de peces en el Golfo de Tehuantepec (Martínez-Muñoz 2012). Los elasmobranquios capturados como pesca incidental son principalmente batoideos demersales que no tienen importancia económica en la región (Tapia-García y García-Abad 1998; Martínez-Muñoz 2012). Los registros indican que 32 especies de batoideos habitan en el Golfo de Tehuantepec, lo cual corresponde al 76.2% de las especies de batoideos reportadas para el Pacífico mexicano (McEachran y Notarbarloto di Sciara 1995; Amezcua-Linares 1996; Castro-Aguirre y Espinosa Pérez 1996; Carrera-Fernández *et al.* 2012).

De acuerdo con la Lista Roja de la Unión Internacional para la Conservación de la Naturaleza (UICN) (http://www.iucnredlist.org, visitada el 20 de enero de 2020), seis especies de batoideos registradas en el Golfo de Tehuantepec están catalogadas como Casi Amenazadas: *Aetobatus laticeps* (Gill, 1865), *Narcine vermiculatus* Breder 1928, *Pseudobatos leucorhynchus* (Günther 1867), *Mobula munkiana* Notarbartolo di Sciara 1987, *M. mobular* (Bonnaterre, 1788), y *M. thurstoni* (Lloyd 1908); tres especies, están listadas como Vulnerables: *M. birostris* (Walbaum 1792), *M. tarapacana* (Philippi 1892) y *Diplobatis ommata* (Jordan y Gilbert 1890); mientras que la especie *Pristis pristis* (Linnaeus 1758), esta listada como En Peligro Crítico. No existen datos suficientes para evaluar el estado de otras nueve especies que se capturan con frecuencia en la pesquería de camarón: *Hypanus longus* (Garman 1880), *Narcine entemedor* Jordan y Starks 1895, *Pseudobatos glaucostigmus* (Günther 1867), *Zapteryx xyster* Jordan y Evermann 1896, *Urotrygon aspidura* (Jordania y Gilbert 1882), *U. chilensis* (Günther 1872), *U. munda* Gill, 1863, *U. nana* Miyake y McEachran 1988 y *U. rogersi* (Jordan y Starks 1895).

Los batoideos constituyen una parte importante en la transferencia de energía en las redes tróficas de ecosistemas marinos bentónicos, demersales y pelágicos (Wetherbee y Cortés 2004, Ebert y Bizarro 2007), controlando las poblaciones de otras especies y manteniendo el equilibrio de los recursos marinos (Ferretti et al. 2013). La información de batoideos en el Golfo de Tehuantepec es escasa y se refiere principalmente a su distribución geográfica y el hábitat en donde ocurren (Amezcua-Linares 1996; Castro-Aguirre y Espinosa Pérez 1996; Robertson y Allen 2015). La mayoría de estas especies no tienen importancia económica; sin embargo, se enfrentan a una explotación incidental grave asociada con la pesquería de camarón (McEachran y Notarbarloto di Sciara 1995; Tapia-García y Gutiérrez-Díaz 1998; López-Martínez *et al.* 2012). Las especies capturadas como fauna de acompañamiento del camarón han sido pobremente documentadas, lo que genera una falta de información sistemática y confiable de estas especies; y de cómo sus poblaciones están siendo afectadas (López-Martínez *et al.* 2012).

Esta situación es particularmente preocupante en el caso de los elasmobranquios ya que son considerados especies vulnerables a la sobreexplotación debido a sus estrategias de historia de vida (p. ej. crecimiento lento, edad de madurez sexual tardía, gran longevidad, fecundidad baja), los cambios en las interacciones ecológicas (por ejemplo depredación y competencia), diferente exposición a la pesca (p. ej. capturabilidad, valor comercial, agrupaciones de las crías) y la susceptibilidad a otros estresores, como la degradación del hábitat y la contaminación (Holden y Tucker 1974; Stevens *et al.* 2000; Marongiu *et al.* 2017). Entre los elasmobranquios, las especies de batoideos parecen extremadamente vulnerables a tales factores estresantes, probablemente debido a su distinta morfología (un cuerpo grande que las hace más capturables) y a un comportamiento gregario, lo que las hace vulnerables a casi todas las artes de pesca para especies demersales, desde redes de enmalle hasta redes de arrastre costeras y marinas (Bellodi *et al.* 2017).

# II. Objetivos

**General:** Generar información de la composición de especies de batoideos capturados con redes de arrastre en el Golfo de Tehuantepec, las asociaciones que forman y su distribución, la ecología reproductiva de un pez guitarra y las anomalías morfológicas de batoideos en la región.

**Específicos:**

1. Identificar los batoideos capturados con redes de arrastre en el Golfo de Tehuantepec.
2. Determinar la composición, abundancia y biomasa de los batoideos capturados con redes de arrastre de fondo.
3. Establecer las asociaciones de batoideos en el Golfo de Tehuantepec y la estructura de estas comunidades.
4. Determinar cuáles factores ambientales influyen en las asociaciones de batoideos detectadas.
5. Establecer la distribución estacional y batimétrica de los diferentes estados de madurez de la guitarra bruja en el Golfo de Tehuantepec.
6. Establecer la talla de madurez por sexo, la fecundidad, la duración del ciclo reproductivo (vitelogéneis y embriogénesis), la temporada y tallas de nacimiento de la guitarra bruja.
7. Registrar la presencia de la(s) especie(s) no registradas anteriormente en la región.

   Registrar las anomalías morfológicas encontradas en batoideos de la región.

# III. Presentación de la tesis

Una amplia porción de la zona costera y marina del Golfo de Tehuantepec se encuentra inexplorada por los científicos y un gran número de grupos taxonómicos han sido ignorados en los estudios recientes (López-Pérez *et al.* 2012). Entre estos grupos se encuentran los peces batoideos, los cuales son frecuentemente capturados como fauna de acompañamiento en la pesquería de camarón y descartados como especies sin valor comercial. El presente estudio aporta información de los batoideos demersales del Golfo de Tehuantepec. El documento está compuesto por cuatro artículos que detallan información referente a un nuevo registro para la región, las anomalías morfológicas encontradas en diferentes especies de batoideos, la distribución y composición de las asociaciones, además de la ecología reproductiva de una especie de guitarra de la región.

El primer artículo aborda los cuatro primeros objetivos de este trabajo, y corresponde al artículo requisito de egreso para obtener el grado de Doctora en Ciencias. En este documento se caracterizan las asociaciones de batoideos en las áreas de pesca del camarón a lo largo de la plataforma continental. En el manuscrito se abordaron una serie de preguntas íntimamente relacionadas: (1) ¿Cuál es la composición, abundancia y biomasa de los batoideos capturados con redes de arrastre en el Golfo de Tehuantepec?; (2) ¿Existen asociaciones espacio-temporales en términos de la composición, abundancia y biomasa de batoideos en el Golfo de Tehuantepec?; (3) ¿Cuántas asociaciones se identifican y cuál es la estructura de estas comunidades de batoideos?; y (4) ¿Qué factores ambientales influyen en las asociaciones s detectadas? Esta información podría servir como referencia para identificar las tendencias de la década pasada; además de constituir una base de referencia para las tendencias actuales y futuras en esta área.

El segundo artículo aborda el objetivo 5 y 6 de este trabajo. El documento describe la ecología reproductiva de la guitarra bruja *Zapteryx xyster*; la cual está catalogada en la Lista Roja de la UICN (Unión Internacional para la Conservación de la Naturaleza) como una especie con datos insuficientes para evaluar su riesgo de extinción.

El artículo tres aborda el objetivo 7 de este trabajo. Este escrito describe la presencia de la raya redonda denticulada *Urotrygon cimar* (López y Bussing, 1998) en el Golfo de Tehuantepec a partir de 101 especímenes capturados en 2009 y 2010. Con este registro, se cuenta con un total de 16 especies de batoideos capturados con arrastres de fondo, mismos que fueron usados para establecer las asociaciones (ver artículo 1, página 11).

En el cuarto artículo se aborda el último objetivo. Este escrito describe las anomalías morfológicas encontradas en 15 ejemplares de vida libre y tres embriones del género *Urotrygon.* Estas anomalías consisten en aletas pectorales con desarrollo incompleto o no fusionadas de la parte anterior, anoftalmia, ausencia de un clasper, desarrollo anormal del hígado y neoplasia en el hígado). Se analiza la localización de los ejemplares en el área de estudio y su posible causa.

La autora y los tutores esperamos que esta pequeña aportación sirva como base para tomar las medidas de manejo y conservación de las especies de batoideos demersales en el Golfo de Tehuantepec.

# IV. Artículo 1: Distribución de las asociaciones de batoideos demersales en la plataforma continental del Golfo de Tehuantepec (artículo requisito de egreso)

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# Distribution of batoid demersal assemblages on the continental shelf of the Gulf of Tehuantepec

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**Abstract.** Information on the relationship between batoid demersal assemblages and environmental factors is scarce. We captured a total of 23 414 batoids belonging to 16 species with bottom trawls at 243 sampling stations in the Gulf of Tehuantepec, Mexico. The species *Urotrygon rogersi*, *Urotrygon chilensis* and *Narcine vermiculatus* represented 70.1% of the abundance and 46.3% of the biomass. Five batoid assemblages were identified using hierarchical cluster and similarity profile analyses. Four assemblages were located at depths less than 40 m and one assemblage was located at depths between 40 and 62 m. The main batoid group was located in front of the most important lagoon complexes. The abundance biomass comparison method indicated that small species were dominant in terms of abundance in most assemblages. The set of environmental conditions and habitat characteristics (longitude, depth and sea surface temperature) present in the Gulf of Tehuantepec predicted important changes in the batoid community and affected its spatiotemporal distribution pattern.

**Additional keywords:** abundance, biomass, bottom trawls, demersal zone.

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## Introduction

The Gulf of Tehuantepec is one of three Central American areas in the Eastern Tropical Pacific with high productivity levels (Ortega-García *et al.* 2000). This productivity is the result of a combination of physical and dynamic conditions, where the most important factor is the effect of the winds that blow with great force from November to January. There is a marked seasonality in oceanographic conditions (Lluch-Cota *et al.* 1997; Tapia-García *et al.* 2007; Barton *et al.* 2009) due to these winds that affects the composition and distribution of phytoplankton (Robles-Jarero and Lara-Lara 1993; Lluch-Cota *et al.* 1997; Lara-Lara *et al.* 1998; Meave del Castillo and Hernández-Becerril 1998), zooplankton (Ayala-Duval *et al.* 1996; Färber-Lorda *et al.* 2004), benthic invertebrates (Gamboa-Contreras and Tapia-García 1998) and demersal ichthyofauna (Tapia-García 1998; Martínez-Muñoz 2012; Núñez-Orozco *et al.* 2013).

Fish are the most abundant fishing resource in the Gulf of Tehuantepec. It has been estimated that the total fish biomass is 457 679 tonnes (Mg), most of which is underused or unexploited (Acal and Arias 1990; Comisión Nacional de Acuacultura y Pesca 2017). The greatest commercial fish catches are obtained by the tuna fishery, with an average of 15 950 Mg year$^{-1}$, and the shark fishery, with an average of 4392 Mg year$^{-1}$ (Comisión Nacional de Acuacultura y Pesca 2017). However, the largest volume of fish is caught incidentally in the shrimp fishery using bottom trawls. The shrimp fishery captures ~4000 tonnes of shrimp per year, compared with 118 624 tonnes of fish (Tapia-García and García-Abad 1998; Comisión Nacional de Acuacultura y Pesca 2017). Teleosts represent ~87% of fish bycatch, whereas elasmobranchs represent ~13% of bycatch (Martínez-Muñoz 2012). The elasmobranchs caught as bycatch are primarily demersal batoids that have no economic importance in the region (Tapia-García and García-Abad 1998; Martínez-Muñoz 2012). Records indicate that 33 species of batoid fishes inhabit the Gulf of Tehuantepec (McEachran and Notarbarloto di Sciara 1995; Amezcua-Linares 1996; Castro-Aguirre and Espinosa-Pérez 1996; Carrera-Fernández *et al.* 2012; Torres-Huerta *et al.* 2013; Robertson and Allen 2015), which corresponds to 78.6% of batoid species reported for the Mexican Pacific.

According to the International Union for Conservation of Nature (IUCN) Red List (http://www.iucnredlist.org, accessed 18 December 2018), six batoid species recorded in the Gulf of Tehuantepec, namely *Aetobatus narinari* (Euphrasen, 1790), *Narcine vermiculatus* Breder, 1928, *Pseudobatos leucorhynchus* (Günther, 1867), *Mobula munkiana* Notarbartolo di Sciara, 1987, *Mobula japonica* Müller & Henle, 1841 and *Mobula thurstoni* (Lloyd, 1908), are listed as Near Threatened; three species, namely *Mobula birostris* (Walbaum, 1792); *Mobula tarapacana* (Philippi, 1892); and *Diplobatis ommata* (Jordan & Gilbert, 1890), are listed as Vulnerable; and one species, namely *Pristis pristis* (Linnaeus, 1758), is listed as Critically Endangered. There are insufficient data to evaluate an additional nine species that are frequently captured in the shrimp fishery: *Hypanus longus* (Garman, 1880), *Narcine entemedor* Jordan & Starks, 1895, *P leucorhynchus* (Günther, 1867), *Zapteryx xyster* Jordan & Evermann, 1896, *Urotrygon aspidura* (Jordan & Gilbert, 1882), *Urotrygon chilensis* (Günther, 1872), *Urotrygon munda* Gill, 1863, *Urotrygon nana* Miyake & McEachran, 1988 and *Urotrygon rogersi* (Jordan & Starks, 1895).

Information on batoids of the Gulf of Tehuantepec is scarce and refers primarily to geographic distribution and habitat (Amezcua-Linares 1996; Castro-Aguirre and Espinosa-Pérez 1996; Robertson and Allen 2015). Most of these species are not characterised as economically important; however, they face serious incidental exploitation due to the high fishing effort associated with the shrimp fishery (McEachran and Notarbarloto di Sciara 1995; Tapia-García and Gutiérrez-Díaz 1998; López-Martínez *et al.* 2012). The species caught as bycatch in the shrimp fishery have not been well documented, which results in a lack of systematic and trustworthy information on these species and how their populations are being affected (López-Martínez *et al.* 2012). This situation is particularly worrisome in the case of elasmobranchs, because they are considered species vulnerable to overexploitation due to their K-selected life history strategy (i.e. slow growth, late attainment of sexual maturity, long life spans, low fecundity), changes in ecological interactions (e.g. predation and competition), different exposure to fishing (e.g. catchability, availability, commercial value, breeding clusters) and susceptibility to other stressors, such as habitat degradation and pollution (Holden and Tucker 1974; Stevens *et al.* 2000; Marongiu *et al.* 2017). Among elasmobranchs, batoid species appear extremely vulnerable to such stressors, probably due to their distinct morphology (a large body that makes them more catchable) and gregarious behaviour, which makes them vulnerable to almost every fishing gear for demersal species, from trammel nets to coastal and offshore trawls (Bellodi *et al.* 2017).

The present study characterised the demersal batoid assemblages in shrimp fishery areas along the continental shelf in 2009 and 2010, from Salina Cruz to Puerto Madero, at depths between 16 and 62 m. Based on this information, the following questions were investigated: (1) what is the composition, abundance and biomass of batoids captured with bottom trawls in the Gulf of Tehuantepec; (2) are there spatiotemporal assemblages in terms of composition, abundance and biomass of batoids; (3) how many assemblages can be identified and what is the structure of the batoid community; and (4) what environmental factors determine the detected assemblages? This information could serve to identify trends over the past decade, and could also be used as a reference for current and future trends in this area.

## Materials and methods

The study area comprised the continental shelf of the Gulf of Tehuantepec, between Salina Cruz, Oaxaca (95°10′50″E, 16°7′89″N), and Río Suchiate, Chiapas (92°14′30″W, 16°13′N), Mexico (Fig. 1). This area is characterised by having a very narrow continental shelf on the western end and a very wide shelf on the eastern end (Carranza-Edwards *et al.* 1998). The most abundant sediment type is sand, which is widely distributed from Salina Cruz to Puerto Madero at depths between 30 and 100 m. There are also bands of mud, muddy sand and sandy mud parallel to the coast on the western end of the study area (Morales de la Garza and Carranza-Edwards 1995; Tapia-García *et al.* 2007).

The most notable characteristic of the area is the presence of strong winds that blow from the north, known locally as *Tehuanos*, which pass as a wind jet through the Chivela pass (depression of the mountain chain on the Isthmus of Tehuantepec). These winds have a direct effect on the ocean surface of the Gulf of Tehuantepec, generating anticyclonic and cyclonic gyres on each side of the wind jet (Trasviña and Barton 1997; Gallegos-García and Barberán-Falcón 1998; Chapa-Balcorta *et al.* 2015). The lateral mixing of these waters favours spawning, nursing and feeding in several species, some of which have commercial value (Trasviña *et al.* 1995; Trasviña and Barton 1997; Fernández-Álamo and Färber-Lorda 2006).

Three sampling trips were conducted in December 2009, March 2010 and June 2010 between Salina Cruz, Oaxaca (95°10′50″W, 16°7′89″N), and Puerto Madero, Chiapas (92°14′30″W, 16°13′00″N; Fig. 1). Each sampling trip lasted 15 days on average. Bottom trawls were conducted over the continental shelf at depths between 16 and 62 m. In all, 243 bottom trawls were made over an area covering ~5296 km$^2$; 84 trawls in December 2009 and 90 trawls in March 2010 were performed from the vessel *R/V UMAR*, and 69 trawls were performed from the vessel *C/V FIPESCO 22* in June 2010. The nets used were 18 m long with a 5-cm mesh size; different tow speeds (ranging from 2.2 to 11.1 km h$^{-1}$) and times (ranging from 2 to 4.5 h) were used at each station. The start and end point of each trawl were recorded using a global positioning system (GPS) device. The horizontal aperture (14 m from the *R/V UMAR* and 15 m from the *C/V FIPESCO 22*) was calculated using the method proposed by Prado and Dremière (1988). The total area covered was calculated, and the abundance and biomass were standardised to a sampled area of 10 000 m$^2$. Captured individuals were identified to species level, counted and weighed.

Depth was recorded *in situ* using an echo sounder. Sea surface temperature (SST) was obtained from Level 3 (L3) SST_11 daytime satellite images with a spatial resolution of 4.63 km, obtained from the Aqua moderate-resolution imaging spectroradiometer (MODIS) satellite sensor corresponding to the month of sampling. These images were obtained from the SeaWiFS Project (NASA/Goddard Space Flight Center, see

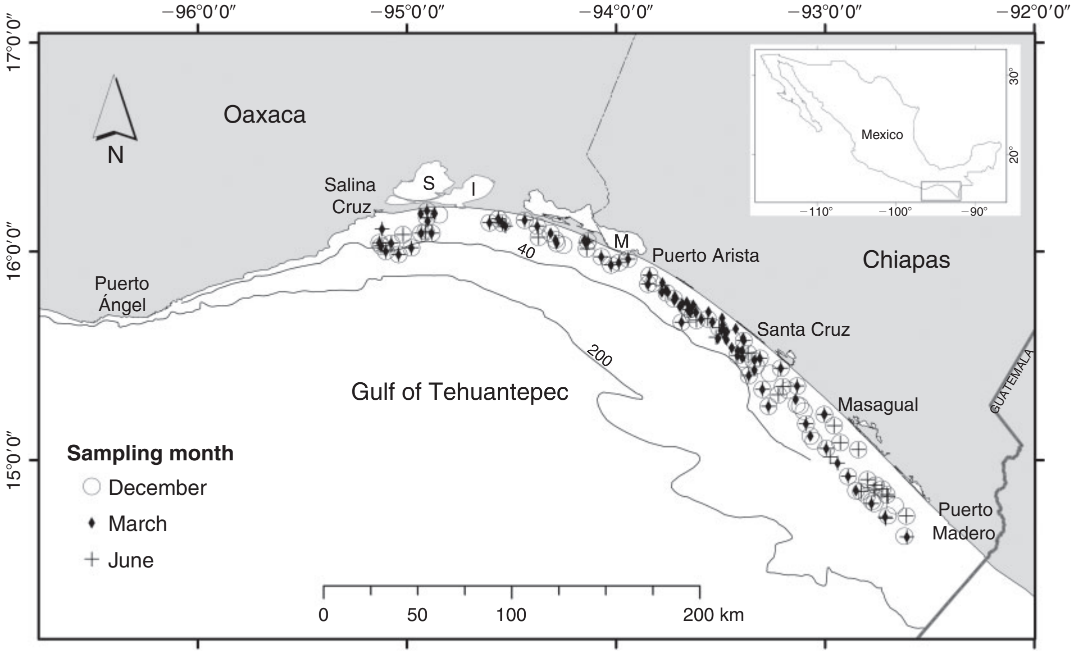

**Fig. 1.** Location of the 243 bottom trawls in the Gulf of Tehuantepec. S, Superior Lagoon; I, Inferior Lagoon; M, Mar Muerto Lagoon.

https://oceancolor.gsfc.nasa.gov/SeaWiFS/, accessed 15 June 2018) and processed using SeaDAS (SeaWiFS Data Analysis System, https://seadas.gsfc.nasa.gov) software. A map of sediments of the Gulf of Tehuantepec was obtained from Morales de la Garza and Carranza-Edwards (1995). This map was digitised and georeferenced using ArcGIS software (Environmental Systems Research Institute, Redlands, CA, USA) to obtain information for each station. This software was also used to create abundance and biomass maps for each sampling trip and for the most abundant species.

Cumulative species curves were constructed using the Clench (1979) equation to evaluate whether the number of bottom trawls analysed was large enough to appropriately describe batoid composition. The order in which samples were added to the curve was randomised 999 times to smooth the entry of new species. The coefficient of determination was used as an indicator of the goodness of fit, and slope values below 0.1 were considered asymptotic.

Data for species abundance and biomass, as well as environmental variables (latitude, longitude, SST, depth and sediment type) were analysed using PRIMER statistics package for Windows (ver. 6, PRIMER-e, see www.primer-e.com). Data matrices of species abundance and biomass were constructed for each bottom trawl. A square-root transformation was performed on the matrices to normalise data and avoid bias (Clarke and Warwick 2001). The Bray–Curtis index was used to quantify the similarity in species composition between sampling locations. A hierarchical CLUSTER analysis was applied to the matrices to characterise the spatial patterns of the batoid community during each sampling trip, using the average grouping model to group samples. The significance of group formation in the cluster analysis was determined using the similarity profile with the SIMPROF routine in PRIMER 6, which applies a permutation test to each node of the dendrogram to identify significant assemblage patterns in samples that were not structured *a priori* (Clarke *et al.* 2008). A total of 1000 permutations was used to calculate an average similarity profile; 999 simulated profiles were generated, and the chosen significance level was 5%.

Similarity percentage analysis (SIMPER) was used to identify the species that contributed the most to the average similarity or dissimilarity between the assemblages and months of sampling. For each sampling trip, the environmental variables were prescreened for multicollinearity using draftsman plots, and any subsets of strongly collinear variables ($>0.95$) were reduced to a single representative variable. After this selection, only longitude, SST and depth were retained. A correlation analysis between biotic and environmental data (BIOENV) was used to estimate the influence of habitat configuration (latitude, longitude, SST, depth, sediment type) on the spatial distribution of the batoid assemblages. This process selects the environmental variables that maximise the degree of correlation (Spearman's ρ) between the biotic and environmental similarity matrices (Bray–Curtis for biota and Euclidean distance for environmental variables; Clarke and Warwick 2001).

