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Recomendaciones para el manejo de las pesquerías de tiburones y rayas, a partir de la distribución y abundancia en las capturas por barcos camaroneros en el Pacífico de Costa Rica

Tesis sometida a la consideración del Programa de Maestría Académica en Gestión Integrada en Áreas Costeras Tropicales

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RESÚMENES

*Capítulo 1. Diversidad y distribución de elasmobranquios asociados a la pesca de arrastre de camarón del Pacífico de Costa Rica, Centroamérica.*Los elasmobranquios forman parte de la fauna acompañante de la pesca de camarón en zonas tropicales. Sin embargo, en Costa Rica no existe información acerca de la comunidad demersal de elasmobranquios, como por ejemplo estadísticas de capturas y composición de especies. El objetivo general de este capítulo es analizar los patrones de diversidad y distribución de la comunidad de elasmobranquios asociada a la pesca de arrastre de camarón del Pacífico de Costa Rica. Se analizaron 217 arrastres entre marzo del 2010 a septiembre del 2011, en las cuales se capturaron 3283 elasmobranquios de 23 especies. El ámbito de tallas de los individuos capturados fue de 8.8-138.0 cm LT. La profundidad fue el factor más importante en la estructuración de la comunidad de elasmobranquios; la riqueza de especies, abundancia y proporción de hembras fueron significativamente mayores en zonas someras (menos de 50 m). El tamaño de cada especie aumentó en forma significativa con la profundidad. Durante el periodo de estudio, el mayor esfuerzo de pesca comercial se presentó en aguas someras. Como consecuencia se puede deducir que la pesca de arrastre de camarón tiene un impacto fuerte sobre los elasmobranquios en Costa Rica.

Capítulo 2. Ecología reproductiva de Raja velezi, Mustelus henlei, Zapteryx xyster y Torpedo peruana asociados a la pesca de arrastre de camarón del Pacífico de Costa Rica, Centroamérica. *Raja velezi*, *Mustelus henlei*, *Zapteryx xyster* y *Torpedo peruana* fueron las especies de elasmobranquios más abundantes en las capturas de la pesca de arrastre de aguas profundas de Costa Rica. En este capítulo se examina la ecología reproductiva de estas especies, ya que la información acerca de las estrategias de historia de vida puede ser utilizada como una herramienta para identificar especies vulnerables y aplicar medidas precautorias de manejo. Entre el 2010 y el 2011 se analizó una muestra 751 individuos de *R. velezi*, 569 de *M. henlei*, 394 de *Z. xyster* y 157 de *T. peruana*. Las tallas de madurez sexual estimadas fueron de: 52-56 cm LT para *R. velezi*, 39-43 cm LT para *M. henlei*, 45-47 cm LT para *Z. xyster,* y 54-65 cm LT para *T. peruana*. Se detectó una correlación positiva entre la fecundidad y el tamaño de la hembra en *M. henlei* y *Z. xyster*, que presentaron camadas de 1-12 embriones y 1-9 embriones respectivamente. Todas las especies presentaron una segregación por tallas y sexo, principalmente en relación con la profundidad. La mayoría de hembras grávidas se encontró en zonas someras (>50 m) a lo largo de la costa Pacífica. Sin embargo, el Humedal Nacional Térraba-Sierpe (HNTS), el Golfo de Nicoya y los humedales de Manuel Antonio-Quepos presentaron grandes agregaciones de hembras grávidas e individuos inmaduros y por lo tanto podrían estar funcionando como hábitats esenciales para estas especies de elasmobranquios. Nuevas propuestas para las estrategias de manejo deberían reducir el esfuerzo de pesca y proteger estos hábitats importantes para tiburones y rayas.