The dominance and biodiversity pattern of batoids were analysed graphically for each assemblage using k-dominance cumulative curves based on species abundances, which means that Assemblage A can be considered to exhibit more dominance than Assemblage B if, for all possible values of k, the k-dominance of A is greater than or equal to the k-dominance of B. Dominance is the reverse of equitability and has an inverse relationship with diversity (Lambshead *et al.* 1983). The abundance biomass comparison (ABC) method was used to compare dominance in terms of abundance with dominance

**Table 1. Batoid species caught in the Gulf of Tehuantepec and their global International Union for Conservation of Nature Red List assessment status (as of 15 February 2017; http://www.iucnredlist.org, accessed 18 December 2018)**

Comparison of abundance (number of specimens) and biomass of the batoid species caught with bottom trawls in the Gulf of Tehuantepec during three sampling trips. NT, near threatened; LC, least concern; DD, data deficient; NE, not evaluated

| FAMILY and species | Red List status | December 2009 | | March 2010 | | June 2010 | |
|---|---|---|---|---|---|---|---|
| | | Abundance (*n*) | Biomass (kg) | Abundance (*n*) | Biomass (kg) | Abundance (*n*) | Biomass (kg) |
| NARCINIDAE | | | | | | | |
| *Narcine entemedor* Jordan & Starks, 1895 | DD | 101 | 28.8 | 73 | 43.1 | 85 | 28.8 |
| *Narcine vermiculatus* Breder, 1928 | NT | 1762 | 84.6 | 1288 | 84.3 | 1228 | 72.8 |
| RHINOBATIDAE | | | | | | | |
| *Pseudobatos glaucostigmus* (Jordan & Gilbert, 1883) | DD | 9 | 3.2 | 13 | 4.9 | – | – |
| *Pseudobatos leucorhynchus* (Günther, 1867) | NT | 546 | 92.5 | 1484 | 249.2 | 227 | 39 |
| *Zapteryx xyster* Jordan & Evermann, 1896 | DD | 20 | 9.9 | 100 | 58.1 | 15 | 4.7 |
| DASYATIDAE | | | | | | | |
| *Hypanus longus* (Garman, 1880) | DD | 75 | 199 | 213 | 254 | 32 | 68.6 |
| GYMNURIDAE | | | | | | | |
| *Gymnura marmorata* (Cooper, 1864) | LC | 82 | 27 | 232 | 125.6 | 90 | 21.1 |
| AETOBATIDAE | | | | | | | |
| *Aetobatus narinari* (Euphrasen, 1790) | NT | 101 | 143.9 | 22 | 27 | 40 | 64.8 |
| RHINOPTERIDAE | | | | | | | |
| *Rhinoptera steindachneri* Evermann & Jenkins, 1891 | LC | 50 | 57.1 | 91 | 82.3 | 300 | 341.6 |
| MOBULIDAE | | | | | | | |
| *Mobula munkiana* Notarbartolo-di-Sciara, 1987 | NT | – | – | 2 | 2.1 | – | – |
| UROTRYGONIDAE | | | | | | | |
| *Urobatis halleri* (Cooper, 1863) | LC | 7 | 3.3 | 6 | 4.4 | – | – |
| *Urotrygon aspidura* (Jordan & Gilbert, 1882) | DD | 99 | 6.2 | 121 | 13.7 | 68 | 3.1 |
| *Urotrygon chilensis* (Günther, 1872) | DD | 1910 | 159.2 | 2719 | 334.3 | 1190 | 118.6 |
| *Urotrygon cimar* López S. & Bussing, 1998 | NE | 105 | 5.4 | 449 | 28.9 | 71 | 5.2 |
| *Urotrygon nana* Miyake & McEachran, 1988 | DD | 851 | 23.6 | 479 | 16.4 | 626 | 17 |
| *Urotrygon rogersi* (Jordan & Starks, 1895) | DD | 1025 | 224.1 | 3873 | 668.3 | 1129 | 70.6 |

in terms of biomass (Clarke 1990). Briefly, at a normal state without disturbance, the community is dominated by slow-growing, large and late-maturing species, and therefore the biomass curve is above the abundance curve. When there is a perturbation, fast-growing, small, early maturing and opportunistic species dominate, so that the biomass curve is below the abundance curve. The W statistic represents the area between the two curves. Thus, a negative value ($<0$) indicates that the biomass curve is below the abundance curve and suggests a disturbed community. A positive value ($>0$) indicates an undisturbed community, and a value close to zero ($\sim 0$) indicates a community with a moderate disturbance (Warwick 1986; Clarke and Warwick 2001).

## Results

During the sampling period 23 414 batoids (4150 kg) belonging to eight families and 16 species were recorded (Table 1). The species accumulation curves for each sampling trip are shown in Fig. 2; the Clench model slope values were $<0.1$, with $R^2 > 0.9$. There was a total of 15 estimated species in December, 16 in March and 12 in June. Therefore, we obtained over 95% of the batoid composition in the Gulf of Tehuantepec in this study.

The Urotrygonidae family was the best represented in terms of number of species ($n = 6$), abundance (64.0%) and biomass (43.4%). The species *U. rogersi*, *U. chilensis* and *N. vermiculatus* were the most abundant during the three sampling trips, representing 70.1% of total abundance, whereas *U. rogersi*, *U. chilensis*, *H. longus* and *Rhinoptera steindachneri* represented 65.8% of total biomass.

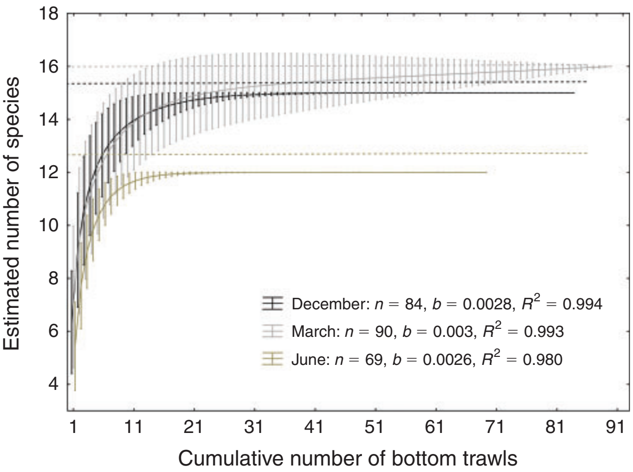

**Fig. 2.** Accumulation curve for batoid species caught with bottom trawls in the Gulf of Tehuantepec, Mexico. Data are the mean ± 95% confidence interval. Each curve corresponds to a sampling trip (December, March and June), with the number of bottom trawls ($n$), slope ($b$) and coefficient of determination ($R^2$) indicated.

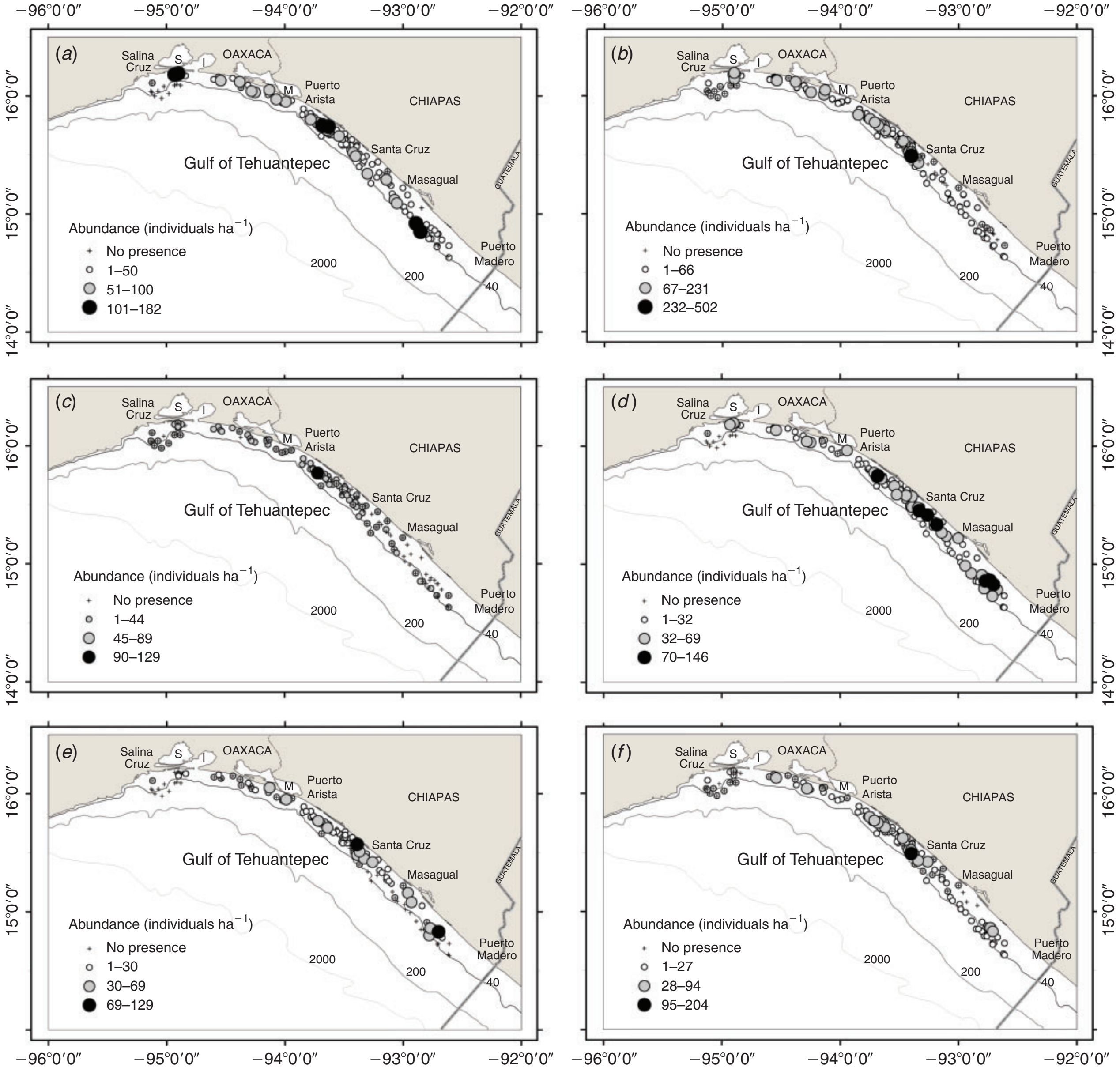

**Fig. 3.** Abundance distribution maps of the most important batoid species in the Gulf of Tehuantepec: (*a*) *Urotrygon chilensis*, (*b*) *Urotrygon rogersi*, (*c*) *Urotrygon cimar*, (*d*) *Narcine vermiculatus*, (*e*) *Urotrygon nana* and (*f*) *Pseudobatos leucorhynchus.* S, Superior Lagoon; I, Inferior Lagoon; M, Mar Muerto Lagoon.

Fig. 3 shows abundance maps for the six most abundant batoid species in the Gulf of Tehuantepec; the data correspond to the abundance during the three sampling trips. *U. chilensis* was homogeneous over the study area, with three equidistant high abundance points. *U. cimar* was distributed approximately homogeneously at low abundances, with a high abundance point near Puerto Arista. Most *U. rogersi* individuals were located between Mar Muerto Lagoon and Santa Cruz, whereas the greatest *N. vermiculatus*, *U. nana* and *P. leucorhynchus* concentrations were found off the eastern coast of the Gulf of Tehuantepec, between Puerto Arista and Masagual, which highlights the considerable abundances found in front of Santa Cruz.

In terms of seasonal variation, the greatest abundance (11 165 specimens) and total biomass (1996 kg) of batoids were recorded in March 2010, representing 48.5 and 50.9% of total capture respectively (Table 1).

Longitude, depth and SST best explained the seasonal variation in the batoid community in December 2009 ($\rho_w = 0.587$; Table 2). These three variables explained 62% of the variation in the abundance and biomass of batoids, whereas in March and June 2010 the variables of longitude and depth explained 66 and 62% of the variation in the abundance and biomass of batoids respectively. Longitude alone was the best single environmental predictor of differences in batoids.

**Table 2. BIOENV analysis, showing the best variable combinations**

Data show Spearman correlations ($\rho_w$) for each sampling trip. All combinations are significant. Lon, longitude; SST, sea surface temperature; Dep, depth

| Combinations | Abundance | | | Biomass | | |
|---|---|---|---|---|---|---|
| | December 2009 | March 2010 | June 2010 | December 2009 | March 2010 | June 2010 |
| Lon–SST–Dep | 0.617 | 0.642 | | 0.617 | 0.607 | |
| Lon–Dep | 0.609 | 0.663 | 0.521 | 0.615 | 0.642 | 0.515 |
| Lon | 0.487 | 0.566 | 0.447 | 0.495 | 0.588 | 0.445 |

CLUSTER analysis identified two main groups during the three sampling trips; the first corresponded to locations with depths between 36 and 62 m (Fig. 4) and the second corresponded to locations at depths between 16 and 40 m. SIMPROF applied to the species abundance data identified four significantly different assemblages ($P < 0.01$) in December 2009 and March 2010, and three assemblages in June 2010; these can be observed in the CLUSTER dendrograms (Fig. 4*a*–*c*). The biomass data offered similar results; therefore, we only present the cluster results obtained for abundances. Four assemblages were identified in December 2009 and March 2010. These assemblages were categorised as upper intermediate shelf-dwellers (UIS), sandy bottom off Oaxaca (SBO), shallow water off Chiapas (SWC) and sandy bottom off Chiapas (SBC). The assemblages of June 2010 were classified as UIS, SBO and sandy bottom and shallow water off Chiapas (SBSW).

The SBO assemblage was located off the eastern Oaxaca coast and part of the western Chiapas coast, in front of the most important lagoon systems, namely Superior, Inferior and Mar Muerto (Fig. 5). The smallest spatial extension of this assemblage occurred in March 2010, and the largest spatial extension was observed in June 2010 (Fig. 5*c*). This assemblage occurred mainly over sandy bottoms, at a mean depth of 29 m (Table 3). The UIS assemblage occurred off the eastern Oaxaca coast, in front of Salina Cruz and the Superior Lagoon. It was distributed primarily over sandy mud bottoms at a mean depth of 45 m with SST variations of up to 5°C (Table 3).

The SWC and SBSW assemblages were located off the Chiapas coast (Fig. 5). The SBSW occupied the SWC and SBC areas found in December 2009 and March 2010. The SWC and SBSW assemblages were distributed over a region with a variety of sediments composed of sand, silty sand, sandy silt and silt (Table 3). The mean depths of the SWC and SBSW assemblages were 29 and 31 m respectively, with mean SSTs of 29.6 and 30.4°C respectively. The SBC assemblage was located off the western Chiapas coast between Santa Cruz and Puerto Madero, over sandy and silty sediments, at a mean depth of 29.4 m and mean SST of 29.4°C.

The k-dominance curve indicated that the SBO assemblage was the most diverse in terms of batoid fish species (Fig. 6). The UIS assemblage showed high species dominance (Fig. 6). The SBC assemblage was second in terms of diversity in December 2009, and first in species dominance in March 2010. The greatest abundance and average biomass were recorded in March 2010 in the SBO and SWC assemblages (Table 3), especially in the region between Puerto Arista and Santa Cruz (Fig. 5).

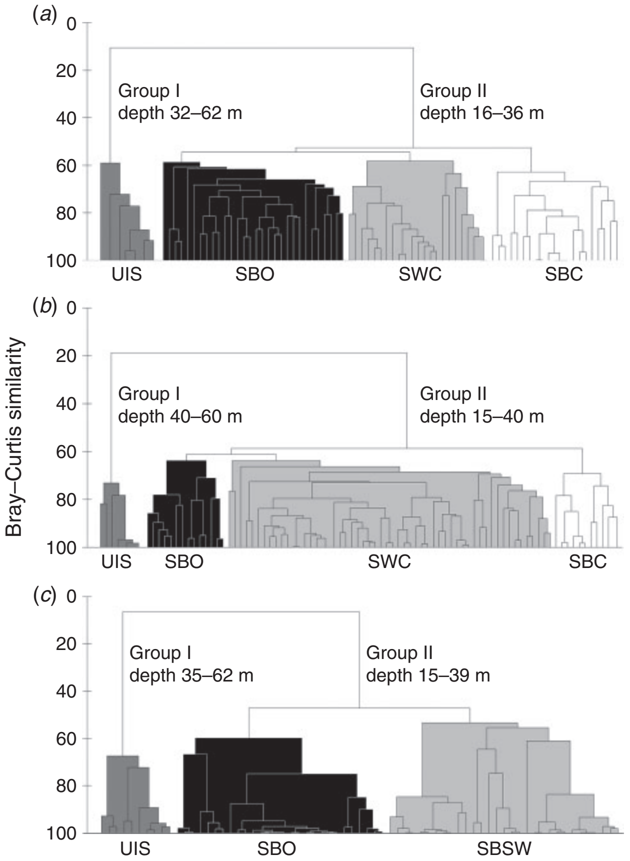

**Fig. 4.** Cluster analysis conducted using abundance values recorded during three sampling trips: (*a*) December 2009, (*b*) March 2010 and (*c*) June 2010. SBO, sandy bottoms off Oaxaca; UIS, upper intermediate shelf-dwellers; SWC, shallow water off Chiapas; SBC, sandy bottoms off Chiapas; SBSW, sandy bottoms and shallow water off Chiapas.

The similarity in species composition of the assemblages (SIMPER, average similarity: 64–77%) indicated homogeneous assemblages (Table 4). The species *U. chilensis*, *U. rogersi* and *N. vermiculatus* contributed significantly to the similarity between SBO, SBC, SWC and SBSW, providing over 48% of similarity. Other species, such as *U. nana*, *Urotrygon cimar*, *U. aspidura*, *Gymnura marmorata*, *N. entemedor*, *R. steindachneri*, *H. longus*, *A. narinari* and *P. leucorhynchus*, contributed less than 18% to similarity. The species *Z. xyster*, *N. entemedor*, *H. longus* and *U. cimar* represented over 80%

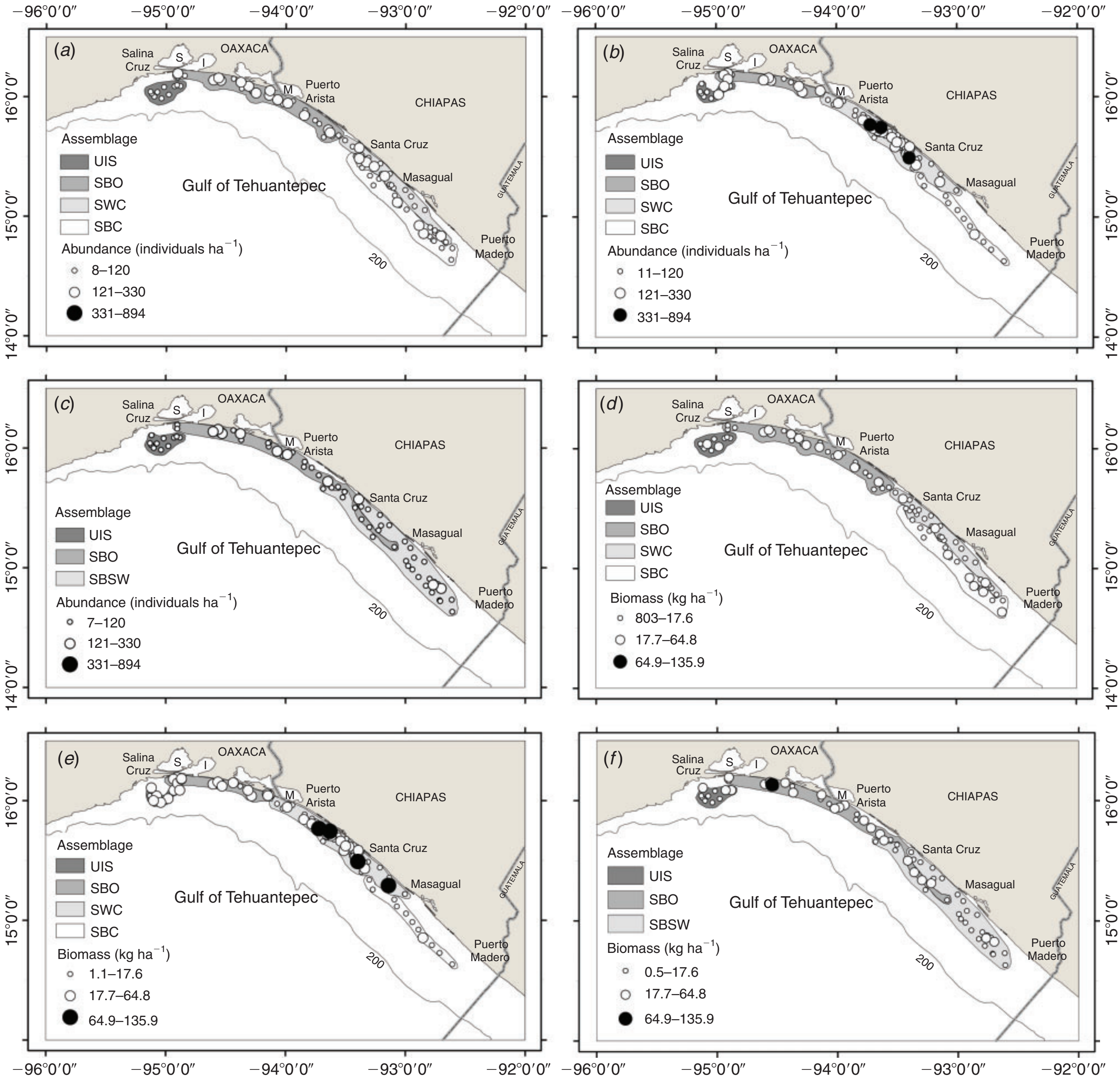

**Fig. 5.** (*a–c*) Abundance maps and (*d–f*) standardised biomass of three sampling trips in the Gulf of Tehuantepec in December 2009 (*a*, *d*), March 2010 (*b*, *e*) and June 2010 (*c*, *f*). SBO, sandy bottoms off Oaxaca; UIS, upper intermediate shelf-dwellers; SWC, shallow water off Chiapas; SBC, sandy bottoms off Chiapas; SBSW, sandy bottoms and shallow water off Chiapas; S, Superior Lagoon; I, Inferior Lagoon; M, Mar Muerto Lagoon.

similarity in the UIS assemblage. Values of dissimilarity of >75% were observed between UIS and SBO, as well as among SBC, SWC and SBSW.

The abundance and biomass curves indicated that biomass was slightly below abundance in most assemblages and the negative value of the *W* statistic indicated that these communities exhibited disturbance (Fig. 7). The biomass and abundance coincided slightly and the positive value (close to zero) of the *W* statistic indicated that three communities (SBC and UIS in December 2009, and SBO in March 2010) exhibited a moderate degree of disturbance.

## Discussion

In this study, 16 of the 33 batoid species recorded for the Gulf of Tehuantepec were captured using bottom trawling. Of the 17 unrecorded species, 6 are demersal: *Hypanus dipterurus* (Jordan & Gilbert, 1880); *Urobatis concentricus* Osburn & Nichols, 1916; *U. munda* Gill, 1863; *Pseudobatos prahli* Acero & Franke, 1995; *Pseudobatos planiceps* Garman, 1880; and *Aetomylaeus asperrimus* (Gilbert, 1898). These species are probably distributed in waters less than 16 m deep or more than 62 m deep (outside the range of this study). The remaining 11

**Table 3. Characteristics of the study sites**

Mean (±s.e.m.) of environmental and ecological parameters per assemblage, obtained from cluster analysis (see Fig. 2) of samples obtained over the continental platform of the Gulf of Tehuantepec. The assemblages were as follows: sandy bottoms off Oaxaca (SBO), upper intermediate shelf-dwellers (UIS), shallow water off Chiapas (SWC), sandy bottoms off Chiapas (SBC) and sandy bottoms and shallow water off Chiapas (SBSW). SST, sea surface temperature

| | December 2009 | | | | March 2010 | | | | June 2010 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | SBO | SWC | SBC | UIS | SBO | SWC | SBC | UIS | SBO | SBSW | UIS |
| Environmental parameter | | | | | | | | | | | |
| Latitude | 15°57′17″ ± 0°10′39″ | 15°15′55″ ± 0°17′10″ | 15°2′19″ ± 0°17′11″ | 16°2′44″ ± 0°2′23″ | 16°7′54″ ± 0°3′3″ | 15°40′58″ ± 0°11′14″ | 15°0′23″ ± 0°13′29″ | 16°2′35″ ± 0°2′32″ | 15°51′57″ ± 0°17′34″ | 15°7′54″ ± 0°21′29″ | 16°2′44″ ± 0°2′23″ |
| Longitude | 94°7′18″ ± 0°24′32″ | 93°6′33″ ± 0°14′34″ | 92°59′17″ ± 0°17′10″ | 95°1′7″ ± 0°5′26″ | 94°34′5″ ± 0°17′43″ | 93°36′32″ ± 0°16′26″ | 92°57′34″ ± 0°12′32″ | 95°2′31″ ± 0°5′29″ | 93°59′53″ ± 0°30′7″ | 93°3′48″ ± 0°28′50″ | 95°1′7″ ± 0°5′26″ |
| SST (°C) | 28.7 ± 0.7 | 29.2 ± 0.1 | 29.2 ± 0.1 | 26.7 ± 0.2 | 27.5 ± 0.8 | 29.1 ± 0.4 | 29.5 ± 0.07 | 26.0 ± 0.4 | 30.8 ± 0.4 | 30.4 ± 0.3 | 30.6 ± 0.08 |
| Depth (m) | 29.5 ± 4.9 | 27.2 ± 3.9 | 37.6 ± 3.9 | 45.4 ± 9.6 | 24.6 ± 5.5 | 27.8 ± 4.6 | 38.5 ± 4.1 | 43.2 ± 12.9 | 29.3 ± 5.7 | 31.4 ± 8.2 | 45.4 ± 9.6 |
| Sediment type (%) | | | | | | | | | | | |
| Sandy bottom | 86.7 | – | 61.9 | – | 71.4 | 40.0 | 75.0 | – | 82.1 | 30.0 | – |
| Sandy mud bottom | 13.3 | 8.7 | 28.6 | – | 28.6 | 34.6 | 25.0 | – | 17.9 | 26.7 | – |
| Mud sandy bottom | – | 82.6 | 9.5 | 100.0 | – | 23.6 | – | 100 | – | 36.6 | 100.0 |
| Mud bottom | – | 8.7 | – | – | – | 1.8 | – | – | – | 6.7 | – |
| Ecological parameters | | | | | | | | | | | |
| Number of species | 10 | 9 | 8 | 5 | 12 | 10 | 5 | 8 | 8 | 7 | 3 |
| Abundance (individuals ha$^{-1}$) | 88 ± 38 | 63 ± 53 | 94 ± 58 | 22 ± 14 | 135 ± 75 | 145 ± 148 | 50 ± 44 | 81 ± 33 | 110 ± 53 | 63 ± 67 | 24 ± 12 |
| Biomass (kg ha$^{-1}$) | 16.0 ± 12.4 | 15.9 ± 14.6 | 6.7 ± 6.8 | 13.8 ± 6.8 | 27.7 ± 8.8 | 25.1 ± 26.5 | 5.4 ± 4.8 | 24.9 ± 11.1 | 23.5 ± 13.3 | 5.4 ± 6.7 | 14.0 ± 9.5 |

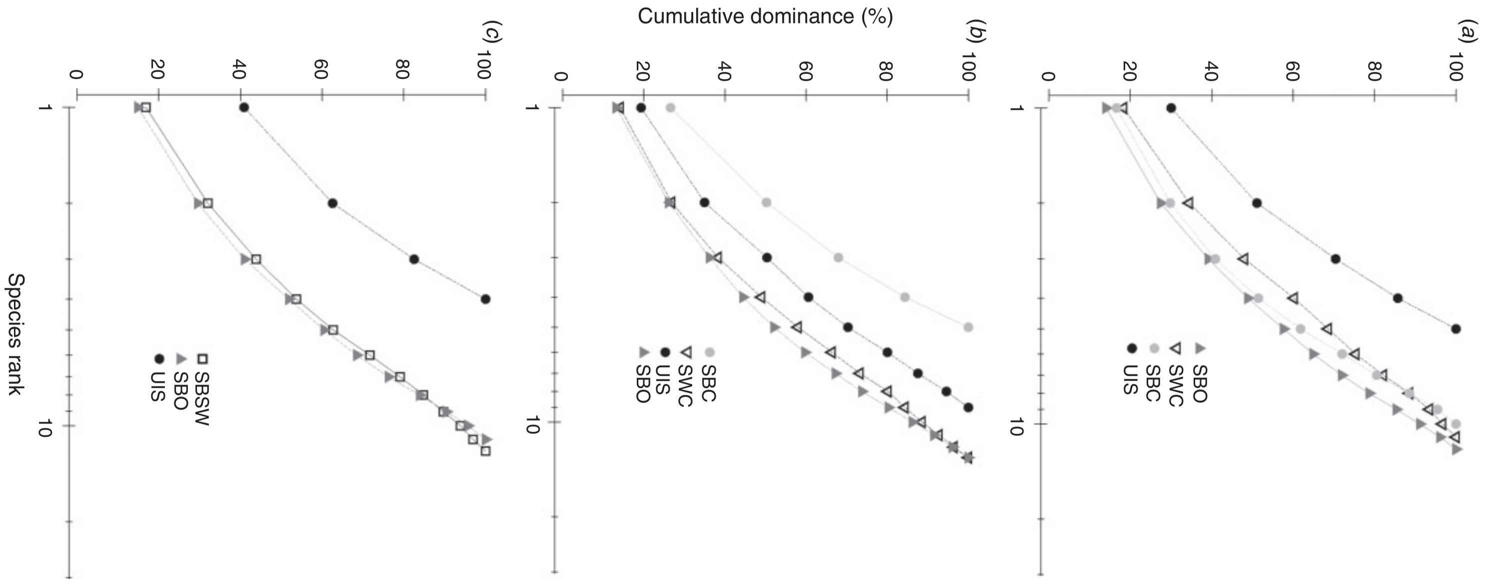

**Fig. 6.** Dominance curves for batoid communities in the Gulf of Tehuantepec based on total abundance in (*a*) December 2009, (*b*) March 2010 and (*c*) June 2010. SBO, sandy bottoms off Oaxaca; UIS, upper intermediate shelf-dwellers; SWC, shallow water off Chiapas; SBC, sandy bottoms off Chiapas; SBSW, sandy bottoms and shallow water off Chiapas.