Capítulo 3. Tiburones y rayas como fauna acompañante en pesquerías tropicales de arrastre de camarón: una revisión de la situación actual acerca de la investigación y medidas de manejo para el Pacífico de Costa Rica, Centroamérica. Se realizó un análisis del manejo en Centro América para los elasmobranquios como fauna acompañante del camarón. En base a este análisis e investigaciones biologico-pesqueras realizadas en Costa Rica, se elaboraron recomendaciones de manejo para la captura incidental de elasmobranquios en la pesca de arrastre del país. Se determinó que las medidas actuales de manejo que benefician a los tiburones y rayas están orientadas a la reducción del esfuerzo de pesca, la regulación de las artes de pesca, el manejo de datos pesqueros y la investigación. Sin embargo, regulaciones específicas para este grupo taxonómico en la pesca de arrastre son inexistentes en Centroamérica. Existen tres acciones principales para la conservación de elasmobranquios en la pesca de arrastre: (1) Reducir el impacto de la pesca de arrastre en el medio ambiente, (2) reducir la mortalidad de tiburones y rayas, (3) evaluar las especies vulnerables a las presiones de pesca de arrastre. Las propuestas de manejo deberían ser regionales, debido a que los elasmobranquios se caracterizan por ámbitos de distribución amplios y transfronterizos.

ABSTRACT

*Chapter 1. Diversity and distribution of elasmobranchs associated with the shrimp-trawling fishery, Pacific of Costa Rica, Central America.*Elasmobranchs are a common component of the bycatch in tropical bottom trawling fisheries. However, basic data such as catch records and species composition of demersal elasmobranchs are lacking in Costa Rica. The present study examined the diversity and distribution patterns of the elasmobranch community associated with the trawling fishery operating along the Pacific coast of Costa Rica. A total of 217 trawls were analyzed between March 2010 and September 2011, resulting in 3283 elasmobranchs from 23 species. Sizes of the elasmobranchs caught as bycatch ranged from 8.8-138.0 cm TL. Depth was the main factor shaping the elasmobranch community; species richness, abundance and biomass were significantly higher at shallower depths. Species size was positively correlated with both depth range and average depth. During the study period, the highest commercial fishing effort occurred in shallow areas. As a consequence, the shrimp-trawling fishery of Costa Rica has a strong impact on elasmobranchs.

*Chapter 2. Reproductive ecology of Raja velezi, Mustelus henlei, Zapteryx xyster and Torpedo peruana associated with the shrimp trawling fishery along the Pacific coast of Costa Rica.*In data-deficient fisheries such the shrimp trawling fishery operating along the Pacific coast of Costa Rica, knowledge of the life history strategies can be used as a valuable tool to identify vulnerable species and apply precautionary measures that could ensure their long-term conservation. We studied the reproductive ecology of *Raja velezi*, *Mustelus henlei*, *Zapteryx xyster* and *Torpedo peruana* associated with the Costa Rican trawling fleet. A total of 217 trawls were analyzed at a depth of 25-350 m from March 2010 to September 2011. During this period, a sample size of 751 *R. velezi*, 569 *M. henlei*, 394 *Z. xyster* and 157 *T. peruana* was obtained. The size at sexual maturity was estimated as: 52-56 cm TL for *R. velezi*, 39-43 cm TL for *M. henlei*, 45-47 cm LT for *Z. xyster,* and 54-65 cm LT for *T. peruana*. Fecundity was found to increase with female length. Litter size varied between 1 and 12 embryos in *M. henlei*, and between 1 and 9 embryos in *Z. xyster*. Size and sexual segregation was observed in all species, mainly related to depth. Most gravid females were found in depths >50 m along the Pacific coast. However, shallow coastal waters near the Golfo de Nicoya, the Quepos-Manuel Antonio wetlands and the Humedal Nacional Térraba-Sierpe presented larger aggregations of gravid females and immature individuals and may function as part of the essential habitats for these elasmobranchs species. Management strategies should be oriented towards the reduction of the fishing effort, and should implement measures to protect these essential shark and ray habitats.

*Chapter 3. Sharks and rays as bycatch in tropical shrimp trawling fisheries: review of the current research situation and management measures for Pacific Costa Rica and Central America.*In this chapter we make management recommendations based on a regional overview of the management framework for elasmobranch bycatch on the shrimp fishery and the biological information generated in a research programconducted in Costa Rica. Current management strategies that benefit sharks and rays are oriented towards the reduction of fishing effort, regulation of fishing gear, management of fisheries data and research. However, specific regulations on bycatch within the shrimp fishery are extremely rare, and regulations for elasmobranch bycatch are non-existent in Central America. The review of the shrimp fishery's management framework in Central America and ecological research conducted in the region indicate that three main issues should be addressed in order to improve elasmobranch conservation: (1) Reduction of the fishery trawling impact on the environment, (2) Long-term conservation of sharks and rays, (3) Assessment of species vulnerability towards current shrimp fishing pressure. Shrimp trawl fisheries in Central America are very similar and therefore management proposals should be regional.

PREFACIO

El tiburón se ha aprovechado desde la época prehistórica, mediante el consumo de su carne, aletas, cartílago, hígado y piel (Walker 2005). En años recientes, la mayoría de tiburones son tomados en pesquerías multi-específicas que tienen como objetivo principal algún teleósteo de mayor importancia económica (Walker 2005). Las pesquerías de tiburón se pueden clasificar como: "pesquerías costeras de línea y transmallo", "pesquería incidental de arrastre demersal", "pesquería incidental de aguas profundas", "pesquería pelágica incidental" (principalmente pesca de palangre y de cerco) y "pesquerías de agua dulce" (Walker 2005).

La pesca de arrastre demersal es responsable por el 50% de los descartes mundiales (Kelleher 2005). Esta técnica captura condrictios con una baja capacidad de escaparse de las redes, tales como los Squaliformes, Triakidae, Echinorhinidae y Batoidea. En la mayoría de los países, no existen regulaciones acerca de la cantidad de tiburones y rayas que se puede extraer incidentalmente. Tampoco se registran las capturas incidentales, ó si se registran estas se consideran dentro de categorías más amplias (i.e., "tiburones y rayas") (Walker 2005) que no proporcionan información suficiente para lograr un manejo adecuado del recurso (Stevens *et al.* 2000). Se han documentado casos en los que la abundancia de tiburones y rayas ha disminuido como consecuencia de su captura incidental no regulada. Un ejemplo es la reducción drástica en el tamaño de las poblaciones de rayas en el mar Irlandés en los últimos 20 años, debido a la pesca por arrastre (Dulvy *et al.* 2000). Sin embargo, en algunos casos, el uso de este arte de pesca genera beneficios para los carroñeros y depredadores, al aumentar la disponibilidad de alimento (Stevens *et al.* 2000).

La atención pública que ha recibido la captura incidental de especies carismáticas como las tortugas y los delfines ha logrado reducir estas capturas (FAO 2009). A nivel mundial, se han reducido los descartes debido a la disminución de la captura incidental en los países desarrollados y al aprovechamiento de una mayor proporción de la captura incidental en los países en vías de desarrollo (Kelleher 2005). En las aguas templadas se han logrado establecer mecanismos muy exitosos para reducir la captura de biomasa sin valor comercial(Clucas 1997, Kelleher 2005). Sin embargo, estos mecanismos no se han logrado implementar en los trópicos debido a la gran diversidad de organismos (Clucas 1997). Países en vías de desarrollo como Chile han logrado reducir sus tasas de descarte al exigir que toda la captura incidental se desembarque en los puertos. En Centroamérica aún no se han logrado implementar medidas de este tipo, por lo que aún presenta altos niveles de descartes (Kelleher 2005).

La pesca de elasmobranquios genera impactos directos e indirectos sobre los ecosistemas marinos (Stevens *et al.* 2000). Estos autores aseguran que uno de los efectos directos más notorios es la desaparición de las clases de talla superiores y la disminución en la abundancia total de la especie. Los programas de monitoreo a largo plazo de tiburones en Australia, Nueva Zelanda y Sudáfrica han establecido que las poblaciones tienden a declinar y luego se estabilizan(Stevens *et al.* 2000). Aunque la causa de este fenómeno no ha sido comprobada, se especula que es consecuencia de la sobrexplotación de una comunidad residente y la posterior captura de inmigrantes (Stevens *et al.* 2000). Sin embargo, es posible que los tiburones aprendan a evitar las redes que se ponen en lugares fijos. También se han documentado cambios indirectos causados por la eliminación de depredadores, eliminación de presas y liberación competitiva (Stevens *et al.* 2000).