**Table 4. Results of similarity percentage analysis (SIMPER) among assemblages, showing the species that contributed most to the differences**
SBO, sandy bottoms off Oaxaca; UIS, upper intermediate shelf-dwellers; SWC, shallow water off Chiapas; SBC, sandy bottoms off Chiapas; SBSW, sandy bottoms and shallow water off Chiapas

| Species | Contribution (%) | | | | |
|---|---|---|---|---|---|
| | SBO | UIS | SWC | SBC | SBSW |
| December 2009 | | | | | |
| *Urotrygon chilensis* | 18.59 | | 22.25 | 18.45 | – |
| *Narcine vermiculatus* | 16.93 | | 31.55 | 20.34 | – |
| *Urotrygon rogersi* | 16.69 | | 2.16 | 18.26 | – |
| *Pseudobatos leucorhynchus* | 13.22 | | 8.41 | 18.68 | – |
| *Gymnura marmorata* | 10.6 | | 4.73 | 0.23 | – |
| *Narcine entemedor* | 9.5 | 29.74 | | | – |
| *Urotrygon nana* | 7.34 | | 25.63 | 0.09 | – |
| *Urotrygon cimar* | 3.8 | | | 2.45 | – |
| *Hypanus longus* | 1.22 | 24.17 | 0.29 | 8.27 | – |
| *Zapteryx xyster* | 1.11 | | | | – |
| *Urotrygon aspidura* | 0.75 | 26.36 | 4.16 | | – |
| *Rhinoptera steindachneri* | 0.19 | | | 0.52 | – |
| *Aetobatus narinari* | 0.06 | | 0.83 | 12.7 | – |
| *Pseudobatos glaucostigma* | | 14.56 | | | – |
| *Urobatis halleri* | | 5.16 | | | – |
| March 2010 | | | | | |
| *Urotrygon rogersi* | 21.27 | | 17 | 20.66 | – |
| *Urotrygon chilensis* | 14.46 | | 19.77 | 29.73 | – |
| *Narcine vermiculatus* | 13.02 | | 14.46 | 27.07 | – |
| *Gymnura marmorata* | 11.79 | | 5.28 | | – |
| *Urotrygon cimar* | 11.25 | 22.9 | 11.7 | 4.68 | – |
| *Rhinoptera steindachneri* | 9.66 | | | | – |
| *Urotrygon aspidura* | 6.21 | | | | – |
| *Hypanus longus* | 5.94 | 17.58 | 2.94 | | – |
| *Pseudobatos leucorhynchus* | 2.64 | | 16.23 | | – |
| *Narcine entemedor* | 2.53 | 18.82 | 0.1 | | – |
| *Zapteryx xyster* | 0.59 | 27.71 | 0.05 | | – |
| *Pseudobatos glaucostigma* | 0.53 | 7.7 | | | – |
| *Urotrygon nana* | 0.09 | | 11.86 | | – |
| *Aetobatus narinari* | | | 0.23 | 17.85 | – |
| *Rhinoptera steindachneri* | | | 0.23 | | – |
| June 2010 | | | | | |
| *Urotrygon chilensis* | 23.76 | | – | – | 22.81 |
| *Urotrygon rogersi* | 23.44 | 1.04 | – | – | 10.35 |
| *Narcine vermiculatus* | 16.04 | | – | – | 38.77 |
| *Urotrygon cimar* | 8.49 | | – | – | |
| *Rhinoptera steindachneri* | 8.15 | | – | – | |
| *Gymnura marmorata* | 7.69 | | – | – | 0.44 |
| *Narcine entemedor* | 7.3 | | – | – | |
| *Urotrygon nana* | 2.38 | | – | – | 10.56 |
| *Pseudobatos leucorhynchus* | 1.94 | 2.9 | – | – | 13.94 |
| *Hypanus longus* | 0.66 | | – | – | |
| *Aetobatus narinari* | 0.15 | | – | – | 0.81 |
| *Zapteryx xyster* | | 96.07 | – | – | |
| *Urotrygon aspidura* | | | – | – | 2.32 |

unrecorded species are pelagic, reef-associated, estuarine or deep-water species (Allen and Robertson 1994; Castro-Aguirre and Espinosa-Pérez 1996; Robertson and Allen 2015; R. Froese and D. Pauly, FishBase, ver. 10/2017, see www.fishbase.org, accessed 20 September 2018).

The 16 batoid species captured in the Gulf of Tehuantepec formed four assemblages during the *Tehuanos* wind season (December and March) and three assemblages during the rainy season (June). These batoid assemblages coincide with the community of fish, crustaceans and cephalopods identified by Bianchi (1991). The SBO and SBC assemblages are part of what was called by Bianchi (1991) the ‘sandy bottom community’, which extends from Salina Cruz, Mexico, to San José, Guatemala. The SWC assemblage corresponded to the coastal water community located between San Marcos, Mexico, and the central Guatemala region. The UIS assemblage identified in this study from 12 stations covering a small area ($\sim$215 km$^2$) in front of Salina Cruz was part of the 'upper intermediate shelf' community, which is one of the most extensive associations described by Bianchi (1991).

Depth and longitude were the main characteristics that determined the structure of the batoid community of the Gulf of Tehuantepec, although temperature played an important role early in the *Tehuanos* wind season. Studies of elasmobranch assemblages that cover a wide depth range (up to 1700 m) have indicated that depth is the main factor that determines the distribution of elasmobranchs (Massutí and Moranta 2003; Gouraguine *et al.* 2011; Bottari *et al.* 2014; Clarke *et al.* 2016). The present study covered a lower depth range (from 16 to 62 m) over a wide geographic region that has been classified into three hydrographic regimes (Lavín *et al.* 1992; Trasviña *et al.* 1995; Chapa-Balcorta *et al.* 2015): (1) a western regime characterised by the presence of mesoscale eddies and coastal upwelling that transports colder and saltier water than the typical eastern tropical waters; (2) a central regime directly affected by great mixing generated by the *Tehuanos* winds; and (3) an eastern regime, which is less affected by the *Tehuanos*, and maintains the surface thermohaline characteristics of Eastern Tropical Pacific Ocean waters. Several studies performed on demersal fauna assemblages over wide geographic areas have linked the demersal community structure to environmental variability (Bianchi 1991, 1992*a*, 1992*b*; Fariña *et al.* 1997*a*, 1997*b*; Labropoulou and Papaconstantinou 2004).

Generally, the greatest species richness, diversity, abundance and biomass of batoids were located in the central region of the Gulf of Tehuantepec (in the SBO assemblage), between Salina Cruz and Puerto Arista, at a mean depth of 27 m. This coincides with the largest biomass of zooplankton (Färber-Lorda *et al.* 1994; Ayala-Duval *et al.* 1996), benthic invertebrates (Gamboa-Contreras and Tapia-García 1998) and demersal fish (Acal and Arias 1990; Tapia-García 1998; (Martínez-Muñoz 2012) reported for the central region of the Gulf of Tehuantepec. The high productivity in the western and central regions of the gulf are due primarily to upwelling and vertical mixing processes, as subsuperficial waters bring high concentrations of phosphates, silicates, nitrites and nitrates, giving rise to a trophic web that feeds a rich biological community (Robles-Jarero and Lara-Lara 1993; Ortega-García *et al.* 2000; Chapa-Balcorta *et al.* 2015).

The greatest diversity, abundance and biomass of batoids, and of other fish and invertebrates in the central region of the Gulf of Tehuantepec, indicate that the distribution of potential prey could also be an important element that could affect habitat selection by batoids. Feeding studies of batoids in the Gulf of Tehuantepec have indicated that the main prey of four species (*U. chilensis*, *U. rogersi*, *N. vermiculatus* and *R. steindachneri*) recorded in this study were amphipods, ophiurans, decapods, polychaetes, stomatopods, molluscs and fish (Guzmán-Castellanos 2010; Díaz-Carballido 2011, 2015). Several authors have shown that the heterogeneous distribution of benthic and demersal batoids overlapped the regions of greatest abundance of potential prey, such as invertebrates and fish, in several regions of the Atlantic (Holden and Tucker 1974; Skjæraasen and Bergstad 2000; Lucifora *et al.* 2012).

The lowest values of abundance and biomass of batoids in the central region of the Gulf of Tehuantepec occurred early during the *Tehuanos* wind season (December). Several factors appear to contribute to this geographical differentiation (depth, SST and longitude). The presence of strong *Tehuanos* winds in this region of the gulf results in changes to the water column, leading to mixing of the surface layer (50–60 m) and considerable variability in both temperature (up to 10°C), salinity (up to 2.2 PSU) and dissolved oxygen (up to 3.0 mL L$^{-1}$; Trasviña *et al.* 1995; Tapia-García *et al.* 2007). Observations conducted in the western region of the Gulf of Tehuantepec during a *Tehuanos* event (A. M. Torres-Huerta, unpubl. data) showed a great number of batoids concentrated in shallow waters (depth 4 m), possibly in search of warm waters rich in dissolved oxygen. We hypothesised that the decrease in temperature and dissolved oxygen during the *Tehuanos* winds could influence vertical movements of the batoids towards adjacent waters in search of optimal ecophysiological niches. Physiologically, water temperature is considered the most important variable that influences the metabolism, reproduction, somatic growth, horizontal and vertical distribution, behaviour and short-term habitat use of fishes (Carey *et al.* 1971; Magnuson *et al.* 1979; Neill 1979). In addition, dissolved oxygen has been considered the dominant ecological factor determining macrobenthic biomass and species composition in the upwelling area off Peru and northern Chile (Rosenberg *et al.* 1983; Gutiérrez *et al.* 2006). Seasonal movement patterns prompted by changes in temperature have been observed in elasmobranch species such as *Mustelus henlei* (Gill, 1863), *Myliobatis californicus* Gill, 1865, *Triakis semifasciata* Girard, 1855 and *Pseudobatos productus* (Ayres, 1854) off the California coast (Hopkins and Cech 2003; Espinoza *et al.* 2011; Farrugia *et al.* 2011). Although in the present study we only have abundance and biomass data, it would be important to continue with studies on the effect of *Tehuanos* winds on batoid dispersion.

The species composition in the SBO, SBC, SWC and SBSW assemblages was homogeneous, with over 90% similarity. *U. chilensis*, *N. vermiculatus*, and *U. rogersi* were the most abundant species, with a wide distribution along the study area at depths up to 42 m. These three species represented 70.1% of the abundance of demersal batoids in the Gulf of Tehuantepec, with the greatest concentrations of *U. chilensis* and *U. rogersi* in the central region and the greatest concentrations of *N. vermiculatus* in the eastern region. *N. vermiculatus* and *U. chilensis* were characterised previously by Tapia-García and García-Abad (1998) as very abundant species in the gulf. Species from the *Narcine* and *Urotrygon* genus are the most abundant species in the demersal batoid community in regions adjacent to the Gulf of Tehuantepec, such as Guatemala, Costa Rica and Colombia (Ixquiac-Cabrera *et al.* 2009; Clarke *et al.* 2016; Navia and Mejía-Falla 2016).

Other less abundant species, such as *U. nana*, *R. leucorhynchus*, *G. marmorata*, *R. steindachneri* and *A. narinari*, had the greatest concentrations of individuals in the central region of the Gulf of Tehuantepec (between Puerto Arista and Masagual). These species have also been reported as having a low abundance at depths less than 50 m in the Pacific region of Costa Rica (Clarke *et al.* 2016). Finally, the assemblage found over the greatest depths (USI) was composed primarily by the species

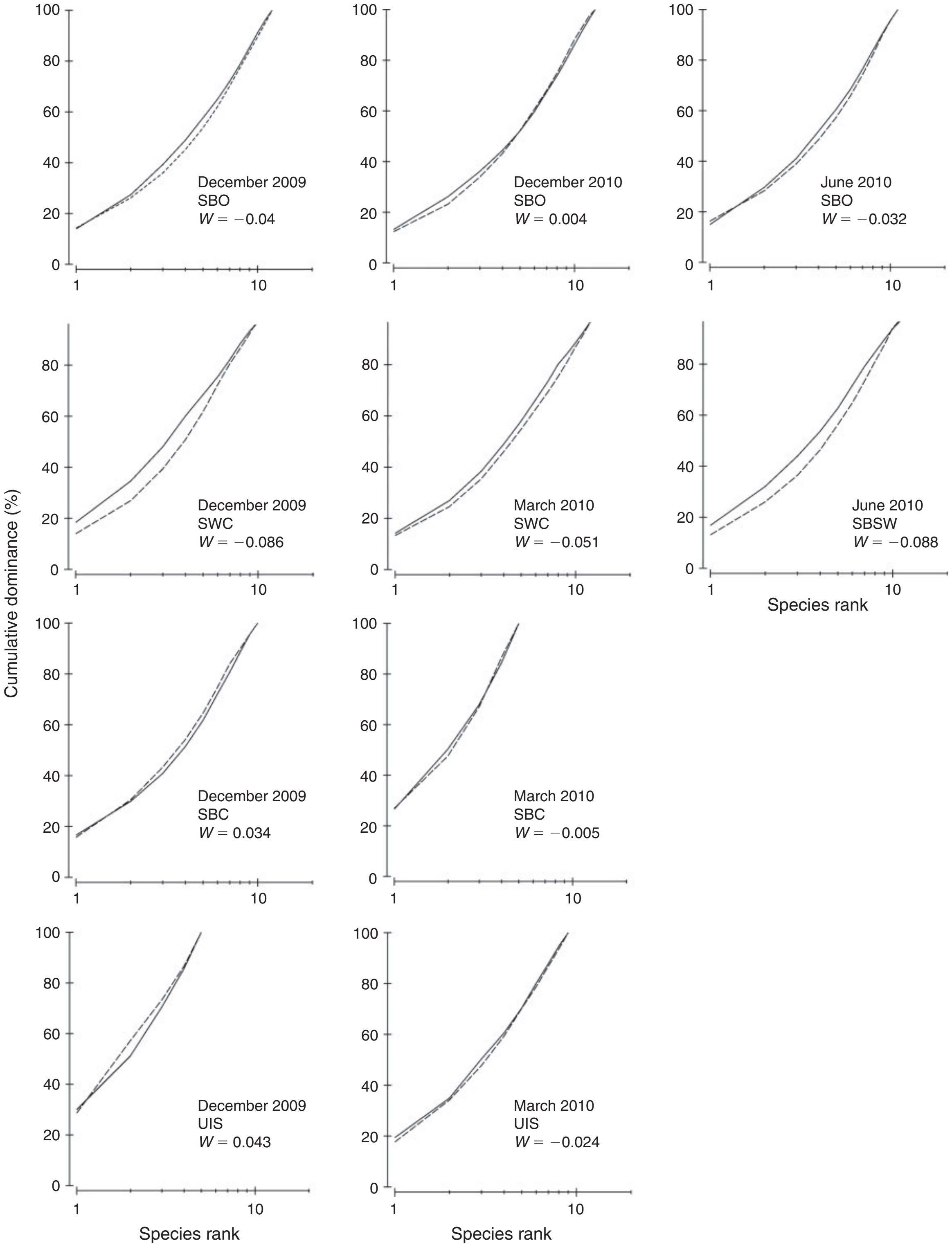

**Fig. 7.** Abundance biomass comparison curves for abundance (continuous line) and biomass (dashed line), and *W* values obtained for each batoid assemblages. SBO, sandy bottoms off Oaxaca; UIS, upper intermediate shelf-dwellers; SWC, shallow water off Chiapas; SBC, sandy bottoms off Chiapas; SBSW, sandy bottoms and shallow water off Chiapas.

*P. glaucostigma*, *N. entemedor*, *Z. xyster* and *H. longus*. The last three species were also distributed over shallower waters (SBO and SWC) although at low abundances (<3.0%).

The ABC curves suggested that the greater part of the batoid assemblages identified in this study were communities with a moderate degree of ecological stress because the abundance curve was above the biomass curve. This indicated that the small species (e.g. *U. chilensis*, *U. rogersi* and *N. vermiculatus*) dominated by number but not by biomass. Ecological stress can be a consequence of anthropogenic and natural perturbations; some of these perturbations include the effects of bottom trawl fishing, seasonal changes in recruitment or changes in the life cycle of species (Kaiser *et al.* 2000, 2002; Thrush *et al.* 2006). The dominance of small-sized batoid species taken as bycatch in the shrimp fishery coincides with records obtained in the Gulf of California, the Guatemala coast, Costa Rica, Colombia and Argentina (Tamini *et al.* 2006; Ixquiac-Cabrera *et al.* 2009; López-Martínez *et al.* 2010; Clarke *et al.* 2016; Navia and Mejía-Falla 2016).

Future studies should evaluate the disturbances (physical, biological, from fisheries etc.) that are leading to ecological stress in the batoid community of the Gulf of Tehuantepec. This is important because at least four batoid species recorded in this study (*A. narinari*, *N. vermiculatus*, *P. leucorhynchus* and *M. munkiana*) are classified by the IUCN as Near Threatened, and eight species (*H. longus*, *N. entemedor*, *P. leucorhynchus*, *Z. xyster*, *U. aspidura*, *U. chilensis*, *U. nana* and *U. rogersi*) are classified as Data Deficient (http://www.iucnredlist.org, accessed 15 February 2019). Soft bottoms offer optimal habitat for batoids and play a key role in the vulnerability to extinction of these species, because soft bottoms are subject to great fishing pressures (Moore 2017).

## Conflicts of interest

The authors declare that they have no conflicts of interest.

## Declaration of funding

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# V.Artículo 2: Ecología reproductiva de *Zapteryx xyster* Jordan y Evermann, 1896 en el Golfo de Tehuantepec

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# Reproductive ecology of the witch guitarfish *Zapteryx xyster* Jordan & Evermann, 1896 (Chondrichtyes: Trygonorrhinidae) in the Gulf of Tehuantepec, Mexican Pacific

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**Abstract.** From January 2008 to December 2009, 451 specimens of witch guitarfish *Zapteryx xyster* were caught in the Gulf of Tehuantepec. Total weight, total length (TL), sex, maturity stage and catch depth were recorded for each specimen. Maturity stage distribution exhibited significant differences with respect to depth. The data indicated that adults migrated towards shallow waters (25–37 m) to reproduce, starting in February. Males reached maturity at 44 cm TL, whereas females reached maturity at 48 cm TL. Witch guitarfish females are synchronous; therefore, ovulation and mating begin in March and parturition begins in April. Females showed a 2-year cycle with consecutive vitellogenesis and gestation. Fecundity was five to eight embryos (mean six embryos) and the sex ratio of embryos was 1 : 1. Birth occurred in April and May, with an average size at parturition of 17.3 cm TL. There was sexual dichromatism between males and females during the breeding period, and sexual polymorphism in adult females. The incidental catch of the witch guitarfish during courtship and mating threatens the survival of this species.

**Additional keywords:** batoids, distribution, reproduction, sexual dichromatism.

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## Introduction

After sawfishes, guitarfish are the elasmobranchs most susceptible to total global extinction (Dulvy *et al.* 2014). There are currently 60 known species of guitarfish worldwide, of which 20 are included as threatened in the International Union for Conservation of Nature (IUCN) Red List (http://www.iucnredlist.org, accessed 16 July 2019), of species (Moore 2017; Eschmeyer and Fong 2019). Five guitarfish species of the *Pseudobatus* genus and two species of the *Zapteryx* genus are distributed in the eastern Pacific Ocean (Robertson and Allen 2015; Moore 2017). According to information from the IUCN, there is insufficient data to evaluate the risk of extinction of 71.4% of these species. Guitarfish inhabit shallow coastal waters over soft sediments where intensive fisheries directed towards other species with greater economic value are located (McEachran and Notarbarloto di Sciara 1995; Moore 2017).

The witch guitarfish *Zapteryx xyster* Jordan & Evermann, 1896 is a viviparous aplacental batoid (Dulvy and Reynolds 1997) that inhabits coastal shallow waters up to a depth of 400 m over a great diversity of habitats, such as reefs and soft, sandy and rocky bottoms (Clarke *et al.* 2014; Robertson and Allen 2015). The distribution range of this species has not been well defined because of the considerable morphological similarity with the banded guitarfish *Zapteryx exasperata* (Jordan & Gilbert, 1880) and because the geographical range of these two species overlaps (Ebert 2003). A recent study indicated that

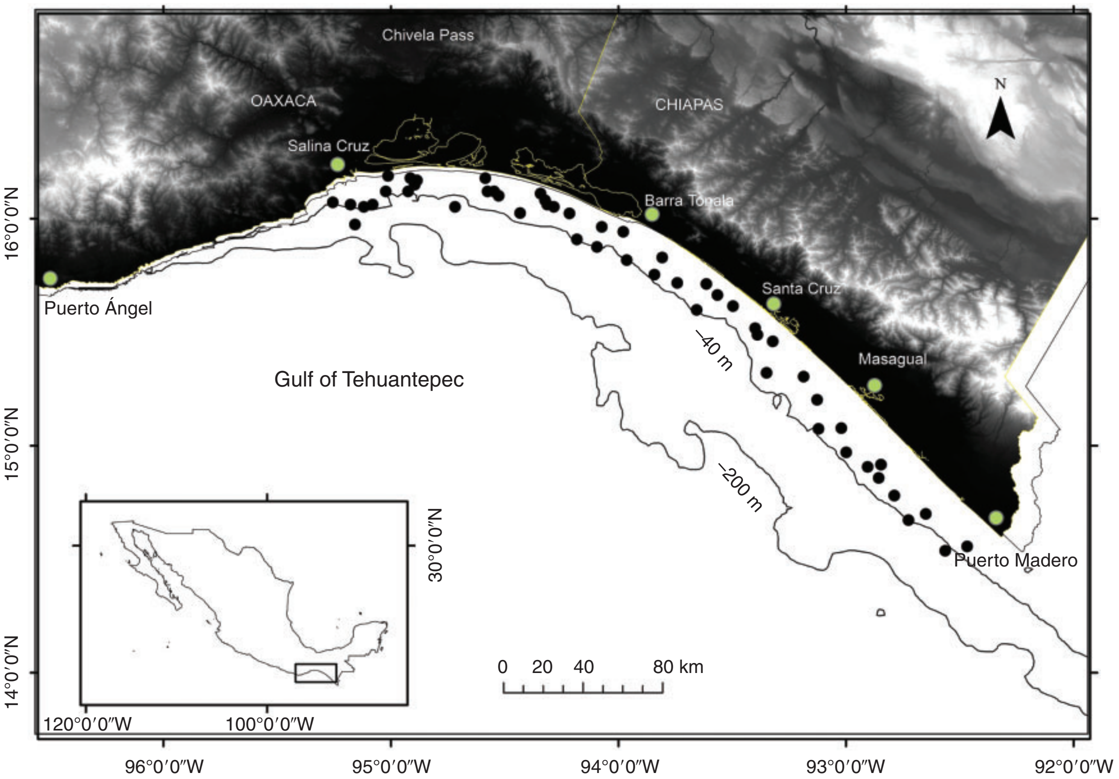

**Fig. 1.** Study area in the Gulf of Tehuantepec. Black circles indicate the location of bottom trawls where the 451 specimens of witch guitarfish were captured.

the coast of Sinaloa, Mexico, could be the main region where the two species overlap, as documented by records of hybrids possibly resulting from a cross between banded guitarfish females from the Gulf of California and witch guitarfish males from the south (Castillo-Páez *et al.* 2017).

The presence of banded guitarfish in the Gulf of Tehuantepec has been recorded by several authors (Castro-Aguirre and Espinosa-Pérez 1996; Tapia-García and García-Abad 1998; Corro-Espinoza and Ramos-Carrillo 2004), but a photograph of a witch guitarfish in the study of Corro-Espinoza and Ramos-Carrillo (2004) suggests that there is erroneous species identification. This historical erroneous identification has prevented understanding of the geographical limits of the distribution of this species, as well as essential aspects of its biology. More current records for the Gulf of Tehuantepec have indicated that the witch guitarfish can be found between Salina Cruz, Oaxaca, and Puerto Madero, Chiapas (Torres-Huerta *et al.* 2019).

The witch guitarfish is caught incidentally in bottom trawl nets used in the shrimp fishery in the Gulf of Tehuantepec. The witch guitarfish represents 0.6% of abundance and 1.9% of batoid biomass bycatch and has no economic value (Tapia-García and García-Abad 1998; Torres-Huerta *et al.* 2019). Recent studies in Costa Rica reported that this species had intermediate to high productivity and was highly susceptible to capture by bottom trawl nets, making it a vulnerable species (Clarke *et al.* 2016, 2018). There are no studies on witch guitarfish in the Mexican Pacific; therefore, the objective of this study was to generate information on the vertical distribution and reproductive biology of this species, which is catalogued as data deficient in the IUCN Red List of species.

## Materials and methods

### Study site

The sampling area was located in the Gulf of Tehuantepec, in the southern Mexican Pacific, between 14°30′ and 16°12′N, and between 92°00′ and 95°25′W (Fig. 1). This region encompasses ~125 000 $\text{km}^2$ off the Oaxaca and Chiapas coasts (Gallegos-García and Barberán-Falcón 1998). The continental shelf of the Gulf of Tehuantepec is 360 km long and narrow on the western end (~12 km wide), whereas on the eastern end it is wider (~45 km). The coastline has several lagoon systems, with the most important being Superior Lagoon, Inferior Lagoon and Mar Muerto Lagoon. These systems contribute nutrients, organic matter and sediments of continental origin to the ocean (Lavín *et al.* 1992).

There are two climatic seasons in the area: a dry season from November to April and a rainy season from May to October. *Tehuanos* winds blow from the Gulf of Mexico during the dry season and intensify when they cross the Chivela Pass (a depression of the mountain chain on the Isthmus of Tehuantepec), creating oceanic fronts and offshore upwellings over an area measuring ~200 $\text{km}^2$ (Lavín *et al.* 1992; Barton *et al.* 1993; Ortega-García *et al.* 2000). The most intense *Tehuanos* have been reported from November to January, with maximum wind speeds of ~35 $\text{m s}^{-1}$ and typical durations of

1–5 days (Blackburn 1962; Romero-Centeno *et al.* 2003). The lateral mixing of these waters creates favourable conditions for spawning, nursery and feeding areas for several species, some of which have commercial value (Trasviña and Barton 1997; Fernández-Álamo and Färber-Lorda 2006).

### Specimen collection

The witch guitarfish individuals examined in this study were obtained from 354 bottom trawls done with the research vessel *UMAR* and the fishing vessel *FIPESCO 22* from January 2008 to December 2009. Each sampling cruise lasted 10 days on average, and trawls were performed randomly over the continental platform at depths between 19 and 62 m. Trawls were performed using shrimp nets with an 18-m mouth and 3.4-cm mesh size and a rigid turtle excluder device (TED). Each trawl lasted 2–4 h at a speed of 1 to 1.5 m $s^{-1}$. The geographic position of each trawl was recorded using a global positioning system (GPS), and depth was recorded *in situ* using an echo sounder.

Witch guitarfish were frozen at –15°C to avoid decomposition. Specimens caught were identified based on descriptions of Jordan and Evermann (1896), Robertson and Allen (2015) and Last and Séret (2016). The following characteristics were considered relevant: (1) a broad rhombic disc; (2) a bluntly pointed snout; (3) a black blotch on the posterior angle of the inferior pectoral fin; and (4) one pair of ocelli on the central pectoral fins, ocelli white or yellowish centrally with darker margin; a second pair of ocelli on the pectoral fins near the posterior angle, a third pair of ocelli midway between the second ocelli and the median line of the back and several fainter ocelli on the back anteriorly.

### Collection of reproductive data

The total weight (g), total length (TL; cm), sex and the number of ocelli on the disc were recorded. Sex was identified by the absence (in females) or presence (in males) of a clasper (copulatory organ) on the pelvic fins. In males, testis length, clasper length (from the posterior end of the cloaca to the extreme distal end of the clasper), degree of calcification (uncalcified, partially calcified or calcified), rotation capability (<360 or 360° rotation) and the presence of spermatic fluid when pressing the pelvic belt were recorded. Ovary length, width of the oviductal gland and diameter of the largest oocyte were measured in females. The diameter of uterine eggs, the number of embryos per uterus, TL and the sex of each embryo in pregnant females were also recorded. The reproductive organs of specimens of the two sexes were analysed macroscopically using the classification proposed by Acero *et al.* (2008) and Colonello *et al.* (2011). An empirical scale was constructed considering three reproductive stages for the two sexes (juvenile, subadult and adult), with four variants in adult females (see Table S1, available as Supplementary material to this paper).

Clasper length, testicle length, ovary length and oviductal gland width were graphed as a function of TL to analyse changes associated with sexual maturity. The ovarian cycle and gestation period, as well as the time of ovulation, mating and birth, were estimated by analysing the diameter of the largest oocyte, total embryo length and the TL of the neonates with respect to time. Uterine fecundity was estimated by counting the number of eggs or embryos in the uterus of 18 females caught from November to May. Birth size was calculated on the basis of the average of the difference between the size of the largest embryo and the smallest neonate. The pattern of ocelli observed during the different maturity stages was described.

### Data analysis

The sex ratio was calculated by counting the total number of individuals of each sex and dividing the number of females by the number of males. The hypothesis of an equal sex ratio (1 : 1) for each month, maturity stage and embryos was analysed using Pearson's Chi-Square test. The size distribution was analysed using Intercooled Stata (ver. 9.0, see https://www.stata.com). A bandwidth of 2.0 cm was used for females and a bandwidth of 1.4 cm was used for males.

The mean (±s.d.) catch depth was calculated for each maturity stage and sex. Normality was evaluated using a Kolmogorov–Smirnov test. A non-parametric Kruskal–Wallis test and *post hoc* Kruskal–Wallis test were used to compare the catch depth of different maturity stages. A Mann–Whitney *U*-test was used to compare catch depth between sexes. Two-sided $P < 0.05$ was considered significant for both tests.

The *a* (intercept) and *b* (slope) parameters of the relationship between TL (cm) and total weight ($W_t$; g) were estimated for males and females through the logarithmic transformation of the following equation:

$$W_t = a(TL)^b$$

This relationship was used to determine whether growth was isometric ($b = 3$) or allometric (negative if $b < 3$ and positive if $b > 3$; Rickers 1975). To verify whether $b$ differed significantly from 3, Student's *t*-test ($\alpha = 0.05$) was used and the parameters of the two sexes were compared using analysis of covariance (ANCOVA). Statistical analyses were performed using Statistica (ver. 12, see https://www.statsoft.de).

The size at 50% maturity of males and females was calculated using the following logistic model in the sizeMat package (J. Torrejon-Magallanes, see https://cran.rproject.org/web/packages/sizeMat/vignettes/sizeMat.html#load-data) in R software (ver. 3.5.2, see https://www.r-project.org):

$$Y = \left[1 + e^{(a+bX)}\right]^{-1}$$

where $Y$ is the proportion of mature individuals and $X$ is TL (cm; Hosmer and Lemeshow 2000).

## Results

### Sex ratio and size frequency

In all, 451 witch guitarfish were caught: 177 specimens were female and 274 were male. Most specimens (74.4%) were caught between February and April (Fig. 2). There was a significant difference ($P < 0.02$, Pearson's Chi-Square test; Table 1) in the female : male ratio in January, February and March. All life stages were found (neonates, juveniles, subadults and adults); 52.0% of females and 64.2% of males were classified as adults.

The TL of females ranged from 15.2 to 69.5 cm, whereas that of males ranged from 15.8 to 58 cm. Table 2 shows the TL range for each maturity stage. According to size–frequency distribution, most females were adults measuring between 51 and 54.8 cm TL (Fig. 3*a*), whereas most males were adults between 49 and 50.9 cm TL (Fig. 3*b*).

### *Catch depth*

Female and male witch guitarfish were caught at depths of 20–57 m. Non-pregnant adult females had the greatest bathymetric distribution range (26–57 m; median ± s.d., 31 ± 9 m), whereas neonate males and females were found at depths ranging from 21 to 27 m (median ± s.d., depth 24 ± 1 and 23 ± 1 m respectively). Juveniles and subadults of both sexes were found at depths between 28 and 49 m (median ± s.d., depths 43 ± 4 and 36 ± 5 m for juvenile females and males respectively; 44 ± 2 and 36 ± 4 m for subadult females and males respectively). Pregnant females and adult males were caught at depths ranging from 24 and 37 m depth (median ± s.d., depth 27 ± 4 and 29 ± 3 m respectively). The depth at catch differed significant between maturity stages ($H_{8,451} = 255.93$, $P < 0.001$, Kruskal–Wallis test). *Post hoc* pairwise comparisons indicated that there were significant differences among the depths at which non-pregnant adult females, neonates (both sexes), juvenile females and adult males were caught ($P < 0.02$).

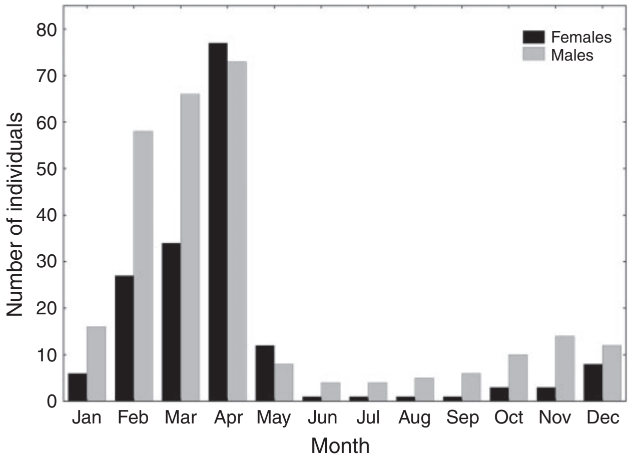

**Fig. 2.** Monthly abundance of witch guitarfish captured using bottom trawl nets in the Gulf of Tehuantepec.

**Table 2. Total length (TL) by maturity stage of the witch guitarfish *Zapteryx xyster* in the Gulf of Tehuantepec**

| | Sample size | TL (cm) | | |
|---|---|---|---|---|
| | | Minimum | Maximum | Mean |
| Maturity | | | | |
| Females | | | | |
| Neonates | 5 | 15.2 | 17.5 | 16.6 |
| Juveniles | 66 | 19 | 46.6 | 36.3 |
| Subadults | 14 | 46.2 | 49.6 | 48.1 |
| Non-pregnant | 69 | 49.4 | 69.5 | 56.2 |
| Pregnant with embryos | 10 | 49.8 | 64 | 54.9 |
| Pregnant with encapsulated uterine eggs | 11 | 50.2 | 65.2 | 55.4 |
| Post-partum | 2 | 50.6 | 57.8 | 54.2 |
| Males | | | | |
| Neonates | 8 | 15.8 | 17.7 | 16.7 |
| Juveniles | 80 | 21.5 | 43 | 34.7 |
| Subadults | 10 | 43 | 47.6 | 45.2 |
| Adults | 176 | 45 | 58 | 50.8 |

**Table 1. Number of males and females of witch guitarfish *Zapteryx xyster*, by month of capture and maturity stage, caught with bottom trawl nets in the Gulf of Tehuantepec**

| | Observed frequency (*n*) | | Sex ratio (females : males) | Chi-Square test | |
|---|---|---|---|---|---|
| | Females | Males | | $\chi^2$ | *P*-value |
| Sampling month | | | | | |
| January | 6 | 17 | 0.4 : 1.0 | 5.26 | 0.022 |
| February | 26 | 59 | 0.4 : 1.0 | 12.81 | <0.001 |
| March | 35 | 65 | 0.5 : 1.0 | 9.00 | 0.003 |
| April | 76 | 73 | 1.0 : 1.0 | 0.06 | 0.806 |
| May | 13 | 8 | 1.0 : 0.6 | 1.19 | 0.275 |
| June | 2 | 3 | 0.7 : 1.0 | 0.20 | 0.655 |
| July | 3 | 2 | 1.0 : 0.7 | 0.20 | 0.655 |
| August | 1 | 5 | 0.2 : 1.0 | 2.66 | 0.102 |
| September | 1 | 6 | 0.2 : 1.0 | 3.57 | 0.059 |
| October | 3 | 10 | 0.3 : 1.0 | 3.76 | 0.052 |
| November | 3 | 14 | 0.2 : 1.0 | 3.76 | 0.052 |
| December | 8 | 12 | 0.7 : 1.0 | 0.80 | 0.371 |
| Maturity | | | | | |
| Neonates | 5 | 8 | 0.6 : 1.0 | 0.69 | 0.405 |
| Juveniles | 66 | 80 | 0.8 : 1.0 | 1.34 | 0.247 |
| Subadults | 14 | 10 | 1.0 : 0.7 | 0.66 | 0.414 |
| Adults | 92 | 176 | 0.5 : 1.0 | 26.32 | <0.001 |

### Allometry and sexual dimorphism

The slope of the relationship between TL and $W_t$ was 3.09 for females and 2.62 for males. The *t*-test indicated that the slope was equal to 3 for females ($t = 0.74$, d.f. $= 84$, $P = 0.459$) and less than 3 for males ($t = -4.94$, d.f. $= 114$, $P < 0.01$). This means that female TL increased proportionally to $W_t$, whereas in males length increased more than weight. The ANCOVA indicated significant differences between males and females ($F_{1,199} = 527.25$, $P < 0.01$).

### Length at maturity

The logistic model of length at maturity for males showed that a TL of 43.6 cm (confidence interval (CI) 42.8–44.3 cm) represented 50% of mature males (Fig. 4*a*); the smallest male with maturity signs measured 43 cm TL. For females, the logistic model indicated that 48.2 cm TL (CI 47.3–49 cm TL) represented 50% of mature females (Fig. 4*b*); the smallest female with signs of maturity measured 46 cm TL.

### Sexual bathymetric segregation, gestation period, ovarian cycle and fecundity

Most (81.7%) adult witch guitarfish were recorded between February and April (reproductive period). Non-pregnant females were caught at depths ranging from 28 to 33 m (median 31.0 m) during this period (breeding period), and at depths ranging from 35 to 54 m (median 43 m) from May to January (non-reproductive period). There was a significant difference in the catch depth of females between the two periods ($P < 0.01$, Mann–Whitney *U*-test; Fig. 5). Adult males were caught at depths ranging from 25 to 37 m (median 33 m) during

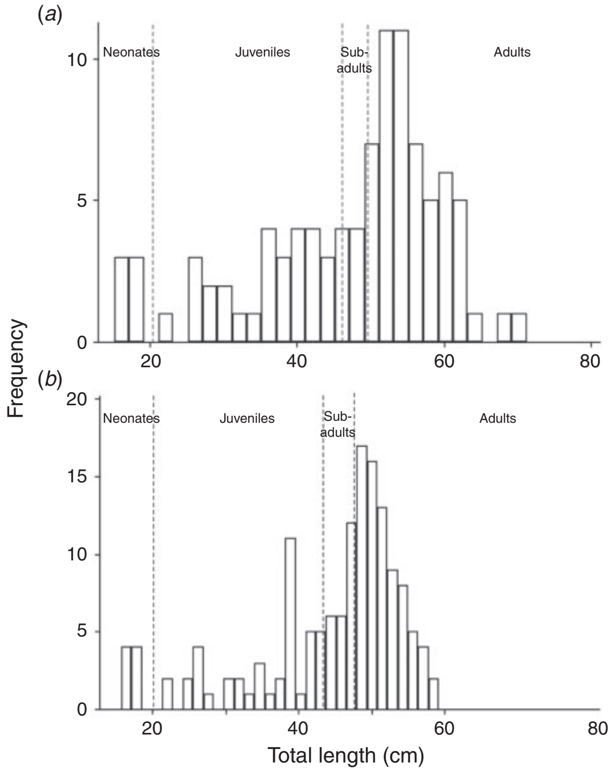

**Fig. 3.** Witch guitarfish size frequency by sex: (*a*) females, (*b*) males. Dashed lines indicate ranges for each maturity stage.

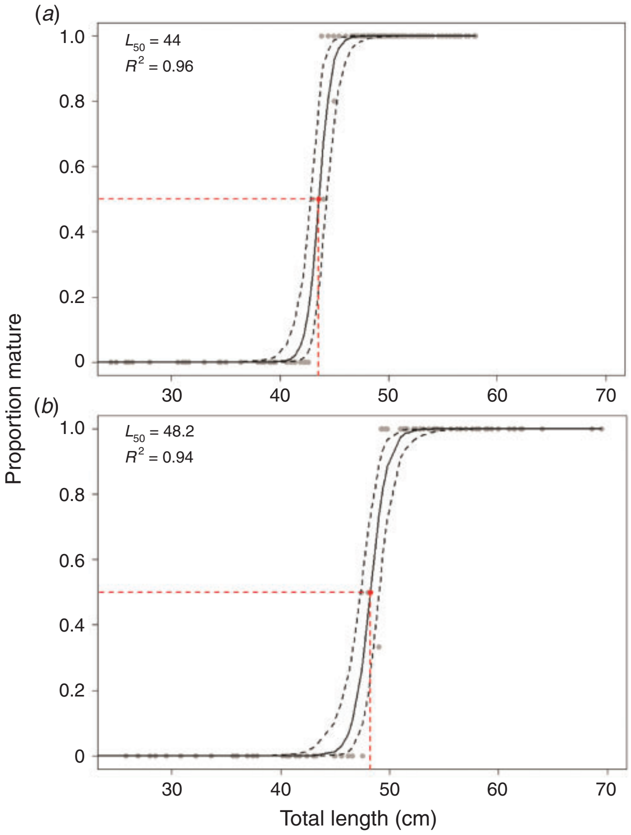

**Fig. 4.** Relationship between cumulative proportion of mature for (*a*) male ($n = 177$) and (*b*) female ($n = 274$) witch guitarfish as a function of total length.

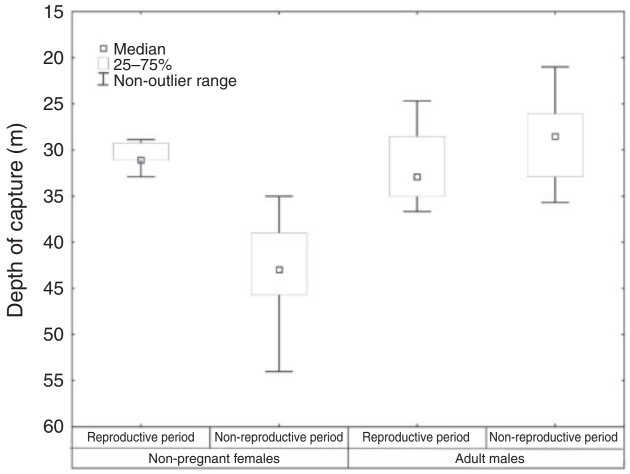

**Fig. 5.** Depth of capture of adult males and non-pregnant females captured during the reproductive (February–April) and non-reproductive (May–January) period.

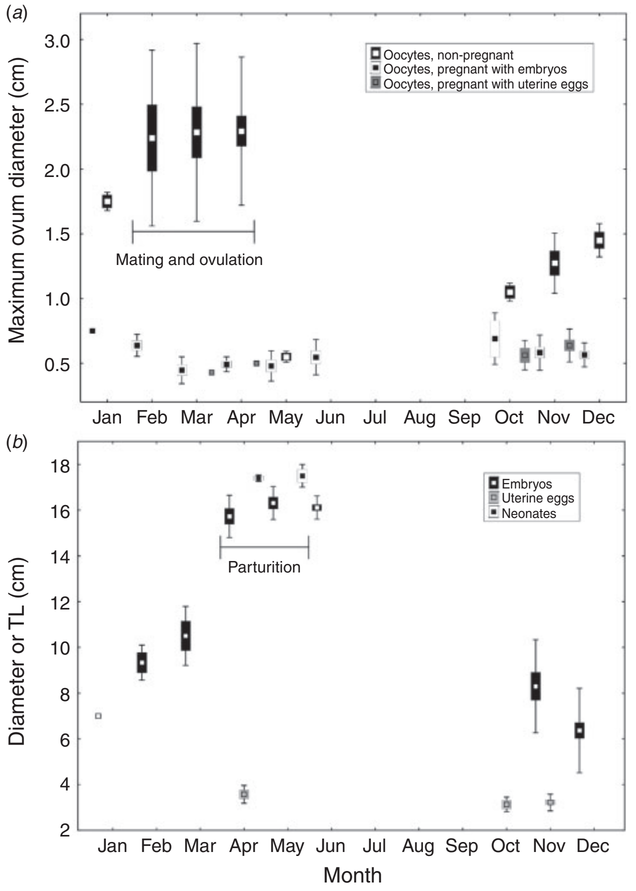

**Fig. 6.** (*a*) Monthly variation in the diameter of the largest oocyte of non-pregnant female witch guitarfish ($n = 69$), pregnant females with embryos ($n = 10$) and pregnant females with uterine eggs ($n = 11$). (*b*) Monthly variation in the diameter of uterine eggs, total length (TL) of embryos of pregnant females ($n = 11$ and 10 respectively) and TL of neonates ($n = 13$). Open boxes represent the mean, closed boxes indicate the s.e.m. and whiskers indicate the s.d. Adult females were not caught from July to September.

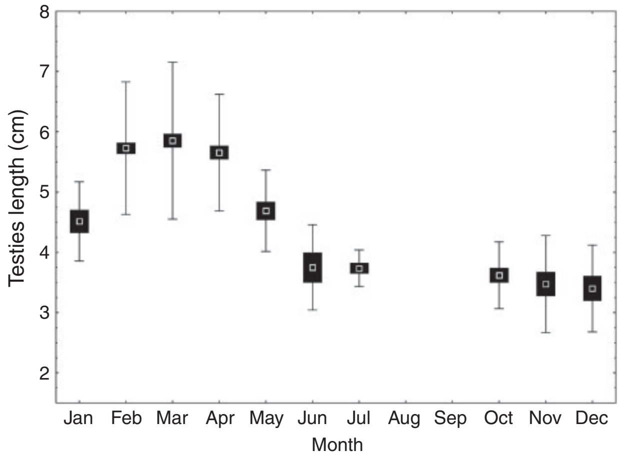

**Fig. 7.** Monthly variation in testis length of adult male witch guitarfish ($n = 112$). Open boxes represent the mean, closed boxes indicate the s.e.m. and whiskers indicate the s.d.

**Table 3. Number of embryos per uterus observed in 10 pregnant females of witch guitarfish *Zapteryx xyster***

TL, total length

| TL (cm) | Number of embryos | |
|---|---|---|
| | Left uterus | Right uterus |
| 48 | 3 | 2 |
| 49.3 | 3 | 2 |
| 49.8 | 3 | 2 |
| 51.4 | 3 | 3 |
| 54.0 | 3 | 3 |
| 56.5 | 3 | Aborted |
| 57.6 | 3 | 3 |
| 58.2 | 4 | 4 |
| 61 | 4 | 4 |
| 64.0 | 4 | 4 |

the reproductive period, and at depths ranging from 21 to 36 m (median 29 m) during the non-reproductive period. There were no significant differences in the catch depth of adult males between the two periods ($P = 0.716$, Mann–Whitney *U*-test).

The maximum oocyte diameter of non-pregnant mature females was greatest from February through April (mean ± s.d. (range) 2.2 ± 0.7 cm (1.2–3 cm) in February, 2.4 ± 0.6 cm (1.6–3.4 cm) in March and 2.3 ± 0.6 cm (1.2–3.4 cm) in April; mean ± s.d. during other months 1.2 ± 0.3 cm; Fig. 6*a*), indicating that ovulation takes place during these months. There was no evidence of concurrent vitellogenesis among pregnant females because maximum vitellogenic oocytes measured less than 0.9 cm during gestation; therefore, the reproductive cycle is likely to be at least biennial.