El impacto negativo que tiene la pesca de tiburones en los ecosistemas marinos es consecuencia del rol tan importante que juegan dentro de la maraña trófica (Cortés 1999). Como depredadores de alto nivel trófico, representan un factor fundamental en la dinámica poblacional de sus presas. Los elasmobranquios que depredan especies con crecimiento lento o que juegan un papel importante en la estructuración y regulación de las comunidades tienen una mayor importancia dentro de los ecosistemas marinos (Heithaus 2004). Los elasmobranquios también influencian el comportamiento de muchas especies, las cuales han desarrollado varias tácticas para evitar encuentros con estos depredadores (Heithaus 2004). Se han documentado varios casos en el norte del Golfo de México (Sheperd and Myers 2005), la costa este de los Estados Unidos (Myers *et al.* 2007) y en Japón (Myers *et al.*2007), en los que los cambios en la estructura trófica o efectos de cascada trófica producidos por la sobre pesca, tienen consecuencias ecológicas y económicas negativas por las relaciones presa-depreador entre tiburones, rayas y moluscos de interés comercial.

Sheperd and Myers (2005) resaltan la posibilidad de que se estén dando cambios en las comunidades de tiburones en otras partes del mundo, especialmente en lugares en donde el esfuerzo pesquero de la flota de palangre y arrastre es igual o mayor que el observado en el Golfo de México. Las probabilidades de que se estén produciendo desequilibrios ecosistémicos en otras partes del mundo aumentan al tomar en cuenta que la mayoría de los países en vías de desarrollo tienen una regulación pesquera menos efectiva que la de Estados Unidos (Sheperd and Myers 2005).

Existen iniciativas en Costa Rica para generar información acerca de los parámetros biológicos de algunas especies de tiburones y rayas. El Programa de Restauración de Tortugas Marinas (PRETOMA) ha liderado investigaciones acerca del estado de las poblaciones de tiburones en la Zona Económica Exclusiva y de las descargas de tiburón por parte de pescadores artesanales en la costa Pacífica (Rojas and Zanella 2006). Sin embargo, no se han realizado investigaciones sobre los tiburones y rayas que son capturados incidentalmente por la flota camaronera en el Pacífico del país. Hoenig y Gruber (1990) aseguran que un conocimiento básico de la historia natural de las especies es vital para alcanzar un manejo sostenible.

La ausencia de información de línea base en Costa Rica impide identificar cambios en las comunidades de elasmobranquios, pero sí nos permite hacerlo con las comunidades demersales. En los últimos cinco años se han observado cambios significativos dentro de la composición de capturas de la flota camaronera que opera en la costa Pacífica de Costa Rica los cuales representan un desequilibrio (Wehrtmann and Nielsen-Muñoz 2009): la abundancia de estomatópodos está aumentando rápidamente hasta alcanzar un 53% de la captura total en el 2008 mientras que la especie objetivo, el camarón camello (*Heterocarpus vicarius*)está desapareciendo.

En respuesta al deterioro de los ecosistemas costeros, la técnica utilizada por la flota semi-industrial camaronera ha sido pescar en aguas más profundas y diversificar sus especies objetivo. En la actualidad, siete barcos conforman la flota semi-industrial camaronera con licencia para pescar en aguas profundas (Bolaños 2005). Las especies objetivo de esta pesquería son *Heterocarpus vicarius* y *Solenocera agassizii*, pero también se capturan altos porcentajes de fauna acompañante (Wehrtmann and Nielsen-Muñoz 2009; Arana *et al.* en prensa). Esta pesquería también ha sufrido las consecuencias de la sobre-explotación de sus recursos, ya que de 72 barcos camaroneros en el país, solamente 52 tienen licencias de pesca actualizadas (Bolaños 2005).

La meta principal de la presente tesis es generar recomendaciones específicas para el uso sostenible de uno de los grupos más vulnerables que componen la fauna de acompañamiento del camarón de profundidad, con el fin de que se incorporen en el manejo de este recurso.Para ello, es necesario tener información de línea base, como por ejemplo, las especies que se están capturando en esta pesquería, y su distribución vertical y horizontal. También es necesario conocer las características biológicas en la dinámica de poblaciones, como estructura de tallas, proporciones sexuales, la talla a primera madurez sexual y patrones espacio-temporales de la condición reproductiva. Esta información será una herramienta importante para elaborar recomendaciones para minimizar el impacto de la pesca sobre este grupo taxonómico.