Because the largest embryos were recorded in April–June (maximum size 17.7 cm TL), parturition most likely takes place during these months. Based on the maximum embryo size and the size of the smallest free-swimming juveniles (17.0 cm TL), size at birth is ~17.3 cm TL. Although no pregnant females were observed from July to September, the timing of ovulation and mating during February–April, increase in embryo size from October to June and timing of parturition in April–June (Fig. 6*b*) indicate that gestation is ~12 months. The presence of uterine eggs (2.8–4.0 cm in diameter) observed in some females in the autumn months could be indicative of embryo diapause or possibly failed fertilisation of ovulated oocytes.

The greatest testicle length was observed in February–April in adult males (mean ± s.d. (range) 5.7 ± 0.5 cm (4.8–6.9 cm) in February, 5.8 ± 0.6 cm (4.8–7.7 cm) in March and 5.7 ± 0.5 cm (5.0–6.6 cm) in April; mean ± s.d. during other months 3.9 ± 0.6 cm; Fig. 7). Males exhibited semen storage in the epididymis between February and May.

The fecundity recorded in 10 pregnant females was 5–8 embryos (mean 6). The sex ratio of embryos was not significantly different from 1 : 1 ($P = 0.70$, Pearson's Chi-Square test). The analysis of fecundity per uterus showed that the three smallest pregnant females (48, 49.3 and 49.8 cm TL; Table 3) had lower fecundity in the right uterus (two embryos).

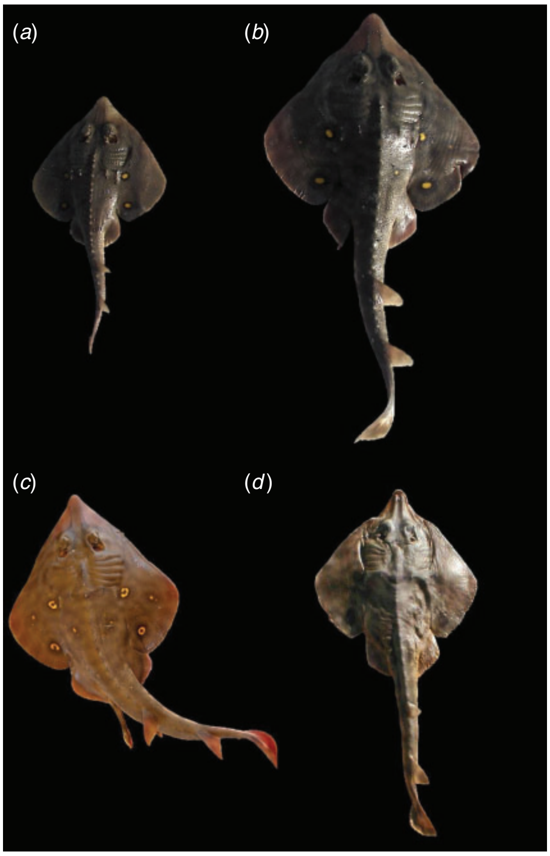

**Fig. 8.** Witch guitarfish *Zapteryx xyster* dorsal view of (*a*) juvenile female 22-cm total length (TL), (*b*) juvenile female 36.9 cm TL, (*c*) mature male 41.3 cm TL and (*d*) pregnant female 64 cm TL.

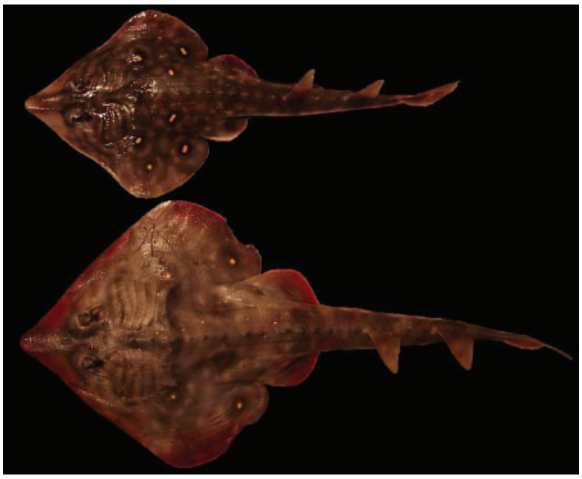

**Fig. 9.** Dorsal view of an adult male (above) and an adult female (below) captured in the Gulf of Tehuantepec showing differences in colouration between reproductive male and female witch guitarfish.

The pregnant females measuring between 51.4 and 57.6 cm TL had three embryos in the right uterus and the three females measuring >58 cm TL had four embryos in each uterus. A mean birth size of 17.3 cm TL was calculated based on the size of the largest embryo (17.7 cm TL) and of the smallest free-living organism (17.0 cm TL), both recorded in May.

### Ocelli pattern

Embryos at an advanced stage of development, neonates and juveniles measuring <35 cm TL had four round ocelli with a yellow centre and black edge. There were two ocelli located in the central part of each side of the disc and two in the posterior part (Fig. 8*a*). Juveniles measuring between 35 and 46.6 cm TL had four ocelli, with some specimens having oval-shaped ocelli. There were also a couple of small round ocelli located in the posterior part of the disc, close to the central body line, and a couple of ocelli on the widest part of the disc (Fig. 8*b*). Subadult and adult males and females had between 4 and 10 ocelli; half the ocelli were located on one side of the disc and the other half were located on the other side; each ocellus had a different shape (Fig. 8*c*). Some ocelli were made up of several smaller ocelli. During the period of reproduction, the colouration of ocelli and the black spots on the body were more conspicuous in adult males than females (Fig. 9). By contrast, eight pregnant females at an advanced stage of embryo development caught during the reproductive period did not have the central part of the ocellus, with only a black spot (Fig. 8*d*), but in females with uterine eggs or in the first stages of embryo development, the centre of the ocellus was yellow.

## Discussion

### Abundance and vertical distribution

Guitarfish are an important component of the demersal fauna of the Gulf of Tehuantepec and are frequently caught as bycatch of the shrimp fishery (Acal and Arias 1990; Tapia-García 1998; Tapia-García and García-Abad 1998; Torres-Huerta *et al.* 2019). The witch guitarfish was not very abundant from May to January, with records of primarily juvenile individuals (<39 cm TL) and adult males (>45 cm TL). Abundance increased in February and March (with dominance of adult males measuring between 45 and 52 cm TL), as well as in April (with dominance of adults of both sexes measuring between 46 and 69 cm TL). Non-pregnant females caught from February to April had the vitellogenic oocytes with the greatest diameter, and males had semen stored in the epididymis. Clarke *et al.* (2016) reported the highest concentrations of witch guitarfish adults at depths between 50 and 100 m in Pacific waters of Costa Rica. Adults are probably concentrated at depths >60 m in the Gulf of Tehuantepec during most of the year and migrate towards shallow waters (depth 25–37 m) to reproduce in February. Seasonal aggregation for reproductive purposes is a characteristic behaviour of elasmobranchs (Carrier *et al.* 1994; Whitney *et al.* 2004; Powter and Gladstone 2009). This has been observed in other species of this genus, such as in the banded guitarfish, which undertakes reproductive migrations towards Bahía Almejas, off the western coast of Baja California (Villavicencio-Garayzar 1995), and towards shallow waters in the Gulf of California (Blanco-Parra *et al.* 2009). After the reproductive period, witch guitarfish adults tended to segregate by sex in the Gulf of Tehuantepec, with females migrating towards greater depths than males. Segregation by sex is a characteristic that has been observed in some batoid species (Villavicencio-Garayzar 1995; Ebert 2005; Clarke *et al.* 2014; Lara-Mendoza and Márquez-Farías 2014).

Catches of pregnant witch guitarfish females at depths <30 m indicate that a preference for shallow waters at this stage. Economakis and Lobel (1998) and Hight and Lowe (2007) suggested that warm and shallow waters increased the body temperature of the pregnant leopard shark *Triakis semifasciata* Girard, 1855 females off the southern Californian coast and the grey shark *Carcharhinus amblyrhynchos* (Bleeker, 1856) in Johnston Atoll, which increased the rate of embryo development. Under the influence of *Tehuanos* winds, surface water flows offshore, which causes mixing and upwelling of subsurface water. The result is a temperature drop of up to 8°C at the centre of the Gulf of Tehuantepec, which limits the availability of warm waters at depths >25 m (Barton *et al.* 1993; Trasviña and Barton 1997; Chapa-Balcorta *et al.* 2015). We hypothesise that pregnant females stay in waters <30 m deep in order to find warm water during the *Tehuanos* wind season. This would allow embryo development to conclude so that offspring can be born at the beginning of April.

The records obtained during this study showed evidence of an apparent juvenile segregation by size. That is, witch guitarfish offspring were distributed in shallow waters (depths <30 m) and, as their TL increased (to the subadult stage), they were captured in deeper waters (mean depth 44 m). Segregation by size was reported previously for this species by Clarke *et al.* (2014) for the Pacific waters of Costa Rica. These authors reported that depth was the main factor affecting the segregation patterns of witch guitarfish. Other studies performed on sharks have suggested that segregation by size could be linked to numerous environmental and biological variables specific to each location (Klimley and Nelson 1984; Klimley 1987; Robbins 2007) that together could enhance habitat with higher prey diversity for each age or maturity stage (Klimley 1987; Sims 2003; Kock *et al.* 2013). This could decrease intraspecific competition and risk of predation (Hoare *et al.* 2000; Heupel *et al.* 2004), enabling the metabolic needs (e.g. for growth and reproduction) of each age or maturity stage to be fulfilled (Klimley 1987; Sims 2005; Wearmouth and Sims 2010).

### Dimorphism and sexual maturity

The information obtained in this study indicated differences in TL (11.5%), $W_t$ (8.5%) and length at maturity (8.3%) between adult males and females. Differences between males and females of the same species are common characteristics observed in elasmobranchs with viviparous reproduction (Sims 2005; Wearmouth and Sims 2010). The advantage of reaching greater TL is that it allows adult females to have more space available in the body cavity for the growth of oocytes or embryos (Klimley 1987; Parsons *et al.* 2008) and a larger liver to cover energetic costs during vitellogenesis, oocyte maturation and gestation (Klimley 1987; Lucifora *et al.* 2002; Mabragaña *et al.* 2002; Oddone and Velasco 2006).

Male witch guitarfish reached maturity at a smaller size than females (43.6 *v.* 48.2 cm TL respectively). This coincides with another report for this species by Clarke *et al.* (2014), who stated that males reached maturity at between 42 and 47 cm TL, compared with 47–52 cm TL for females, in Costa Rica. Dimorphism in the length of sexual maturity has also been observed in other species in the Family Trygonorrhinidae (Villavicencio-Garayzar 1995; Marshall *et al.* 2007; Blanco-Parra *et al.* 2009; Colonello *et al.* 2011).

We found that adult male witch guitarfish can be distinguished from females by their ocelli during the reproductive period. Adult males have ocelli with a yellow centre and black edge on the back of the body that are brighter than those of adult females. Sexual dichromatism (differences in colouration of the two sexes) has been observed in the nurse shark *Ginglymostoma cirratum* (Bonnaterre, 1788) during courtship and mating, with males being considerably darker than females (Klimley 1980). In many vertebrates such as fishes, birds, lizards and primates, bright colours are widely considered a product of sexual selection, through mating preferences of the opposite sex for brightly coloured individuals (Darwin 1871; Andersson 1986; Cotton *et al.* 2006). Reproductive period colouration in males shows that sexual dichromatism may play an important social role in sex recognition (Cooper and Greenberg 1992).

Observations from the present study indicate that ocelli with a yellow centre and black edge were more frequent in non-pregnant females, whereas ocelli lacking yellow colouration were more frequent in pregnant females. Absence of a yellow centre in the adult female ocelli could be related to pregnancy. Sexual polymorphism (in the colouration of males and females of the same species) has been observed in lacertids and some mammals (Galán 2000; Wyatt 2014). Galán (2000) suggested that changes in the colouration of pregnant females could serve to avoid chasing and mating attempts by males during pregnancy. Therefore, differences in colouration between adult witch guitarfish females could play an important role in sexual recognition during the reproductive period.

### Reproductive cycle and fecundity

Witch guitarfish females are synchronous; therefore, ovulation and mating begin in March and parturition begins in April. The presence of pregnant females without concurrent vitellogenesis and non-pregnant mature females during the same period is indicative of a 2-year cycle with consecutive vitellogenesis and gestation. This means that females are pregnant during 1 year; they give birth and do not ovulate or mate again until 1 year later. Biennial cycles with consecutive vitellogenesis and gestation have been reported for many of the sharks of the genus *Carcharhinus*, some hammerheads (e.g. *Sphyrna mokarran* Rüppell, 1837 and *Sphyrna zygaena* Linneus, 1758), the nurse shark (*G. cirratum* Bonnaterre, 1788) and the American cownose ray (*Rhinoptera bonasus* (Mitchill, 1815); Castro 2009; Pérez-Jiménez 2011).

The presence of uterine eggs in the witch guitarfish in April, October and November could indicate a probable embryo diapause period. This reproductive strategy allows adjustment of the birth of offspring to the most favourable time of the year, which maximises survival probability and the reproductive success of species (Waltrick *et al.* 2014). This strategy has been documented for at least 16 species, 8 of which are guitarfishes (Waltrick *et al.* 2012). Future studies could confirm whether the witch guitarfish exhibits embryo diapause based on examinations of non-pregnant adult females from May to October.

Witch guitarfish pups were born in April–June; the size at birth ranged between 15.2 and 17.5 cm TL (mean 16.9 cm TL), and the sex ratio was 1 : 1. The greatest biomass of invertebrates and demersal fish in the Gulf of Tehuantepec was recorded from March to August (Gamboa-Contreras and Tapia-García 1998; Tapia-García 1998), so the presence of neonates beginning in April could be linked to the abundance of possible prey.

The smallest pregnant females (between 48 and 50 cm TL) had low fecundity in the right uterus. This could be related to: (1) the space available in the body cavity, which is small at smaller sizes (Klimley 1987); and (2) the fact that the digestive system and liver are on the right-hand side of the coelom, which further reduces the available space. The disc-shaped morphology of batoids restricts the coelomic space, which restricts the uterine capacity even more (Musick and Ellis 2005). The fecundity of the two uteri was equal in witch guitarfish females measuring >58 cm TL, and these females reached their maximum fecundity (eight embryos). The maximum fecundity coincided with reports for this species in Costa Rica of Clarke *et al.* (2014). This means that as well as the banded guitarfish (seven embryos), the witch guitarfish is a species with intermediate fecundity among the species of the Family Trygonorrhinidae (*Zapteryx brevirrostris*: 2 embryos; *Aptychotrema rostrata*: 20 embryos; Villavicencio-Garayzar 1995; Blanco-Parra *et al.* 2009; Colonello *et al.* 2011; Kyne *et al.* 2016).

### *Future considerations*

The incidental catch of witch guitarfish during its reproductive cycle using bottom trawl nets could have negative effects on the reproductive success and long-term viability of this species. According to Musick (1999) and Stevens *et al.* (2000), catches of large organisms could lead to changes in the size structure and reproductive potential of species, increasing vulnerability to overexploitation (Mucientes *et al.* 2009; Jacoby *et al.* 2012). There are annual shrimp fishery closures in Mexico that begin in March and end in September (Secretaría de Agricultura, Desarrollo Rural, Pesca y Alimentación 2013), which indirectly provide partial protection for the reproductive cycle of the witch guitarfish (March and April). However, the adult male catch during February and perhaps part of March could make this species vulnerable, because more males than females were captured. According to Simpfendorfer *et al.* (2002) and Mucientes *et al.* (2009), there is differential sexual exploitation in species such as the blue shark *Prionace glauca* (southern Pacific Ocean) and the mako shark *Isurus oxyrinchus* (northern Atlantic Ocean) because the two sexes exhibit different seasonal distribution patterns, which could contribute to population decreases.

Bottom trawl nets used in the shrimp fishery of the Gulf of Tehuantepec have TEDs. According to Eayrs (2007), TEDs prevent animals larger than 20 cm TL from entering the codend of the net. However, 94% of witch guitarfish caught measured between 20 and 69.5 cm TL. Management regulations should take into account the need to adapt TEDs to decrease the mortality of adult male witch guitarfish during their reproductive period, which would be an important step in the conservation of this species.

## Conflicts of interest

The authors declare that they have no conflicts of interest.

## Declaration of funding

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**Supplementary material**

# Reproductive ecology of the witch guitarfish *Zapteryx xyster* Jordan & Evermann, 1896 (Chondrichtyes: Trygonorrhinidae) in the Gulf of Tehuantepec, Mexican Pacific

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**Table S1. Empiric scale of maturity proposed for witch guitarfish *Zapteryx xyster*, based on macroscopic observations of the reproductive system of both sexes**

| Maturity stage | Males | Females |
|---|---|---|
| Juvenile | Thin white testicle, little blood irrigation. Flaccid epididymis. Clasper flaccid at the base. | Thin white ovary, little blood irrigation. Undifferentiated oocytes. No regionalisation between oviduct and uterus. Oviducal gland not well defined. |
| Sub-adult | Firm beige testicle, with apparent development but not sectioned. White epididymis, thin and long. Clasper partially calcified and rotation less than 360°. | Ovary has uniform appearance but no visible oocytes. The oviduct is differentiated and compact. The oviducal gland is not well differentiated. |
| Adult | Turgid testicle, with high blood irrigation and pink lobes clearly sectioned. Spiral epididymis, long and whitish. Cranial section of the siphonal sac is thin, becoming thick in the caudal region. Clasper is calcified at the base with 360° rotation, rhipiodon is open and with seminal fluid. | Both ovaries are functional, oocytes and oviducal gland are completely differentiated. Four variants:<br>Non-pregnant female with large ovaries and notable blood irrigation, empty uteri.<br>Pregnant female with small ovaries, uteri with encapsulated uterine eggs.<br>Pregnant female with small ovaries and differentiated embryos in the uterus.<br>Post-partum female with small ovaries and distended uteri. |

# VI. Artículo 3: Presencia de la raya redonda denticulada *Urotrygon cimar* en el Golfo de Tehuantepec

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# Presence of the denticled roundray *Urotrygon cimar* in the Gulf of Tehuantepec, Mexico

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*A total of 101 denticled roundray* Urotrygon cimar *were caught in a large area of the Gulf of Tehuantepec. Sizes ranged from 102 to 282 mm total length. Rays were caught at depths between 17 and 62 m. These records confirm the presence of the denticled roundray off the southern coast of the Mexican Pacific.*

**Keywords:** batoids, Urotrygonidae, Mexican Pacific, distribution

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## INTRODUCTION

A wide portion of the coastal zone of the Gulf of Tehuantepec remains unexplored, and a large number of taxonomic groups have been ignored by recent studies (López-Pérez *et al.*, 2012). Among these groups are the roundrays of the genus *Urotrygon* Gill 1863, which comprises small-sized species (less than 47 cm total length). These rays are frequently caught as by-catch in shrimp fisheries and are discarded as species without commercial value. These species are *Urotrygon aspidura* (Jordan & Gilbert, 1882), *U. chilensis* (Günther, 1872), *U. munda* Gill, 1863, *U. nana* Miyake & McEachran, 1988 and *U. rogersi* (Jordan & Starks, 1895) (Tapia-García & García-Abad, 1998), all of which have very similar morphological characteristics. The main differences are the disc shape and the presence or absence of spines and denticles in the median dorsal part of the disc and tail.

The denticled roundray *Urotrygon cimar* (López & Bussing, 1998) is a tropical benthic species usually associated with soft bottoms (Robertson & Allen, 2002, 2008). The name is derived from them having a round disc with dorsal surface covered densely by dermal denticles of sharp-tipped, moderate sized and stelliform bases, denticles of midline of disc slightly increasingly larger and recurved with their tips facing backwards, and, but not forming distinct rows of enlarged denticles or thorns (López & Bussing, 1998; Robertson & Allen, 2008). Until 2008 its presence in the Central Pacific was only known for Costa Rica, Nicaragua and El Salvador (López & Bussing, 1998; Robertson & Allen, 2008). However, Amezcua-Linares & Amezcua (2009) reported the presence of a female *U. cimar* caught in 1985 in Bahía de Petacalco in the Mexican Pacific, thus increasing its distributional range. During four trips to the Gulf of Tehuantepec a total of 101 specimens of *U. cimar* were collected, including juveniles and adults of both sexes, confirming the presence of this species off the southern coast of the Mexican Pacific.

## MATERIALS AND METHODS

A total of 152 bottom trawls were carried out between October 2009 and October 2010, at depths between 11 and 62 m, using the RV 'UMAR'. The study area comprised the coast between Salina Cruz, Oaxaca (95°10′50″W 16°7′89″N) and Barra de Suchiate, Chiapas (92°14′30″W 16°13′N) (Figure 1). During these sampling trips specimens from the *Urotrygon* genus were found that did not correlate with descriptions of species recorded in the area. The rays were identified as *U. cimar* based on criteria proposed by López & Bussing (1998) and Robertson & Allen (2002, 2008), and by comparison with the specimen from the Ichthyological Collection of the Marine Science and Limnology Institute, Universidad Nacional Autónoma de México (UNAM), catalogue number ICMYL 724.01 (Amezcua-Linares & Amezcua, 2009).

The sex, total length, disc width, disc length, distance from the cloaca to the tip of the caudal fin, and maturity stage of all organisms were recorded. Males had a pair of copulating organs on the pelvic fins. Total length was measured from the tip of the head to the tip of the caudal fin; disc width was measured as the distance between the extreme edges of the pectoral fins; disc length was measured from the tip of the head to the tip of the pectoral fin; tail length was measured from the middle of the cloaca to the tip of the caudal fin. Males and females were classified according to their macroscopic gonadal development. The internal reproductive organs of juveniles were undifferentiated; males had small and flaccid claspers. Adult females had well-differentiated gonads, thick

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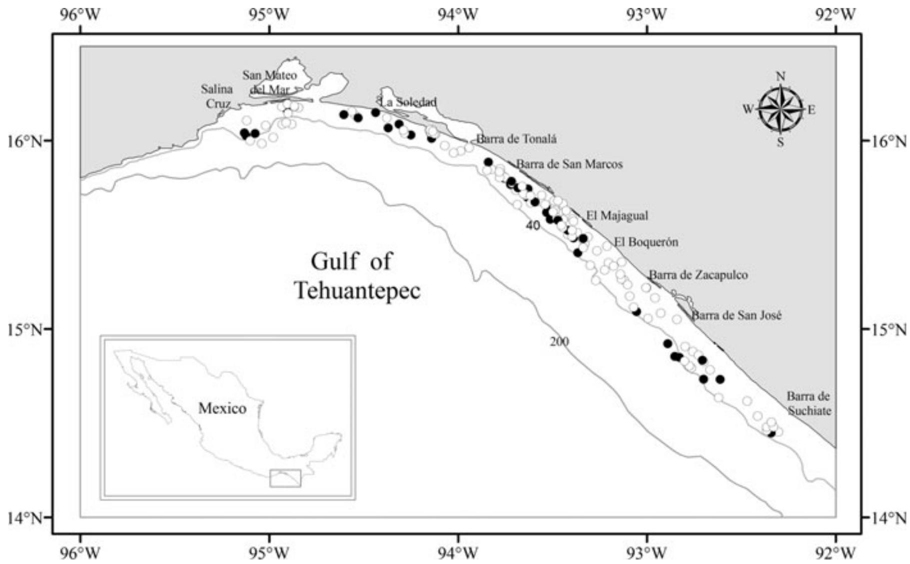

**Fig. 1.** Study area and location of bottom trawls. Black circles show the stations where *Urotrygon cimar* was caught.

oviducts and wide uteri. Adult males had the epididymis rolled along the whole conduct up to the seminal vesicle, stored sperm and completely calcified claspers.

## RESULTS

Of 152 trawls, in 36 were caught 101 denticled roundrays. Sizes ranged between 102 and 282 mm total length (TL). Disc shape was round, with a width of 54 to 61% TL, and disc length ranged from 49 to 57% TL. Morphometric relationship equations showed that disc width increased more than total length (Figure 2; Table 1). Tail length was 44 to 57% TL. The dorsal surface of the disc, tail and upper part of the caudal fin were covered by sharp denticles and star-shaped bases. Denticles were slightly larger on the median disc line, and the inferior surface was smooth (Figure 3). Adults had a dorsal surface of yellow-brown to light brown coloration, irregularly spotted with brown, black, and on rare occasions, light spots. These spots ranged in size from eye-sized to spiracle-sized, and were

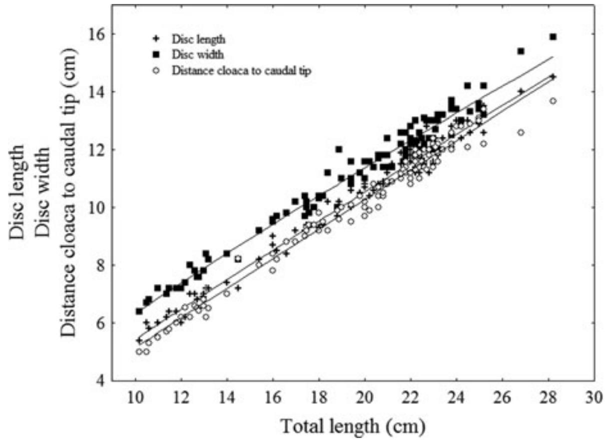

**Fig. 2.** Relationship among three morphometric measurements (disc width, disc length and distance from the cloaca to the tip of the caudal fin) and *Urotrygon cimar* total length.

**Table 1.** Coefficients of three morphometric relationships versus *Urotrygon cimar* total length. Growth patterns are: –A, negative allometry; I, isometry.

| | a | b | $r^2$ | Growth |
|---|---|---|---|---|
| Disc width | 0.900 | 0.84 | 0.98 | –A ($P < 0.01$) |
| Disc length | 0.604 | 0.95 | 0.99 | –A ($P < 0.01$) |
| Tail length | 0.521 | 0.99 | 0.98 | I ($P = 0.77$) |

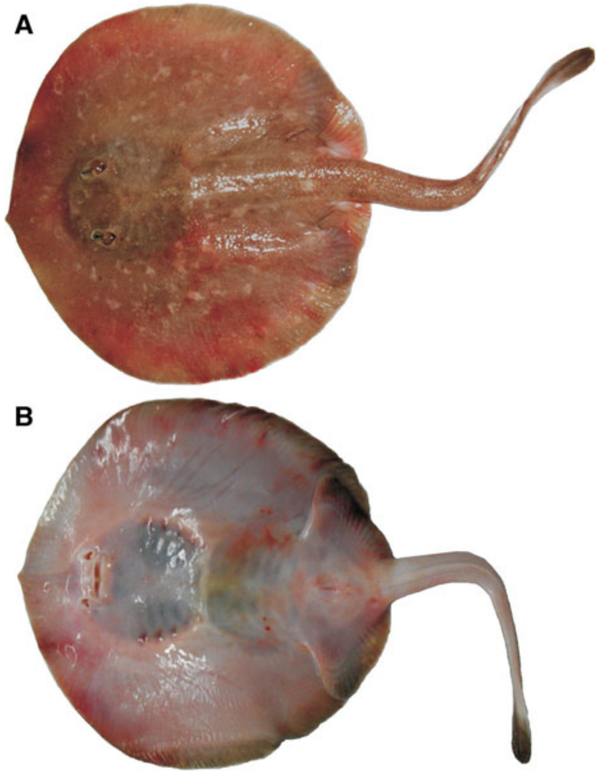

**Fig. 3.** Photograph of female *Urotrygon cimar* caught off Gulf of Tehuantepec: (A) dorsal view; (B) ventral view.

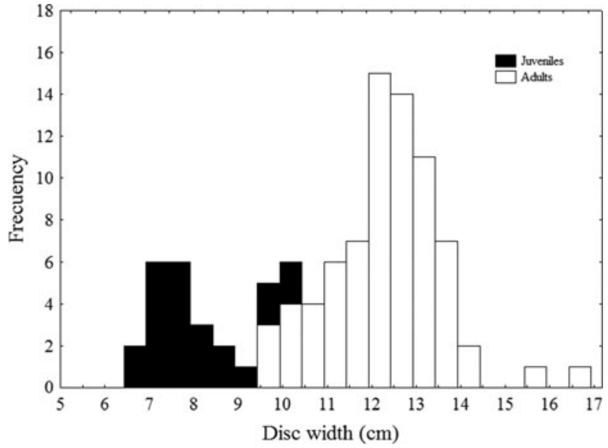

**Fig. 4.** Size–frequency of *Urotrygon cimar* by maturity stage.

common towards the middle line. The ventral side was white and the edge of the disc and posterior edges of the pelvic fins were wide and dark. The caudal fin was brown with dark spots and dark edges. The pupil had a black triangle cover that descended to the centre; this characteristic was more visible in recently caught specimens that were not preserved in alcohol.

Three females containing embryos in advanced stages of development were found. The embryos had the disc surface covered by denticles, which indicates that these organisms born with this characteristic and can be easily separated from juveniles belonging to other species of the *Urotrygon* genus. A specimen of *U. cimar* was deposited at the Marine Fish National Collection of the Biology Institute, UNAM, under the catalogue number CNPE PE16662.

The 101 specimens of *U. cimar* were captured between San Mateo del Mar (94°53′90″W 16°9′06″N) and Barra de Suchiate (92°40′0″W 14°49′00″N), encompassing a distance of 334 km, and depths between 23 and 44 m. An average number of 3 organisms per station were caught, with a range from 1 to 10 specimens per station.

The southern-most specimen was caught close to the frontier with Guatemala (92°41′0″W 14°43′14″N), a distance of 1100 km from the holotype, which was found in Costa Rica (López & Bussing, 1998), 446 km from the limit of the distribution proposed by Robertson & Allen (2002), and 1778 km to the south from the specimen found in Michoacán by Amezcua-Linares & Amezcua (2009).

A percentage of 59% of rays were found between Barra de Tonalá (93°56′47″W, 15°59′13″N) and Barra de Zacapulco (92°5117″W 15°929″N); the remaining 21% were found between Barra de Zacapulco and Barra de Suchiate (92°13′32″W 14°31′47″N) (Figure 4). The following three sampling stations yielded 27% of rays: off la Soledad (94° 9′43″W 16°5′20″N), between Barra de San Marcos and El Majagual (93°29′28″W 15°43′1″N), and off Barra de San José (92°37′52″W 14°55′31″N).

Of 101 specimens caught, 47 were females and 54 males. Females ranged from 67 to 158 mm disc width (DW), and males ranged from 64 to 137 mm DW. Immature individuals measured from 64 to 100 mm DW, and adults measured from 96 to 164 mm DW (Figure 5). Adults measuring from 118 to 128 mm DW were the most abundant (15 individuals). Of 36 adult females, 14 were pregnant; these were observed in December 2009, March 2010 and June 2010. Fecundity was from 1 to 2 embryos. Seven gravid females measuring from 104 to 142 mm DW had one embryo in the left uterus, and seven females measuring from 116 to 164 mm had two embryos in the left uterus. The presence of embryos measuring 64 mm DW and of juveniles of this same size recorded in March 2010 between Barra de San Marcos (93°41′22″W 15°51′32″N) and El Boquerón (93°6′6″W 15°23′43″N) off the Chiapas coast suggests that this area could be a birthing area for the denticled roundray. This study confirms the presence in the Gulf of Tehuantepec of *U. cimar*, and highlights the importance of knowing more about this species' biology, in order to avoid confusing it with other species from the *Urotrygon* genus.

## DISCUSSION

The present study confirms the presence of the denticled roundray *Urotrygon cimar* off the Oaxaca and Chiapas coasts, with over one hundred specimens caught. The denticled roundray is distributed in the southern Mexican Pacific, where it has probably been confused with spiny

**Table 2.** Main characteristics between *Urotrygon cimar* and *Urotrygon munda*.

| **Characteristic** | ***U. cimar*** | ***U. munda*** |
|---|---|---|
| Disc shape | Round | Orbicular |
| Disc anterior margins | Evenly convex with snout slightly projecting | Nearly straight to convex with snout short, weakly pointed |
| Dermal denticles | Top of disc, tail, and top half of tail fin densely covered with moderate sized, sharp denticles with star-shaped bases, slightly larger towards middle of disc | Relatively large, strong, recurved with star-like bases densely covering entire disc and tail |
| Enlarged denticles or thorns along mid-back from mid-disc to tail spine | Absence | 1–2 scattered rows of 18–32 recurved spines |
| Papillary operculum | Pupil with black triangular cover reaching down to its centre, it covers 25% of pupil | Covers more than 50% of pupil |
| Upper surface coloration | Yellow-brown to tan; irregularly spotted with brown or black blotches ranging from size of eye to size of spiracle, densest near midline | Uniform light brown to yellowish brown, tail with faint dusky edges |

roundray *U. munda*. The spiny roundray has been reported in the Gulf of Tehuantepec by Amezcua-Linares (1996), Castro-Aguirre & Espinosa-Pérez (1996), Tapia-García & García-Abad (1998), Robertson & Allen (2002), Corro-Espinosa & Ramos-Carrillo (2004) and Robertson & Allen (2008). However, Corro-Espinosa & Ramos-Carrillo (2004) show a predominance of denticled roundray instead of *U. munda.* None of these studies has reported *U. cimar* in the area.

This confusion could be due to the similar external morphology between the two species. Both are characterized by the presence of dermal denticles spread all over the disc and tail; the difference lies mainly for the presence of enlarged denticles or thorns, which are on the median dorsal line in *U. munda*, while *U. cimar* has no thorns and instead has sharp dermal denticles that are slightly larger on the median line of the disc (López & Bussing, 1998; Robertson & Allen, 2008). A picture of the distribution of *U. munda* is described by Amezcua-Linares (1996) and Robertson & Allen (2008). The disc anterior margins of *U. cimar* are convex forming a disc that is almost round and *U. munda* have anterior margins that are almost straight to convex (Robertson & Allen 2008). In addition, the lid or papillary operculum is triangular in *U. cimar* covering approximately 25% of the pupil, while in *U. munda* it covers more than 50% (López & Bussing, 1998). Table 2 shows the main characteristics which allow the description of these species differences.

It is noteworthy that during this study over 100 bottom trawls were carried out, at depths between 17 and 23 m, during which no *U. munda* specimens were caught. According to Robertson & Allen (2008), *U. munda* occurs between 1 and 51 m depth, which could indicate that *U. munda* is not very abundant at depths under 51 m. The findings of our study emphasize the need to collect specimens at depths under 17 m and over 62 m in order to establish the distributional range of both species.

## ACKNOWLEDGEMENTS

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# VII. Artículo 4: Anomalías morfológicas en rayas del género *Urotrygon* del Golfo de Tehuantepec

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SENCKENBERG

SHORT COMMUNICATION

# Morphological abnormalities of round rays of the genus *Urotrygon* in the Gulf of Tehuantepec

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**Abstract** During three sampling trips carried out over the continental platform of the Gulf of Tehuantepec 15 free-ranging specimens and 3 embryos with morphological abnormalities were collected. Abnormalities consisted of developed pectoral fins that were not fused interiorly, pectoral fins that were not completely developed, anophthalmy, absence of a clasper, an abnormally developed liver, and neoplasia of the liver. Eighty-three percent of specimens were captured relatively close to each other, in waters adjacent to the estuaries of the lagoon systems of La Joya-Buenavista, Carretas-Pereyra and Chantuto-Panzacola, at a depth of between 29.0 and 33.0 m. The presence of organochlorines in the region is a probable cause of morphological abnormalities.

**Keywords** Batoids · Urotrygonidae · Abnormalities · Oaxaca · Chiapas

## Introduction

Shrimp are the main fishing resource in the Gulf of Tehuantepec within the 90 fishing zone (Cervantes-Hernández 2008), which is located between Punta Chipehua and Salina Cruz, Oaxaca (16°00′N, 95°25′W) and Puerto Chiapas, Chiapas (14°42′N, 92°30′W) (Reyna-Cabrera and Ramos-Cruz 1998). The fishing area encompasses a 5988 km$^2$ area over the continental platform. Catches are made at a depth of 9.1 to 72.8 m using trawl nets with a 57.15-mm mesh size (Instituto Nacional de Pesca 2004).

Round rays (genus *Urotrygon*) are frequently captured as bycatch in the shrimp fishery (Tapia-García and García-Abad 1998). They are discarded, however, as they have no commercial value. The *Urotrygon* genus refers to round rays that have pectoral fins fused to the body, forming an oval, almost circular disc, with maximal disc widths (DWs) of 35 cm (McEachran and Sciara 1995). They inhabit mainly coastal waters with sandy and muddy bottoms (Amezcua-Linares 1996; McEachran and Sciara 1995; Robertson and Allen 2008), which increases their vulnerability to being captured with trawl nets.

In the Mexican Pacific Ocean, morphological abnormalities such as incomplete development of the anterior portion of the disc have been reported in the batoid fishes *Dasyatis longa* (Escobar-Sánchez et al. 2009), *Dasyatis dipterura* (Blanco-Parra and Niño-Torres 2011) and *Myliobatis californica* (Ramírez-Amaro et al. 2013). Anophthalmy has been reported in *Urobatis halleri* (Rubio-Rodríguez et al. 2010), functional bicephaly in *Rhinoptera steindachneri* (Castro-Aguirre and Torres-Villegas 1979), and albinism in *Narcine entemedor* (Sandoval-Castillo et al. 2006) and *Myliobatis californica* (De Jesús-Roldan 1990). Morphological malformations in the genus *Urotrygon* have been

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reported in embryos of two gravid females caught off the coast of the central Pacific coast of Colombia (Mejía-Falla et al. 2011). The objective of the present study was to report the abnormalities found in 15 free-living specimens and 3 embryos of the *Urotrygon* genus caught as bycatch in the shrimp fishery of the Gulf of Tehuantepec.

## Material and methods

Three sampling trips were carried out during December 2009, March 2010 and April 2014 to the Gulf of Tehuantepec, between Salina Cruz (95°10′50″W, 16°7′89″N) and Barra de Suchiate (92°14′30″ W, 16°13′N) (Fig. 1). A total of 139 bottom trawls were carried out at a depth of 11 to 62 m using trawl nets with a 52.5-mm mesh size. A total of 931 *Urotrygon chilensis* (Günther, 1872), 514 *U. rogersi* (Jordan and Starks, 1895) and 89 *U. nana* (Miyake and McEachran, 1988) were caught. Specimens were kept frozen at −15 °C until processing. After thawing and examination, six *U. chilensis*, three *U. rogersi*, and two *U. nana*, were found to have external morphological abnormalities. Each organism was dissected; a longitudinal cut was made on the ventral side from the anus to the branchial apertures to detect internal morphological abnormalities.

## Result and discussion

A total of 15 free-living round rays and 3 embryos were found to have morphological abnormalities (Table 1). Free-living specimens comprised ten specimens of *U. chilensis*, three specimens of *U. rogersi* and two specimens of *U. nana*. The embryos comprised two specimens of *U. rogersi* and one *U. chilensis*. A total of 88.9 % of organisms with abnormalities were captured in the coastal waters of Chiapas, in the estuaries of the lagoon systems of La Joya-Buenavista (94°41′21″W, 15°51′31″N) and Chantuto-Panzacola (92°51′13″W, 15°09′22″N), within a 853-km$^2$ area (Fig. 1), at a depth of between 28 and 38 m. Two free-living specimens and an embryo were captured in front of Laguna Superior e Inferior (94°54′16″W, 16°09′40″N) and Mar Muerto (94°18′44″W, 16°05′13″N), at depths between 29.0 and 33.0 m.

The morphological abnormalities found in the *Urotrygon* specimens occurred in the anterior portion of the pectoral fins, the eye, the claspers and the liver. The anterior portion of the pectoral fins of a juvenile *U. chilensis* female measuring 7.7 cm DW was not fused and formed a small notch 0.5 cm deep. A smaller notch was observed under the widest part of the left pectoral fin (Fig. 2a). The anterior portion of the pectoral fins of two *U. chilensis* adults was not fused. One specimen measured 13.0 cm DW (Fig. 2b); its left pectoral fin was well developed with a pointed end, but it was directed 45° counterclockwise. The right pectoral fin ended in a blunt end that was not fused to the left pectoral fin. The

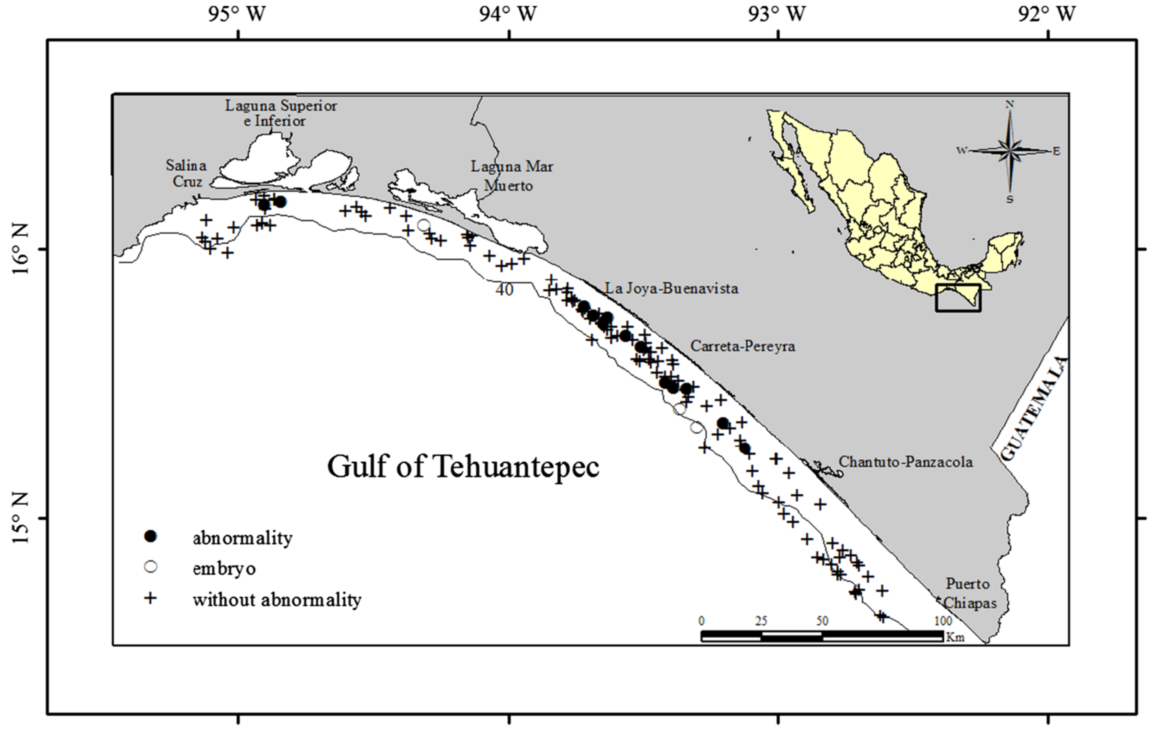

**Fig. 1** Study area with locations of 139 bottom trawls. Black dots indicate records of specimens with morphological anomalies, white dots indicate embryos with anomalies, and crosses indicate trawls with no records of specimens with anomalies

**Table 1** Samples by species, sex, date and location of capture (n. mi. = nautical mile), and type of anomaly found in 15 free-living species and 3 embryos of *Urotrygon*

| Species | Capture day | Sex | Capture site | Specimen | Abnormality |
|---|---|---|---|---|---|
| *U.chilensis* | 03/22/2010 | ♀ | 9.7 n.mi. from Carreta-Pereyra | free-living | Pectoral fins non adherent to the head |
| *U.chilensis* | 03/14/2010 | ♂ | 4.7 n.mi. from La Joya-Buenavista | free-living | Pectoral fins non adherent to the head |
| *U.chilensis* | 12/27/2010 | ♂ | 8.9 n.mi. from laguna Superior-Inferior | free-living | Pectoral fins non adherent to the head |
| *U. rogersi* | 12/27/2010 | ♀ | 8.1 n.mi. from La Joya-Buenavista | free-living | Pectoral fins non adherent to the head |
| *U. nana* | 03/19/2010 | ♀ | 6.8 n.mi. from La Joya-San Mateo del Mar | free-living | Pectoral fins non adherent to the head |
| *U. nana* | 03/15/2010 | ♀ | 7.6 n.mi. from La Joya-San Mateo del Mar | free-living | Anophthalmy |
| *U. rogersi* | 03/14/2010 | ♀ | 14.7 n.mi. from La Joya-Buenavista | free-living | Anophthalmy |
| *U. rogersi* | 03/24/2010 | ♀ | 9.9 n.mi. from La Joya-Buenavista | free-living | Anophthalmy |
| *U.chilensis* | 04/19/2014 | ♂ | 5.8 n.mi. from laguna Superior-Inferior | free-living | Pectoral fins poorly adherent |
| *U.chilensis* | 04/22/2014 | ♂ | 9.4 n.mi. from Carreta-Pereyra | free-living | Absence of a clasper |
| *U.chilensis* | 03/23/2010 | ♀ | 15.3 n.mi. from Carreta-Pereyra | free-living | Pectoral fins non adherent to the head |
| *U.chilensis* | 03/22/2010 | ♂ | 20.0 n.mi. from Mar Muerto | embryo | Pectoral fins non adherent to the head |
| *U. rogersi* | 03/13/2010 | ♂ | 9.6 n.mi. from Carreta-Pereyra | embryo | Pectoral fins non adherent to the head |
| *U. rogersi* | 12/16/2009 | ♀ | 8.3 n.mi. from laguna Superior-Inferior | embryo | Pectoral fins non adherent to the head |
| *U.chilensis* | 04/19/2014 | ♀ | 5.1 n.mi. from Carreta-Pereyra | free-living | Left lobe of the liver of smaller size |
| *U.chilensis* | 04/21/2014 | ♀ | 4.8 n.mi. from Mar Muerto | free-living | Left lobe of the liver of smaller size |
| *U.chilensis* | 04/19/2014 | ♀ | 16.3 n.mi. from Chantuto-Panzacola | free-living | Brilliant black liver |
| *U.chilensis* | 04/22/2014 | ♀ | 11.2 n.mi. from Carretas-Pereyra | free-living | Neoplasia of the liver |

second male measured 13.5 cm DW; the anterior portion of its pectoral fins was not fused and formed a 1.5-cm deep notch (Fig. 2c).

The anterior portion of the pectoral fins of a 24.2-cm DW *U. rogersi* female was incompletely developed; the fins were not fused and there was a notch a little over 3.0 cm deep (Fig. 2d). Two adult *U. nana* females had morphological abnormalities. The first specimen measured 11.2 cm DW; the anterior portion of the pectoral fins was not fused and formed a small notch 0.9 cm deep (Fig. 2e). The second specimen measured 12.2 cm DW and had anophthalmy in the right eye (Fig. 2f). Two adult *U. rogersi* females observed during March 2010 sampling trips, measured 22.6 and 23.6 cm DW, and had undeveloped right eyes, but there are no photographs of these specimens.

A 9.6-cm DW *U. chilensis* juvenile male had the anterior portion of the pectoral fins fused, with a small notch and a depression on the dorsal and ventral sides (Fig. 3a). An adult *U. chilensis* male measuring 16.4 cm DW lacked the left clasper (copulating organ); the right clasper was well developed, it measured 2.9 cm in length and was calcified (Fig. 3b). Two gravid *U. chilensis* females measured 17.4 and 16.8 cm DW. The anterior portion of the pectoral fins of the first female was not fused, forming a 1.5-cm deep notch. This female had a male embryo in her right uterus that measured 5.4 cm DW and was well formed (Fig. 3c). The second female had no malformations; its left uterus contained a 4.8-cm DW male embryo whose anterior portion of the pectoral fins was not fused (Fig. 3d).

Two gravid *U. rogersi* females measured 23.9 and 25 cm DW. The first had a male embryo in each uterus. The embryo in the left uterus measured 4.0 cm DW and was well developed, while the pectoral fins of the embryo in the right uterus were not completely developed; the anterior portion remained free at the height of the first branchial aperture (Fig. 3e). The second gravid female had two well-developed embryos in the left uterus: a 4.2-cm DW female and a 4.3-cm DW male. In the right uterus, a 4.5-cm DW female had a well-developed left pectoral fin, and an incompletely-developed right pectoral fin, with the anterior portion free (Fig. 3f). Both *U. rogersi* embryos were treated with a translucence technique so they appear almost transparent in the figure.

Four adult *U. chilensis* females had morphological abnormalities of the liver. Figure 4a shows a healthy liver from a 16.0-cm DW adult female. Two 19.2- and 15.2-cm DW females had a left lobe of the liver smaller than the right lobe (Fig. 4b and c, respectively). A female measuring 18.9 cm DW had a brilliant black liver (Fig. 4d) and an adult female measuring 18.3 cm DW had neoplasia of the right lobe of the liver (Fig. 4e).