OBJETIVOS

Objetivo general

El objetivo general de este trabajo es elaborar recomendaciones para el manejo de los elasmobranquios, con base en su abundancia y distribución (vertical y horizontal) en las capturas incidentales por los barcos camaroneros en la costa Pacífica de Costa Rica.

Objetivos específicos

Aspectos biológico pesqueros:

A. Determinar la composición de especies de elasmobranquios que forman parte de la captura incidental de la fauna de arrastre.

B. Describir la variación en la proporción de sexos por profundidad

C. Determinar posibles áreas de veda de importancia reproductiva para los elasmobranquios.

Aspectos de manejo:

D. Compilar la información disponible sobre el manejo de elasmobranquios en la región y Latino América

E. Elaborar recomendaciones específicas de manejo para la captura incidental de elasmobranquios por parte de la flota camaronera.

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CHAPTER II

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Figure 3. Linear regressions between elasmobranch community metrics and the depth gradient along Costa Rican Pacific (2010-2011). a)Relationship between the number of elasmobranch species caught per tow and depth ($r^2 = 0.575$, $F = 37.815$, $p =< 0.001$, $y = 2.512 - 0.933x$). b) Abundance (CPUE) of elasmobranchs along the 20-350m gradient ($r^2 = 0.370$, $F = 15.861$, $p =< 0.001$, $y = 2.603 - 0.956x$). c) Biomass (CPUE) of elasmobranchs along the 20-350m gradient ($r^2 = 0.005$, $F = 0.146$, $p = 0.705$, $y = 0.0852 - 0.0153x$).

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Figure 4. Linear regressions between body size and depth of elasmobranch species sampled along the Pacific of Costa Rica, Central America (2010-2011). a) Relationship between average total length and average depth (r^2 = 0.505, F = 14.265, p = 0.002, y = 27.503 + 0.173x). b) Relationship between maximum total length and depth range (r^2 = 0.362, F = 7.373, p = 0.018, y = 44.992 + 0.202x). Each symbol represents a single species: (●) *Diplobatis ommata*, (⬢) *Echinorhinus cookei*, (□) *Mustelus henlei,* (◆) *Mustelus lunulatus*, (■) *Narcine entemedor*, (●) *Narcine vermiculatus*, (○) *Raja equatorialis*, (◇) *Raja velezi*, (■) *Rhinobatos leucorhynchus*, (◆) *Squatina californica*, (▲) *Torpedo peruana*, (△) *Urotrygon aspidura*, (▲) *Urotrygon chilensis,* (▼) *Urotrygon rogersi,* (▽) *Urotrygon nana,* (▼) *Zapteryx xyster.*

Figura 4. Regresiones lineales entre tamaño corporal y profundidad en las species de elasmobranquios, pacífico de Costa Rica, Centroamérica (2010-2011). a) Regresión entre la longitud total promedio y la profundidad promedio por especie (r^2 = 0.505, F = 14.265, p = 0.002, y = 27.503 + 0.173x). b) Regresión entre la longitud total máxima y el ámbito de profundidad de cada especie (r^2 = 0.362, F = 7.373, p = 0.018, y = 44.992 + 0.202x). Cada símbolo representa una especie: (●) *Diplobatis ommata*, (⬢) *Echinorhinus cookei*, (□) *Mustelus henlei,* (◆) *Mustelus lunulatus*, (■) *Narcine entemedor*, (●) *Narcine vermiculatus*, (○) *Raja equatorialis*, (◇) *Raja velezi*, (■) *Rhinobatos leucorhynchus*, (◆) *Squatina* *californica*, (▲) *Torpedo peruana*, (△) *Urotrygon aspidura*, (▲) *Urotrygon chilensis,* (▼) *Urotrygon rogersi,* (▽) *Urotrygon nana,* (▼) *Zapteryx xyster.*

Figure 5. Elasmobranch species composition across depth levels, Pacific of Costa Rica, Central America (2010-2011). Depths: < 50 m (●), 50-100 m (◇), 100-200 m (▲), > 200 m (■). Dotted line indicates the 30% similarity contour. P 61

Figura 5. Composición de species de la comunidad de elasmobranquios por niveles de profundidad y áreas geográficas, pacífico de Costa Rica, Centroamérica (2010-2011). Profundidades: < 50 m (●), 50-100 m (◇), 100-200 m (▲), > 200 m (■). Los círculos indicant un 30% de similitud.