The 139 bottom trawls carried out off the Oaxaca and Chiapas coasts covered a wide area of the coastal zone of the Gulf of Tehuantepec. However, organisms with morphological abnormalities occurred in only 8.6 % of the trawls. These records

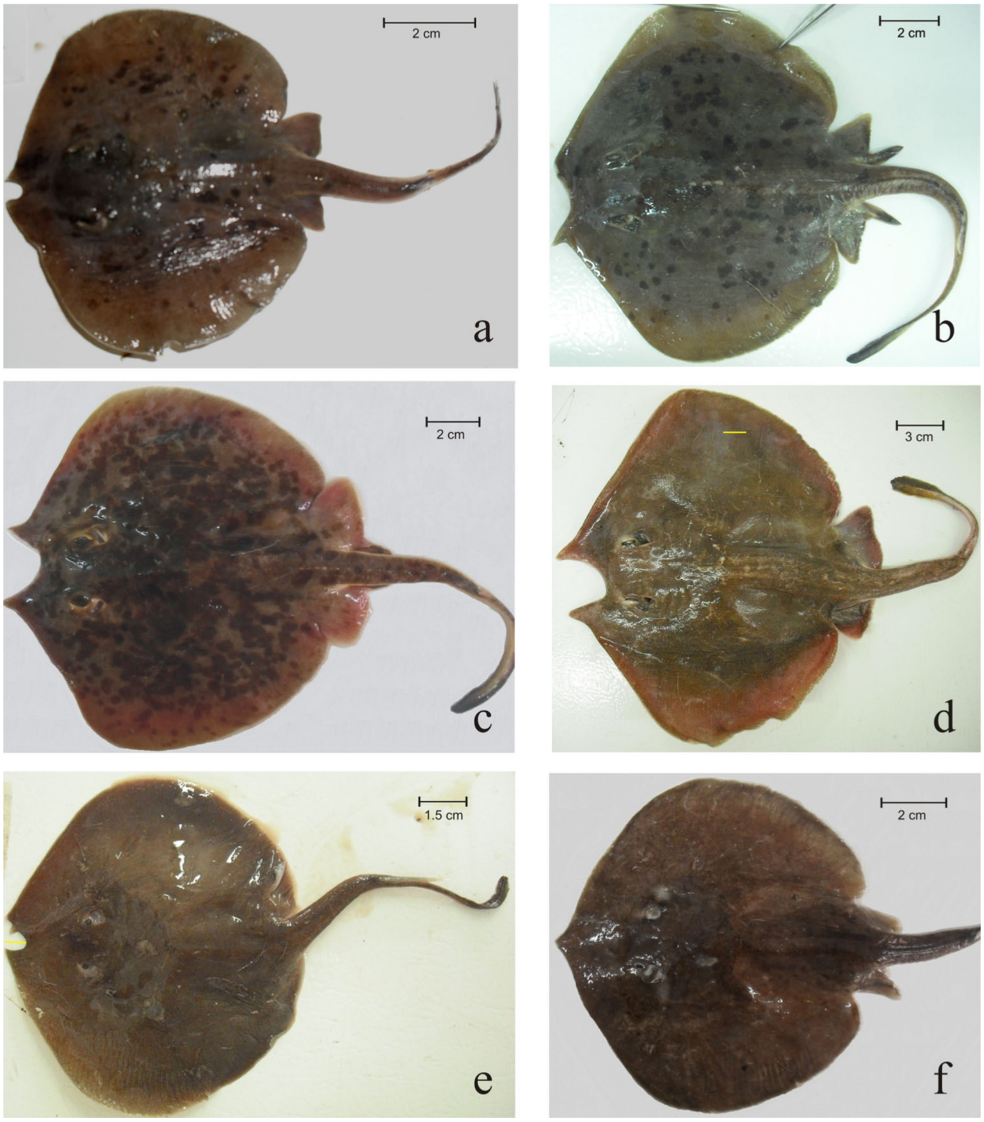

**Fig. 2** Morphological abnormalities of the anterior portion of the pectoral fins in: **a** *U. chilensis* female (7.7 cm DW), **b** *U. chilensis* male (13 cm DW), **c** *U. chilensis* male (13.5 cm DW), **d** *U. rogersi* female (24.2 cm DW), **e** *U. nana* female (11.2 cm DW), and **f** anophthalmy of the right eye of a *U. nana* female (12.2 cm DW)

corresponded to locations that were relatively close to each other and encompassed approximately 25 % of the sampling area. The morphological abnormalities found in *U. chilensis*, *U. rogersi* and *U. nana* correspond to the first report of abnormalities in batoids in the Gulf of Tehuantepec. The abnormalities found were: anterior portion of well-developed pectoral fins not fused, poorly fused anterior portion of the pectoral fins, pectoral fins that were incompletely developed, anophthalmy, absence of a clasper, and liver with abnormal development and neoplasia.

Results indicate that the morphological abnormalities in the anterior portion of the pectoral fins (i.e., not being completely developed or not fused) in embryos of *U. rogersi* and *U. chilensis* do not prevent organisms from reaching sexual maturity, because there were adult specimens of both species that had pectoral fins that were not fused. This is the most common anomaly off the coast of the Gulf of Tehuantepec and does not seem to affect the growth and development of organisms. Mejía-Falla et al. (2011) found *U. rogersi* embryos with morphological abnormalities of the anterior portion of the pectoral fins that were more pronounced than the ones found in this study, which leads the authors to suppose that these organisms had low probabilities of reaching an adult stage. The absence of a clasper found in a male of *U. chilensis* is a rare abnormality that would probably place this organism at a competitive disadvantage with respect to other males during reproduction. This is because in elasmobranchs, the male inserts only one of the two claspers (left or right) during reproduction (Carrier et al. 1994; Chapmana et al. 2003; Nordell 1994; Pratt and Carrier 2001; Whitney et al. 2004), and in batoids, the male inserts the clasper opposite the pectoral fin of the female (left or right) that the male holds during copulation (Chapmana et al. 2003). Therefore, a male with the left clasper absent would be limited during reproduction to holding the female on the left side.

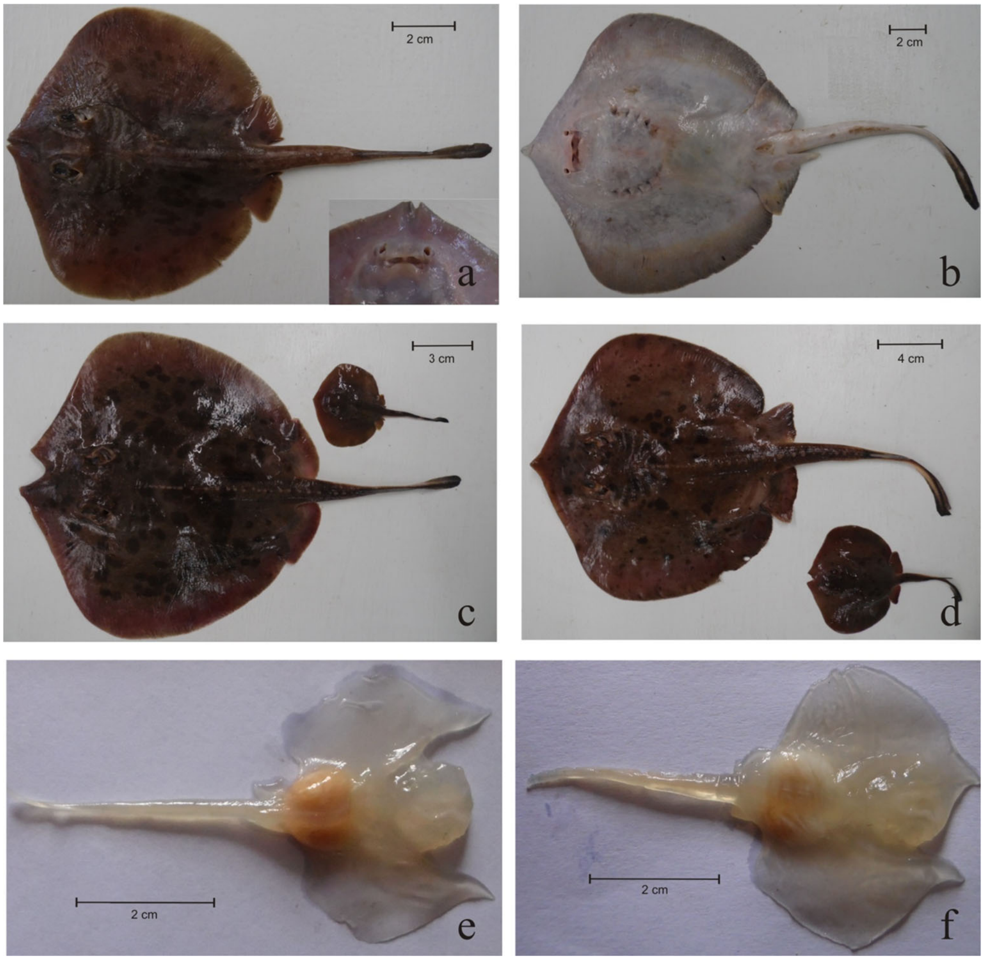

**Fig. 3** Morphological abnormalities in **a** *U. chilensis* male (9.6 cm DW), **b** *U. chilensis* male with absence of the left clasper (16.4 cm DW), **c** *U. chilensis* female and embryo (17.4 and 5.4 cm DW, respectively), **d** *U. chilensis* female and embryo (16.8 and 4.8 cm DW, respectively), **e**, **f** *U. rogersi* embryos (4 and 4.5 cm DW, respectively)

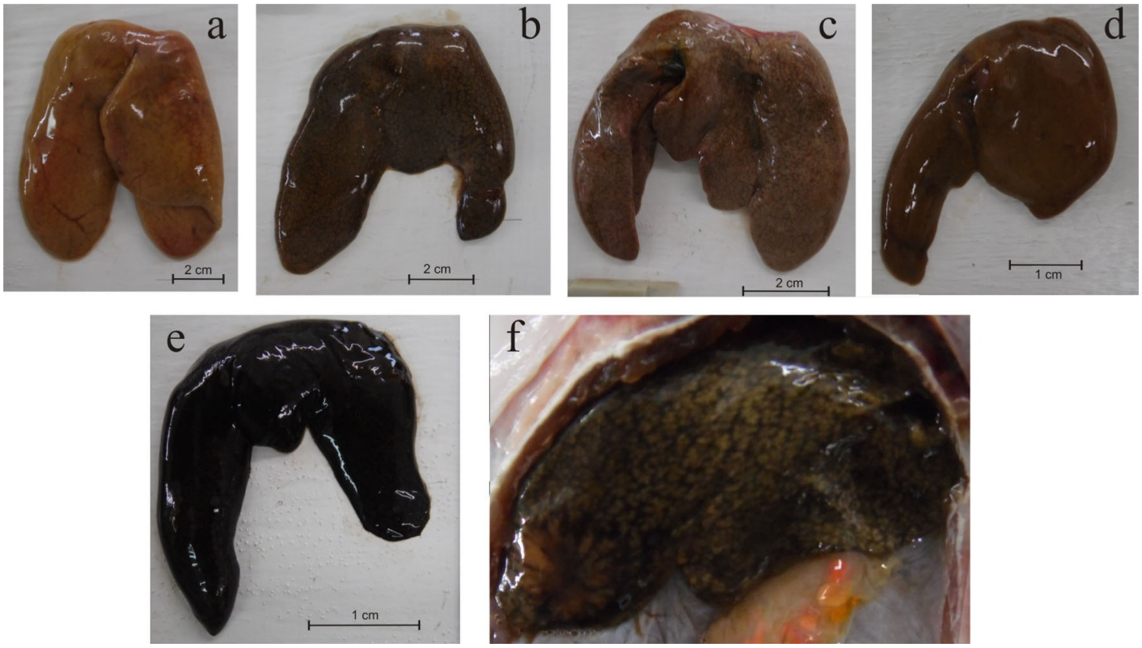

**Fig. 4** Morphological abnormalities of the liver of *U. chilensis* females: **a** healthy liver (16 cm DW), **b**, **c**, **d** left lobe with abnormal development (19.2, 20.2 and 15.2 cm DW), **e** brilliant black liver (18.9 cm DW), and **f** liver with neoplasia of the right lobe (18.3 cm DW)

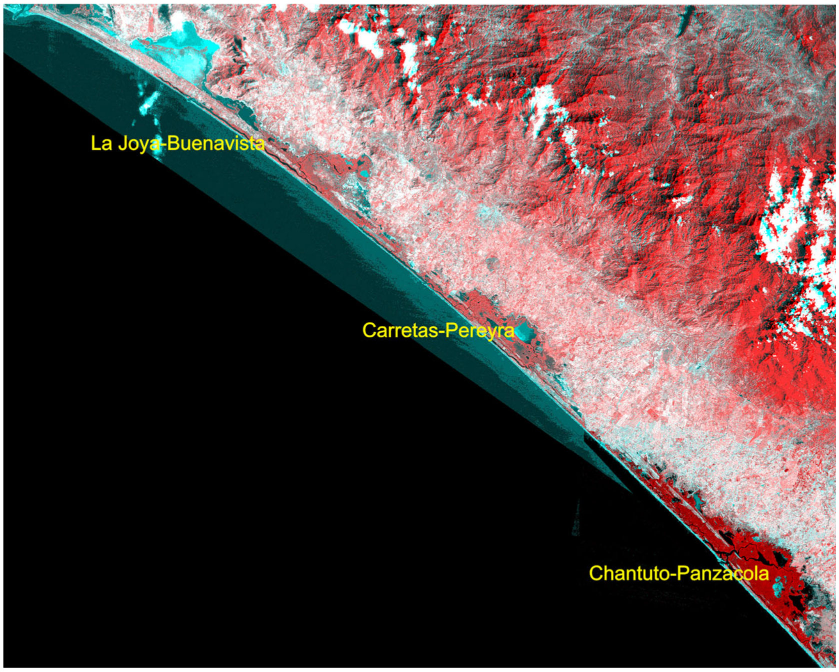

**Fig. 5** Multispectral SPOT image of the Chiapas coast recorded 23 September 1997. Pink hues show crop locations

A total of 83.3 % of recorded abnormalities occurred in the estuaries of the three lagoon systems of Chiapas: La Joya-Buenavista, Carretas-Pereyras and Chantuto-Panzacola. The high incidence of external morphological abnormalities, as well as the presence of livers with abnormal development and neoplasia in this area, leads us to suppose that the abnormalities could probably be due to a pollution problem that has been occurring for several decades in this region. The three lagoon systems are surrounded by an extensive area of mango, plantain, coffee, soy and cotton plantations (Fig. 5), in which there has been indiscriminate use of dichlorodiphenyltrichloroethane (DDT) for over 40 years, not only for pest control in cotton crops, but also for the control of malaria vectors by health brigades (Herrera-Portugal et al. 2008). After the banning of DDT, a great variety of pest-control substances that are banned in other countries and restricted in Mexico have been used in this area (Escobar-Castillejos et al. 2011). These substances adhere firmly to the substrate and are degraded slowly, similarly to DDT (Carvalho 2006; Escobar-Castillejos et al. 2011). Rueda et al. (1997) reported the presence of 16 of these organochlorine substances in the sediment of Chantuto-Panzacola and Carretas-Pereyra. Seven of these compounds were also found in muscle tissue of the shrimp *Litopenaeus vannamei* and of the snapper *Lutjanus novemfasciatus* (Gill, 1862).

Escobar-Sánchez et al. (2009), Mnasri et al. (2010), Ribeiro-Prado et al. (2008) and Rubio-Rodríguez et al. (2010) attributed the cause of morphological abnormalities in batoid fishes to adverse factors such as exposure to pollutants generated by human activities, among them, the presence of heavy metals and sewage discharge. According to Sapozhnikova et al. (2004), organochlorine compounds can influence fish development as well as reproduction and behavior. It is extremely important to carry out studies to determine whether organochlorines are the cause of morphological abnormalities in batoids off the coast of the Gulf of Tehuantepec.

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# VIII. Discusión general

El volumen de captura comercial de los batoideos en el Golfo de Tehuantepec se ha incrementado en un 250% en los últimos 10 años (CONAPESCA 2017), con una captura promedio anual de 433 toneladas. Aunado a esto existe una captura incidental, descartada y no registrada de batoideos en la pesquería de camarón que podría estar superando estos valores. A pesar de esto, los batoideos han sido pobremente documentados, lo que ha generado una falta de información confiable de estas especies en la región.

Los resultados de este trabajo indican que 16 especies de batoideos fueron capturadas con redes de arrastre de fondo en el Golfo de Tehuantepec, entre 16 y 62 metros de profundidad (Torres-Huerta *et al.* 2013; Torres-Huerta *et al.* 2019). Quince de estas especies ya habían sido registradas anteriormente en la región (McEachran y Notarbarloto di Sciara 1995; Amezcua-Linares 1996; Castro-Aguirre y Espinosa Pérez 1996; Carrera-Fernández *et al.* 2012) y solo la raya redonda denticulada *U. cimar* representa un registro adicional a los taxa previamente reportados.

La raya redonda denticulada es una especie tropical con hábitos bentónicos y normalmente se encuentra asociada a fondos blandos (Robertson y Allen 2015). Hasta 2008 solo se tenía conocimiento de la presencia de esta especie en aguas de Costa Rica, Nicaragua y El Salvador (López y Bussing 1998; Robertson y Allen 2015). Sin embargo, Amezcua-Linares y Amezcua (2009) reportan la presencia de una hembra capturada en 1985 en Bahía de Petacalco en el

Pacífico Mexicano. En el Golfo de Tehuantepec se confirma la presencia de la especie con un total de 101 ejemplares, incluyendo juveniles y adultos de ambos sexos. Históricamente esta especie ha sido confundida con la raya redonda áspera *U. munda,* de hecho, Corro-Espinosa y Ramos-Carrillo (2004) muestran una foto de la raya redonda denticulada como raya redonda áspera. Esa confusión puede deberse a que ambas especies son muy parecidas en su morfología externa; las dos especies se caracterizan por la presencia de dentículos esparcidos en todo el disco, siendo la principal diferencia que la raya redonda áspera presenta púas esparcidas en la línea media dorsal, mientras que, la raya redonda denticulada carece de púas y en su lugar sólo presenta dentículos filosos que son ligeramente más grandes en la línea media del disco (López y Bussing 1998; Robertson y Allen 2015).

La raya redonda áspera ha sido reportada para el Golfo de Tehuantepec por Castro-Aguirre y Espinosa-Pérez (1996), Tapia-García y García-Abad (1998), Robertson y Allen (2015), pero ninguno de estos autores registra a la raya redonda denticulada en la región. Es muy importante señalar que durante el desarrollo de este estudio se realizaron más de 300 arrastres de fondo en un intervalo de profundidad de 16 a 62 m y no se capturaron ejemplares de la raya redonda áspera. De acuerdo a Robertson y Allen (2015) la raya redonda áspera se distribuye entre 1-51 m de profundidad, por lo que es importante continuar con los estudios en la región y realizar colectas en profundidades menores a 17 m y mayores a 62 m con el objetivo de establecer la presencia de la raya redonda áspera en el Golfo de Tehuantepec, y de confirmarse su presencia, establecer la amplitud de distribución de ambas especies.

Mediante el estudio de ecología de comunidades de batoideos se determinó que las 16 especies capturadas en el Golfo de Tehuantepec forman cuatro asociaciones durante la temporada de vientos Tehuanos (diciembre a marzo) y tres asociaciones durante la temporada de lluvias (junio). Estas asociaciones de batoideos coinciden con la comunidad de peces, crustáceos y cefalópodos identificados por Bianchi (1991). La asociación de fondos arenosos de Oaxaca (SBO en el artículo) y la asociación de fondos arenosos de Chiapas (SBC en el artículo) son parte de lo que fue llamado por ese autor como la comunidad de fondo arenoso, que se extiende desde Salina Cruz, México, hasta San José, Guatemala. La asociación de aguas costeras de Chiapas (SWC en el artículo) correspondió a la comunidad de aguas costeras ubicada entre San Marcos, México, y la región central de Guatemala. La asociación de la plataforma media superior (UIS en el artículo) identificado en este estudio de 12 estaciones que cubren un área pequeña (aproximadamente 215 km$^2$) frente a Salina Cruz es parte de la comunidad de la "plataforma media superior", que es una de las asociaciones más extensas descritas por Bianchi (1991).

La profundidad y la longitud geográfica son los principales factores que determinan la estructura de la comunidad, aunque la temperatura juega un papel importante al inicio de la temporada de vientos Tehuanos. Los estudios comunitarios de batoideos que cubren un amplio intervalo de profundidad (hasta 1700 m) indican que la profundidad es el principal factor que determina la distribución de los elasmobranquios (Massutí y Moranta 2003; Gouraguine *et al.* 2011; Bottari *et al.* 2014; Clarke *et al.* 2016). El presente estudio cubrió un estrecho intervalo de profundidad (16 a 62 m) en una amplia región geográfica que se ha clasificado en tres regímenes hidrográficos (Lavín *et al.* 1992; Trasviña *et al.* 1995; Chapa-Balcorta *et al.* 2015): (1) un régimen occidental caracterizado por la presencia de giros a mesoescala y de surgencias costeras que transportan agua más fría y salada que las típicas aguas tropicales orientales; (2)

un régimen central directamente afectado por la mezcla generada por los vientos de Tehuanos; y (3) un régimen oriental, menos afectado por los Tehuanos, y mantiene las características termohalinas superficiales de las aguas del Pacífico Tropical Oriental. Varios estudios de asociaciones de fauna demersal realizados en amplias áreas geográficas han vinculado la estructura demersal de la comunidad con el régimen ambiental característico de cada región (Bianchi 1991; Bianchi 1992a; Bianchi 1992b; Farinã *et al.* 1997b; Farinã *et al.* 1997a; Labropoulou y Papaconstantinou 2004)**.**

En general, la mayor riqueza de especies, diversidad, abundancia y biomasa de batoideos se localiza en la región central del Golfo de Tehuantepec (en la asociación SBO), entre Salina Cruz y Puerto Arista, a una profundidad promedio de 27 m. Esto coincide con la mayor biomasa de zooplancton (Färber-Lorda *et al.* 1994; Ayala-Duval *et al.* 1996), invertebrados bentónicos (Gamboa-Contreras y Tapia-García 1998) y peces demersales (Acal y Arias 1990; Tapia-García 1998; Martínez-Muñoz 2012) reportados para la región central del Golfo de Tehuantepec. La alta productividad en la región occidental y central del golfo es principalmente debido a los procesos de surgencia y mezcla vertical, pues las aguas subsuperficiales tienen altas concentraciones de fosfatos, silicatos, nitritos y nitratos, dando lugar a una cadena trófica que alimenta a una rica comunidad biológica (Robles-Jarero y Lara-Lara 1993; Ortega-García *et al.* 2000; Chapa-Balcorta *et al.* 2015).

La mayor diversidad, abundancia y biomasa de batoideos, y de otros peces e invertebrados en la región central del Golfo de Tehuantepec, indican que la distribución de las presas potenciales también podría ser un elemento importante que podría afectar la selección del hábitat por los batoideos. Los estudios de alimentación de los batoideos en el Golfo de

Tehuantepec han indicado que las principales presas de cuatro especies (*U. chilensis, U. rogersi, N. vermiculatus* y *R. steindachneri*) registradas en este estudio fueron anfípodos, ofiuros, decápodos, poliquetos, estomatópodos, moluscos y peces (Guzmán-Castellanos 2010; Díaz-Carballido 2011; Díaz-Carballido 2015). Holden y Tucker (1974), Skjæraasen y Bergstad (2000), Lucifora *et al.* (2012) han demostrado que la distribución heterogénea de los batoideos demersales y bentónicos se sobrepone con las regiones de mayor abundancia de presas potenciales, como invertebrados y peces ().

Los valores más bajos de abundancia y biomasa de los batoideos en la región central del Golfo de Tehuantepec ocurrieron a principios de la temporada de vientos Tehuanos (diciembre). Varios factores parecen contribuir a esta diferenciación geográfica (profundidad, temperatura y longitud). La presencia de fuertes vientos de Tehuanos en esta región del golfo provoca cambios en la columna de agua, generando una mezcla de la capa superficial (50–60 m) y una considerable variabilidad en la temperatura (hasta 10°C), salinidad (hasta 2.2 PSU) y oxígeno disuelto (hasta 3.0 ml L-1) (Trasviña *et al.* 1995; Tapia-García *et al.* 2007). Observaciones realizadas en la región occidental del Golfo de Tehuantepec durante un evento de Tehuanos (A. M. Torres-Huerta, datos sin publicar) muestran un gran número de batoideos concentrados en aguas poco profundas (4 m), posiblemente en busca de aguas cálidas ricas en oxígeno disuelto. En este trabajo se plantea que la disminución de la temperatura y el oxígeno disuelto durante los vientos de Tehuanos podrían influir en los movimientos verticales de los batoideos hacia aguas adyacentes en la búsqueda de áreas con parámetros ecofisiológicos óptimos. Fisiológicamente, la temperatura del agua es considerada la variable más importante que influye en el metabolismo, reproducción, crecimiento somático, distribución horizontal y vertical, comportamiento y uso del hábitat a corto plazo de los peces (Carey *et al.* 1971; Magnuson *et al.* 1979; Neill 1979). Además, el oxígeno disuelto ha sido considerado como el factor ecológico dominante que determina la biomasa macro bentónica y la composición de especies en el área de surgencias de Perú y Chile (Rosenberg *et al.* 1983; Gutiérrez *et al.* 2006). Patrones de movimiento estacionales provocados por los cambios de temperatura se han observado en especies de elasmobranquios como *Mustelus henlei*, *Myliobatis californicus*, *Triakis semifasciata* y *Pseudobatos productos* frente a la costa de California (Hopkins y Cech 2003; Espinoza *et al.* 2011; Farrugia *et al.* 2011)**.** Aunque en el presente estudio sólo se tienen datos de abundancia y biomasa, es importante continuar con estudios sobre el efecto de los vientos Tehuanos en la dispersión de los batoideos.

La composición de especies en las asociaciones SBO, SBC, SWC y SBSW fue homogénea, con más de 90% de similitud. *U. chilensis*, *N. vermiculatus* y *U. rogersi* fueron las especies más abundantes, con una amplia distribución a lo largo del área de estudio en profundidades de hasta 42 m. Estas tres especies representan el 70.1% de la abundancia de batoideos demersales en el Golfo de Tehuantepec, con las mayores concentraciones de *U. chilensis* y *U. rogersi* en la región central y las mayores concentraciones de *N. vermiculatus* en la región oriental. *Narcine vermiculatus* y *U. chilensis* fueron caracterizados previamente por Tapia-García y García-Abad (1998) como especies muy abundantes en el golfo. Las especies del género *Narcine* y *Urotrygon* son las especies más abundantes en la comunidad de batoideos demersales en regiones adyacentes al Golfo de Tehuantepec, como Guatemala, Costa Rica y Colombia (Ixquiac-Cabrera *et al.* 2009; Clarke *et al.* 2016; Navia y Mejía-Falla 2016).

Otras especies menos abundantes como *U. nana, R. leucorhynchus, G. marmorata, R. steindachneri* y *A. laticeps*, tienen las mayores concentraciones de individuos en la región central del Golfo de Tehuantepec (entre Puerto Arista y Masagual). Estas especies también se han reportado con abundancias bajas en profundidades menores a 50 m en la región del Pacífico de Costa Rica (Clarke *et al.* 2016). Finalmente, la asociación determinada en las zonas más profundas (USI), se caracteriza por la presencia de las especies *P. glaucostigma*, *N. entemedor, Z. xyster* y *H. longus*. Las tres últimas especies también se distribuyeron en aguas poco profundas (SBO y SWC), aunque en menores abundancias (< 3.0%).

Las curvas ABC sugieren que la mayor parte de las asociaciones de batoideos identificados en este estudio son comunidades con un grado moderado de estrés ecológico debido a que la curva de abundancia estaba por encima de la curva de biomasa. Esto significa que especies pequeñas (p. ej. *U. chilensis, U. rogersi* y *N. vermiculatus*) dominan en número, pero no en biomasa. El estrés ecológico puede ser consecuencia de perturbaciones antropogénicas y naturales; algunas de estas perturbaciones incluyen los efectos de la pesca de arrastre de fondo, los cambios estacionales en el reclutamiento o los cambios en el ciclo de vida de las especies (Kaiser *et al.* 2000; Kaiser *et al.* 2002; Thrush *et al.* 2006). La dominancia de especies de batoideos de tamaño pequeño capturadas como fauna incidental en la pesca de camarón coincide con los registros obtenidos en el Golfo de California, la costa de Guatemala, Costa Rica, Colombia y Argentina (Tamini *et al.* 2006; Ixquiac-Cabrera *et al.* 2009; López-Martínez *et al.* 2010; Clarke *et al.* 2016; Navia y Mejía-Falla 2016).

Futuros estudios podrían evaluar las alteraciones (físicas, biológicas, de la pesca, etc.) que están provocando el estrés ecológico a la comunidad de batoideos del Golfo de Tehuantepec.

Esto es importante porque al menos cuatro especies de batoideos registradas en este estudio (*A. laticeps, N. vermiculatus, P. leucorhynchus* y *M. munkiana*) son clasificadas por la UICN como Casi Amenazadas, y ocho especies (*H. longus*, *N. entemedor*, *P. leucorhynchus*, *Z. xyster*, *U. aspidura*, *U. chilensis*, *U. nana* y *U. rogersi*) se clasifican como Datos Deficientes (http://www.iucnredlist.org, consultado el 15 de febrero de 2019). Los fondos blandos ofrecen un hábitat óptimo para los batoideos y juegan un papel clave en la vulnerabilidad a la extinción de estas especies, debido a que los fondos blandos están sujetos a grandes presiones de pesca (Moore 2017).

El conocimiento referente a la distribución de los batoideos en el Golfo de Tehuantepec y sus aspectos reproductivos permitirá en un futuro tomar decisiones para el manejo y la conservación de estas especies. En este trabajo se generó información de la ecología reproductiva de la guitarra bruja, la cual es una de las nueve especies del Golfo de Tehuantepec catalogada por la Lista Roja de la UICN con datos insuficientes para evaluar su riesgo de extinción. Las guitarras brujas son un importante componente de la fauna demersal de la región y son frecuentemente capturadas como fauna incidental en la pesquería de camarón (Acal y Arias 1990; Tapia-García 1998; Tapia-García y García-Abad 1998; Torres-Huerta *et al.* 2019). La guitarra bruja es poco abundante de mayo a enero, con registros de individuos principalmente juveniles (< 39 cm de TL) y machos adultos (> 45 cm de TL). Las abundancias se incrementan en febrero y marzo, con predominio de machos adultos con tallas entre 45 y 52 cm de TL, y en abril, con adultos de ambos sexos midiendo entre 46 y 69 cm de TL. Las hembras no grávidas capturadas de febrero a abril presentan el mayor diámetro de ovocitos vitelogénicos y los machos tienen semen almacenado en el epidídimo. Clarke *et al.* (2016)

reportan las concentraciones más altas de adultos de guitarra bruja entre 50 y 100 m de profundidad en las aguas del Pacífico de Costa Rica. Los adultos están probablemente en profundidades > 60 m en el Golfo de Tehuantepec durante la mayor parte del año y migran hacia aguas someras (entre 25 y 37 m) para reproducirse en febrero. Las agregaciones estacionales con fines reproductivos son un comportamiento característico en elasmobranquios (Carrier *et al.* 1994; Whitney *et al.* 2004; Powter y Gladstone 2009). Esto ha sido observado en otras especies de este género, como la guitarra bandeada *Z. exasperata*, la cual realiza migraciones reproductivas hacia bahía Almejas, en la costa occidental de Baja California (Villavicencio-Garayzar 1995), y hacia aguas someras en el Golfo de California Sur (Blanco-Parra *et al.* 2009). Después del período reproductivo, los adultos de la guitarra bruja tienden a segregarse por sexo en el Golfo de Tehuantepec, con las hembras migrando hacia mayores profundidades que los machos. La segregación por sexo es una característica que se ha observado en algunas especies de batoideos. (Villavicencio-Garayzar 1995; Ebert 2005; Clarke *et al.* 2014; Lara-Mendoza y Márquez-Farías 2014).

Las hembras preñadas de la guitarra bruja capturadas en profundidades < 30 m indican una preferencia por aguas someras durante la preñez. Economakis y Lobel (1998), Hight y Lowe (2007) sugieren que las aguas cálidas y someras incrementan la temperatura del cuerpo de las hembras preñadas del tiburón leopardo *Triakis semifasciata* Girard, 1855 en la costa sur de California, y del tiburón gris *Carcharhinus amblyrhynchos* (Bleeker, 1856) en el Atolón Johnston, en el Océano Pacífico Norte, lo cual aumenta la tasa de desarrollo embrionario. Bajo la influencia de los vientos Tehuanos, el agua superficial fluye mar adentro lo cual genera mezcla y surgencia de agua subsuperficial. El resultado es una caída de la temperatura de hasta

8°C en el centro del Golfo de Tehuantepec, lo cual limita la disponibilidad de aguas cálidas en profundidades > 25 m (Barton *et al.* 1993; Trasviña y Barton 1997; Chapa-Balcorta *et al.* 2015). Se puede suponer que las hembras embarazadas permanecen en aguas <30 m de profundidad en busca de aguas cálidas durante la temporada de vientos Tehuanos. Esto les permite a las hembras concluir el desarrollo embrionario para que las crías puedan nacer a partir de abril.

Los registros obtenidos durante este estudio muestran evidencia de una aparente segregación juvenil por talla. Esto significa que las crías de la guitarra bruja se distribuyen en aguas someras (< 30 m) y conforme incrementan su talla (al estado sub adulto) son capturadas en aguas más profundas ($\bar{x} = 44$ m). La segregación por tallas ha sido previamente reportada para esta especie por Clarke *et al.* (2014) para aguas del Pacífico de Costa Rica. Estos autores mencionan que la profundidad es el factor principal que influye en los patrones de segregación de la guitarra bruja. Otros estudios realizados en tiburones han sugerido que la segregación por tamaño podría estar vinculada a numerosas variables ambientales y biológicas específicas de cada región (Klimley y Nelson 1984; Klimley 1987; Robbins 2007), que en conjunto pueden ofrecen mayor diversidad de hábitats y presas para cada talla o estado de madurez (Klimley 1987; Sims 2003; Kock *et al.* 2013). Esto podría disminuir la competencia intraespecífica y el riesgo de depredación (Hoare *et al.* 2000; Heupel *et al.* 2004), lo que permite satisfacer las necesidades metabólicas (por ejemplo, crecimiento y reproducción) de cada edad o etapa de madurez (Klimley 1987; Sims 2005; Wearmouth y Sims 2010).

Los machos adultos de la guitarra bruja pueden distinguirse de las hembras por sus ocelos durante el período reproductivo. Los machos adultos tienen ocelos con un centro amarillo y borde negro en la parte posterior del cuerpo y son más brillantes que los de las hembras adultas. El dicromatismo sexual (diferencias en la coloración de los dos sexos) se ha observado en el tiburón gata *Ginglymostoma cirratum* (Bonnaterre, 1788) durante el cortejo y el apareamiento, con los machos considerablemente más oscuros que las hembras (Klimley 1980). En muchos vertebrados como peces, pájaros, lagartijas y primates los colores brillantes son ampliamente considerados como un producto de la selección sexual, los cuales actúan teniendo a los miembros del sexo opuesto preferentemente apareándose con los individuos de color más brillante (Darwin 1871; Andersson 1986; Cotton et al. 2006). La coloración en el período reproductivo de los machos muestra que el dicromatismo sexual puede desempeñar un papel social importante en el reconocimiento del sexo (Cooper y Greenberg 1992).

Las observaciones de este trabajo indican que los ocelos con el centro amarillo y el borde negro son más frecuentes en las hembras no preñadas, mientras que las hembras preñadas son más frecuentes sin el centro amarillo de los ocelos. La ausencia de un centro amarillo de los ocelos podría estar relacionada con la fase de gravidez. El polimorfismo sexual (diferencias en la coloración entre hembras o machos de una misma especie) ha sido observado en lacértidos y algunos mamíferos (Galán 2000; Wyatt 2014). Galán (2000) sugiere que los cambios en la coloración entre las hembras grávidas pueden tener la función de evitar las persecuciones y los intentos de copula por parte de los machos, una vez que ya han sido fertilizadas. Por lo anterior, se sugiere que las diferencias en la coloración entre hembras adultas del pez guitarra bruja podría estar jugando un importante papel en el reconocimiento sexual durante el periodo reproductivo.

La información obtenida en este trabajo indica diferencias en la longitud total (11.5%), en peso total (8.5%) y en talla de madurez (8.3%) entre machos y hembras de adultos. Las diferencias entre machos y hembras de la misma especie es una característica común que ha sido observada en elasmobranquios con reproducción vivípara (Sims 2005; Wearmouth y Sims 2010). La ventaja de alcanzar mayor tamaño permite a las hembras tener más espacio disponible en la cavidad del cuerpo para el crecimiento de los ovocitos o embriones (Klimley 1987; Parsons *et al.* 2008) y un hígado de mayor tamaño para cubrir el gasto energético de las hembras durante la vitelogénesis, la maduración de los ovocitos y la gestación (Klimley 1987; Lucifora *et al.* 2002; Mabragaña *et al.* 2002; Oddone y Velasco 2006).

Los machos de la guitarra bruja alcanzan la talla de madurez a una talla menor (43.6 cm TL) que las hembras (48.2 cm TL). Esto coincide con lo reportado para esta especie por Clarke et al. (2014), quienes mencionan que los machos alcanzan la madurez entre 42 y 47 cm de TL, y las hembras alcanzan la madurez sexual entre 47 y 52 cm TL en Costa Rica. El dimorfismo en la talla de madurez también ha sido observado en otras especies de la familia Trygonorrhinidae (Villavicencio-Garayzar 1995; Marshall *et al.* 2007; Blanco-Parra *et al.* 2009; Colonello *et al.* 2011).

Las hembras de la guitarra bruja son sincrónicas; por lo tanto, la ovulación y el apareamiento comienzan en marzo y el parto comienza en abril. La presencia de hembras grávidas sin vitelogénesis concurrente y hembras adultas no grávidas durante el mismo período es indicativo de un ciclo de dos años con vitelogénesis y gestación consecutiva. Esto significa que las hembras están grávidas durante un año; dan a luz, y no ovulan /aparean de nuevo hasta un año más tarde.

Los ciclos bienales con vitelogéneis y gestación consecutiva han sido reportados en muchas especies de tiburones del género *Carcharhinus*, algunos tiburones martillo (*Sphyrna mokarran* Rüppell, 1837 y *S. zygaena* Linneus, 1758), el tiburón gata (*Ginglymostoma cirratum* Bonnaterre, 1788), y de la raya gavilán (*Rhinoptera bonasus* (Mitchill, 1815)) (Castro 2009; Pérez-Jiménez 2011).

La presencia de huevos uterinos en la guitarra bruja en abril, octubre y noviembre podría indicar un probable periodo de diapausa embrionaria. Esta estrategia reproductiva permite ajustar el nacimiento de las crías al periodo más favorable del año, lo cual maximiza la probabilidad de sobrevivencia y el éxito reproductivo de las especies. Esta estrategia ha sido bien documentada para al menos 16 especies, ocho de las cuales son peces guitarra (Waltrick *et al.* 2012). Trabajos futuros podrían confirmar si la guitarra bruja presenta un periodo de diapausa embrionaria con la examinación de hembras adultas no preñadas de mayo a octubre.

Las crías de la guitarra bruja nacen entre abril y junio; el tamaño al nacer oscila entre 15.2 y 17.5 cm TL ($\bar{x}$=16.9 cm TL), y la proporción sexual fue 1:1 (H:M). La mayor biomasa de invertebrados y peces demersales en el Golfo de Tehuantepec se han registrado de marzo a agosto (Gamboa-Contreras y Tapia-García 1998; Tapia-García 1998), por lo que la presencia de neonatos a partir de abril podría estar relacionada con la abundancia de posibles presas.

Las hembras grávidas más pequeñas (entre 48 y 50 cm LT) presentan una menor fecundidad en el útero derecho, esto podría estar relacionado con: a) el espacio disponible en la cavidad celómica, ya que es menor en tallas más pequeñas (Klimley 1987), y b) el aparato digestivo e hígado se encuentran acomodados del lado derecho del celoma, lo que limita aún más el espacio disponible. La morfología en forma de disco de los batoideos restringe el espacio celómico y con esto se restringe aún más la capacidad uterina (Musick y Ellis 2005). La fecundidad de los dos úteros es igual en hembras que miden más de 58 cm de LT y estas hembras alcanzan su mayor fecundidad (8 embriones). La fecundidad máxima coincide con la reportada para la especie en Costa Rica por Clarke *et al.* (2014). Esto significa que al igual que la guitarra bandeada (siete embriones), la guitarra bruja es una especie con fecundidad intermedia entre las especies de la familia Trygonorrhinidae (*Z. brevirrostris*: 2 embriones, *Aptychotrema rostrata*: 20 embriones) (Villavicencio-Garayzar 1995; Blanco-Parra *et al.* 2009; Colonello *et al.* 2011; Kyne *et al.* 2016).

La captura incidental de la guitarra bruja, durante más de un mes de su periodo reproductivo usando redes de arrastre de fondo podría afectar negativamente el éxito reproductivo y la viabilidad a largo plazo de esta especie. De acuerdo con Musick (1999) y Stevens *et al.* (2000), la captura de los organismos de mayor tamaño puede generar cambios en la estructura de tallas y en el potencial reproductivo, incrementando la vulnerabilidad a la sobreexplotación (Mucientes *et al.* 2009; Jacoby *et al.* 2011). Existe una veda anual a la pesca de camarón en México que comienzan en marzo y termina en septiembre (SAGARPA 2013), por lo que el ciclo reproductivo y el periodo de nacimiento de la guitarra bruja están parcialmente protegido de forma indirecta (marzo y abril). Sin embargo, la captura de machos adultos durante febrero y quizás parte de marzo, podría hacerlos más vulnerables debido a que éstos duplican en número a las hembras capturadas. De acuerdo con Simpfendorfer *et al.* (2002) y Muscientes *et al.* (2009), existe una explotación sexual diferencial en especies como el tiburón azul *Prionace glauna* (capturado en el Océano Pacífico Sur) y en el tiburón mako *Isurus oxyrinchus* (capturado en el Océano Atlántico Norte), debido a que ambos sexos exhiben un patrón de distribución estacional diferente. La explotación de especies marinas que presentan segregación sexual estacional podría tener efectos devastadores en algunas especies, ya que podría contribuir a la disminución de la población (Heppell *et al.* 1999; Muscientes *et al.* 2009; Tovar-Ávila *et al.* 2010). Es de vital importancia realizar un estudio demográfico para evaluar el efecto de la explotación sexual diferencial en los adultos de la guitarra bruja en el Golfo de Tehuantepec.

Las redes de arrastre de fondo usadas en la pesquería de camarón en el Golfo de Tehuantepec cuentan con dispositivos excluidores de tortuga (DET). Los DET tienen un espacio entre barras de 10.2 cm como máximo (SEMARNAT-2016), lo que en teoría debería impedir que los animales de más de 10.2 cm de altura o de anchura entren al copo de la red. Sin embargo, el 94% de las guitarras bruja capturadas tenían entre 20-69.5 cm de longitud total, pero debido a su aplanamiento dorso ventral pasan a través de los DET. Estudios técnicos realizados por el Instituto Nacional de Pesca indican que los DTE funcionan para algunas especies de batoideos, pero no para otras (J. Tovar-Ávila, comunicación personal, 27 de febrero de 2020), por lo que está en fase de prueba la doble relinga, que tiene como objetivo ahuyentar a las rayas antes de que la red pase, y la relinga con rodillos que evita que vaya pegada al fondo. En el futuro esto podría disminuir la mortalidad de los machos adultos durante su periodo reproductivo, lo cual sería un importante paso para la conservación de la guitarra bruja.

Durante los viajes de muestreo realizados en este estudio se recolectaron 15 organismos de vida libre y 3 embriones del género *Urotrygon* con anomalías morfológicas. Estos ejemplares fueron capturados en localidades relativamente cercanas entre sí, ocupando aproximadamente el 25% del área de muestreo. Las anormalidades morfológicas encontradas en *U. chilensis, U. rogersi* y *U. nana* fueron: aletas pectorales no fusionadas en su parte anterior, aletas pectorales sin desarrollo completo, anoftalmía, agenesia de mixopterigio, hígado con desarrollo anormal y neoplasia (Torres-Huerta *et al.* 2015).

El 83.3% de los registros con anormalidades se localizaron frente a las desembocaduras de tres sistemas lagunares de Chiapas: La Joya-Buenavista, Carretas-Pereyras y Chantuto-Panzacola. La alta incidencia de anomalías morfológicas externas, así como la presencia de hígados con desarrollo anormal y neoplasia en esta región podría deberse a la descarga de aguas contaminadas proveniente de la zona terrestre. Los tres sistemas lagunares se encuentran rodeados de una extensa región de cultivos de mango, plátano, café, soya y algodón, en los cuales se ha usado indiscriminadamente el diclorodifeniltricloroetano (DDT) por más de 40 años, no sólo en la agricultura para el control de las plagas del cultivo de algodón, sino también, por las brigadas de salud para el control de vectores del paludismo (Herrera-Portugal *et al.* 2008). Después de la prohibición del DDT en 1972, se ha utilizado adicionalmente en la región una gran variedad de plaguicidas prohibidos en otros países y restringidos en México (Escobar-Castillejos *et al.* 2011). Estas sustancias se adhieren firmemente al suelo y son degradados lentamente, al igual que el DDT (Carvalho 2006; Escobar-Castillejos *et al.* 2011). Rueda *et al.* (1997) reportaron la presencia de 16 de estos plaguicidas organoclorados en sedimento de Chantuto-Panzacola y Carretas-Pereyra. Siete de estos compuestos fueron también encontrados en músculo del camarón *Litopenaeus vannamei* (Boone, 1931) y del pargo *Lutjanus novemfasciatus* Gill, 1862.

Escobar-Sánchez *et al.* (2009), Mnasri *et al.* (2010), Ribeiro-Prado *et al.* (2008) y Rubio-Rodríguez *et al.* (2010) atribuyen la causa de las anomalías morfológicas encontradas en otros peces batoideos a factores adversos como la exposición a contaminantes generados por las actividades humanas. De acuerdo a Sapozhnikova *et al*. (2004), los compuestos organoclorados pueden influir en el desarrollo de los peces, la reproducción y el comportamiento. Es de suma importancia continuar con los estudios para establecer si los organoclorados son la causa de las anomalías morfológicas en batoideos en el Golfo de Tehuantepec.

Este trabajo aporta información relevante de los batoideos del Golfo de Tehuantepec, lo cual da pauta para que futuros estudios consideren abordar las causas de las anomalías morfológicas en la costa de Chiapas, la biología reproductiva de otras especies de batoideos e información adicional que permita entender el estado en el que se encuentran las poblaciones de batoideos de la región. Una cuestión que es de suma importancia para la conservación de los batoideos, es la de hacer mejoras en las redes de arrastre de fondo con el fin de disminuir la captura no solo de los batoideos sino la de otras especies de peces capturadas incidentalmente.

# IX. Conclusiones

- Se registraron trece especies de batoideos demersales y tres especies pelágicas capturadas con redes de arrastre de fondo en el Golfo de Tehuantepec, entre 16 y 62 metros de profundidad.
- Se confirma la presencia de la raya redonda denticulada *U. cimar* en el Golfo de Tehuantepec.
- Las anomalías morfológicas encontradas en *U. chilensis, U. rogersi* y *U. nana* fueron: aletas pectorales no fusionadas en su parte anterior, aletas pectorales sin desarrollo completo, anoftalmía, agenesia de mixopterigio, hígado con desarrollo anormal y neoplasia.
- Las anomalías morfológicas se localizaron frente a las desembocaduras de los sistemas lagunares: La Joya-Buenavista, Carretas-Pereyras y Chantuto-Panzacola. La alta incidencia de estas anomalías morfológicas podría ser debido a la descarga de aguas contaminadas proveniente de la zona terrestre.
- Las 16 especies capturadas en el Golfo de Tehuantepec forman cuatro asociaciones durante la temporada de vientos Tehuanos (diciembre a marzo) y tres asociaciones durante la temporada de lluvias (junio). La profundidad y la longitud geográfica son los factores principales que determinan la estructura de la comunidad, aunque la temperatura juega un papel importante al inicio de la temporada de vientos Tehuanos.

- La mayor riqueza de especies, diversidad, abundancia y biomasa de batoideos se localiza en la región central del Golfo de Tehuantepec (en la asociación SBO), entre Salina Cruz y Puerto Arista, a una profundidad promedio de 27 m.
- La composición de especies en las asociaciones SBO, SBC, SWC y SBSW fue homogénea, con más de 90% de similitud. *U. chilensis, N. vermiculatus* y *U. rogersi* fueron las especies más abundantes, con una amplia distribución a lo largo del área de estudio en profundidades de hasta 42 m. Estas tres especies representan el 70.1% de la abundancia de batoideos demersales, con las mayores concentraciones de *U. chilensis* y *U. rogersi* en la región central y las mayores concentraciones de *N. vermiculatus* en la región oriental.
- La asociación USI, localizada en aguas más profundas, se caracteriza por la presencia de las especies *P. glaucostigma, N. entemedor, Z. xyster* y *H. longus*.
- La mayor parte de las asociaciones de batoideos identificados en este estudio son comunidades con un grado moderado de estrés ecológico debido a que la curva de abundancia estaba por encima de la curva de biomasa. Esto significa que especies pequeñas (p. ej. *U. chilensis, U. rogersi* y *N. vermiculatus*) dominan en número, pero no en biomasa.
- La guitarra bruja es poco abundante de mayo a enero en el Golfo de Tehuantepec, con registros de individuos principalmente juveniles (< 39 cm LT) y machos adultos (> 45 cm LT). Las abundancias se incrementan en febrero y marzo, con predominio de machos adultos con tallas entre 45 y 52 cm de TL, y en abril, con adultos de ambos sexos midiendo entre 46 y 69 cm de TL.

- Las hembras preñadas de la guitarra bruja capturadas en profundidades < 30 m indican una preferencia por aguas someras durante esta condición. Esto les permite a las hembras concluir el desarrollo embrionario para que las crías puedan nacer a partir de abril.
- Los registros obtenidos durante este estudio muestran evidencia de una aparente segregación juvenil por talla. Las crías de la guitarra bruja se distribuyen en aguas someras (< 30 m) y conforme incrementan su talla (al estado sub adulto) son capturados en aguas más profundas ($\overline{x} = 44$ m).
- Los individuos adultos de la guitarra bruja presentan dicromatismo sexual durante el periodo reproductivo. Esto significa que los machos tienen ocelos con un centro amarillo y borde negro en la parte posterior del cuerpo y son más brillantes que los de las hembras adultas.
- Las hembras adultas presentan polimorfismo sexual. Esto significa que los ocelos con el centro amarillo y el borde negro son más frecuentes en las hembras no preñadas, mientras que las hembras preñadas son más frecuentes sin el centro amarillo de los ocelos. La ausencia de un centro amarillo de los ocelos podría estar relacionado con la fase de gravidez.
- La información obtenida en este trabajo indica diferencias en la longitud total (11.5%), en peso total (8.5%) y en talla de madurez (8.3%) entre machos y hembras de adultos. Los machos de la guitarra bruja alcanzan la talla de madurez a una talla menor (43.6 cm TL) que las hembras (48.2 cm TL).
- Las hembras de la guitarra bruja son sincrónicas, la ovulación y el apareamiento comienzan en marzo y el parto comienza en abril. La presencia de hembras grávidas sin vitelogénesis concurrente y hembras adultas no grávidas durante el mismo período es indicativo de un ciclo de dos años con vitelogénesis y gestación consecutiva.

- Las crías de la guitarra bruja nacen entre abril y junio; el tamaño al nacer oscila entre 15.2 y 17.5 cm TL ($\overline{x} =$ 16.9 cm TL), y la proporción sexual es de 1:1 (H:M).
- La captura incidental de la guitarra bruja durante una parte de su periodo reproductivo usando redes de arrastre de fondo podría afectar negativamente el éxito reproductivo y la viabilidad a largo plazo de la guitarra bruja.

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