Figure 6. Species and environmental biplot based on the canonical correspondence analysis. Environmental data: latitude, season and depth. Gray squares represent nominal variables and red arrows represent continuous variables (the length of the vector indicates the strength of the correlation and its direction indicates the relationship with the species). The species (blue solid triangles) are abbreviated as: *Dasyatis longa* (DLO), *Diplobatis ommata* (DOM), *Mustelus henlei* (MHE), *Mustelus lunulatus* (MLU), *Narcine entemedor* (NEM), *Narcine vermiculatus* (NVE), *Raja equatorialis* (REQ), *Raja velezi* (RVE), *Rhinobatus leucorhynus* (RLE), *Squatina californica* (SCA), *Torpedo peruana* (TPE), *Urotrygon aspidura* (UAS), *Urotrygon chilensis* (UCH), *Zapteryx xyster* (ZXY).

Figura 6. Biplot de species y factores ambientales resultante de un análisis de correspondencia canónica. Factores ambientales: latitud, estación, profundidad. Los cuadros representan variables nominales, las flechas representan variables continuas (la longitud del vector indica el grado de la correlación, la dirección indica su relación con las especies). Las especies (triángulos) se abreviaron de la siguiente manera: *Dasyatis longa* (DLO), *Diplobatis ommata* (DOM), *Mustelus henlei* (MHE), *Mustelus lunulatus* (MLU), *Narcine entemedor* (NEM), *Narcine vermiculatus* (NVE), *Raja equatorialis* (REQ), *Raja velezi* (RVE), *Rhinobatus leucorhynus* (RLE), *Squatina californica* (SCA), *Torpedo peruana* (TPE), *Urotrygon aspidura* (UAS), *Urotrygon chilensis* (UCH*)*, *Zapteryx xyster* (ZXY).

CHAPTER II

Figure 1. Map of the geographic areas (A) and trawling locations (B) along the Pacific of Costa Rica, Central America (March 2010 – September 2011).

Figure 1. Mapa de las areas geográficas(A) y sitios de muestreo (B) , pacífico de Costa Rica, Centroamérica (2010-2011).

Figure 2. Estimated size at first maturity for *Raja velezi.* Sexual maturity curves of females (A) and males (B). Red represents females and blue represents males. Correlations between liver weight (C) / gonad weight (D) and total length for both males and females. Correlations between uterus width and total length for females (E) and correlation between clasper size and total length for males (F). **Figura 2.** Talla de madurez estimada para *Raja velezi.* Curvas de madurez sexual para hembras (A) y machos (B). Rojo representa a las hembras y azul representa a los machos. Correlaciones entre la longitud total y el peso del hígado (C)/ peso de las gónadas (D) para hembras y machos. Correlaciones éntre la longitud total y el ancho del útero en hembras (E) y el tamaño de los mixopterigios en machos (F).

Figure 3. Estimated size at first maturity for *Mustelus henlei.* Sexual maturity curves of females (A) and males (B). Red represents females and blue represents males. Correlations between liver weight (C) / gonad weight (D) and total length for both males and females. Correlations between uterus width and total length for females (E) and correlation between clasper size and total length for males (F).

Figura 3. Talla de madurez estimada para *Mustelus henlei.* Curvas de madurez sexual para hembras (A) y machos (B). Rojo representa a las hembras y azul representa a los machos. Correlaciones entre la longitud total y el peso del hígado (C)/ peso de las gónadas (D) para hembras y machos. Correlaciones éntre la longitud total y el ancho del útero en hembras (E) y el tamaño de los mixopterigios en machos (F).

Figure 4. Estimated size at first maturity for *Zapteryx xyster.* Sexual maturity curves of females (A) and males (B). Red represents females and blue represents males. Correlations between liver weight (C) / gonad weight (D) and total length for both males and females. Correlations between uterus width and total length for females (E) and correlation between clasper size and total length for males (F).

Figura 4. Talla de madurez estimada para *Zapteryx xyster.* Curvas de madurez sexual para hembras (A) y machos (B). Rojo representa a las hembras y azul representa a los machos. Correlaciones entre la longitud total y el peso del hígado (C)/ peso de las gónadas (D) para hembras y machos. Correlaciones éntre la longitud total y el ancho del útero en hembras (E) y el tamaño de los mixopterigios en machos (F).

Figure 5. Estimated size at first maturity for *Torpedo peruana.* Sexual maturity curves of females (A) and males (B). Red represents females and blue represents males. Correlations between liver weight (C) / gonad weight (D) and total length for both males and females. Correlations between uterus width and total length for females (E) and correlation between clasper size and total length for males (F).

Figura 5. Talla de madurez estimada para *Torpedo peruana.* Curvas de madurez sexual para hembras (A) y machos (B). Rojo representa a las hembras y azul representa a los machos. Correlaciones entre la longitud total y el peso del hígado (C)/ peso de las gónadas (D) para hembras y machos. Correlaciones éntre la longitud total y el ancho del útero en hembras (E) y el tamaño de los mixopterigios en machos (F).

Figure 6. Relationship between the number of embryos and the total length of the females and litter size of *Mustelus henlei* (A, R^2=0.7951, y=-19.8058+0.4630x), *Zapteryx xyster* (B, R^2=0.9040, y=-9.5569+0.2564x).All variables are log-transformed.

Figura 6. Regresuón entre el número de embriones y la longitud total de la hembra en *Mustelus henlei* (A, R^2=0.7951, y=-19.8058+0.4630x), *Zapteryx xyster* (B, R^2=0.9040, y=-9.5569+0.2564x). Todas las variables fueron transformadas con logaritmo.

Figure 7. Mean abundance ± SE (CPUE, ind./hour) of *Raja velezi, Mustelus henlei, Zapteryx xyster* and *Torpedo peruana* along the Pacific coast of Costa Rica per month(2010-2011).

Figura 7. Abundancia promedio ± SE (CPUE, ind./hora) por mes de *Raja velezi, Mustelus henlei, Zapteryx xyster* y *Torpedo peruana*, pacifico deCosta Rica, Centroamérica (2010-2011).

Figure 8. Mean abundance ± SE (CPUE, ind./hour) of *Raja velezi, Mustelus henlei, Zapteryx xyster* and *Torpedo peruana* in every geographic area and depth level along the Pacific coast of Costa Rica (2010-2011).

Figure 8. Abundancia promedio ± SE (CPUE, ind./hora) por área geográfica y nivel de profundidad de *Raja velezi, Mustelus henlei, Zapteryx xyster* y *Torpedo peruana*, pacifico deCosta Rica, Centroamérica (2010-2011). (2010-2011).

Figure 9. Biplot resulting from a canonical correspondence analysis, of the relationship between five CPUE (ind./hour) of five maturity-sex stages of *Raja velezi* (RVE), *Mustelus henlei* (MHE), *Zaptery xyster* (ZXY) and *Torpedo peruana* (TPE) on the Pacific coast of Costa Rica (2010-2011) and environmental factors. Latitude, longitude, dry season, rainy season and depth acted as independent variables, and species abundance was dependent variable. Arrows indicate continuous variables squares indicate nominal variables and triangles represent each maturity stage-species combination. N: neonate, J: juvenile, M: adult male, F: adult females, G: gravid female.

Figura 9. Biplot resultante de un análisis de correlación canónica de la relación entre la abundancia (CPUE; ind./hora) de cinco estadíos de madurez de *Raja velezi* (RVE), *Mustelus henlei* (MHE), *Zaptery xyster* (ZXY) y*Torpedo peruana* (TPE) y factores ambientales, pacífico de Costa Rica, Centroamérica (2010-2011). Latitud, longitud, profundidad, estación seca y lluviosa fueron las variables independientes y la abundancia de cada estadío madurez-especie fueron las variables dependientes. N: neonato, J: juvenil, M: macho adulto, F: hembra adulta, G: hembra grávida.

Figure 10. Location of gravid females along the Pacific coast of Costa Rica. Bubble sizes indicate the number of gravid females found (A). Proportion of gravid females for *Raja velezi* (B) *Mustelus henlei (*C), and *Zapteryx xyster* (D)along the Pacific coast of Costa Rica. Red represents gravid females and blue represents mature females.

Figure 10. Sitios con hembras grávidasa lo largo de la costa pacífica de Costa Rica. El tamaño de los círculos indica el número encontrado de hembras grávidas. (A). Proporción de hembras grávidas de *Raja velezi* (B) *Mustelus henlei (*C), and *Zapteryx xyster* (D)en el pacífico de Costa Rica. Rojo representa a las hembras grávidas y azul representa a las hembras maduras.

Figure 11. Relative abundance (CPUE – individuals h^{-1}) of mature and immature individuals along the Pacific coast of Costa Rica for *Raja velezi* (A), *Mustelus henlei* (B), *Zapteryx xyster* (C), *Torpedo peruana* (D). Each pie graph represents relative abundance in the established geographic areas. Blue represents the mature stages and yellow represents the immature stages.

Figura 11. Abundancia relativa(CPUE – individuos h^{-1}) de individuos maduros e immaduros, de *Raja velezi* (A), *Mustelus henlei* (B), *Zapteryx xyster* (C), *Torpedo peruana* (D) a lo largo del pacífico de Costa Rica (2010-2011). Cada gráfico de pastel representa la abundancia relativa en cada área geográfica. Azul representa los estadíos maduros y Amarillo los estadíos immaduros.

Figure 12. Relative abundance (CPUE – individuals h^{-1}) of females and males along the Pacific coast of Costa Rica for *Raja velezi* (A), *Mustelus henlei* (B), *Zapteryx xyster* (C),

Torpedo peruana (D). Each pie graph represents relative abundance in the established geographic areas. Red represents females and blue represents males. **Figura 12.** Abundancia relativa (CPUE – individuos h^{-1}) de machos y hembras de *Raja velezi* (A), *Mustelus henlei* (B), *Zapteryx xyster* (C), *Torpedo peruana* (D) a lo largo del pacífico de Costa Rica (2010-2011). Cada gráfico de pastel representa la abundancia relativa en cada área geográfica. Azul representa los machos y rojo las hembras.

CHAPTER I

CHAPTER 1

Diversity and distribution of elasmobranchs associated to the shrimp-trawling fishery, Pacific of Costa Rica, Central America

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ABSTRACT

Elasmobranchs are a common component of the bycatch in tropical bottom trawling fisheries. However, basic data such as catch records and species composition of demersal elasmobranchs are lacking in Costa Rica. The present study examined the diversity and distribution patterns of the elasmobranch community associated to the trawling fishery operating along the Pacific coast of Costa Rica. A total of 217 trawls was analyzed between March 2010 and September 2011, resulting in 3283 elasmobranchs from 23 species. Sizes of the elasmobranchs caught as bycatch ranged from 8.8-138.0 cm TL. Depth was the main factor shaping the elasmobranch community; species richness, abundance and biomass were significantly higher at shallower depths. Species size was positively correlated with both depth range and average depth. In contrast, latitude did not influence the observed variations in the community. During the study period, the highest commercial fishing effort occurred in shallow areas. As a consequence, the shrimp trawling fishery of Costa Rica has a strong impact on elasmobranchs, and thus on the overall marine biodiversity. Future studies should focus on the role of sharks and rays in the structure and dynamics of demersal communities associated with this fishery.

KEYWORDS: *sharks and rays, diversity gradients, bottom trawling fishery, Eastern Tropical Pacific*

INTRODUCTION

Trends inmarine biodiversity are typically associated with latitudinal and depth gradients (Gray 2001, Smith and Brown 2002, Hillebrand 2004). In elasmobranchs, species richness increases with decreasing latitude and peaks in the tropics, where approximately 41% of all species are found (White and Sommerville 2010). A higher diversity of sharks, skates and rays has been detected in shallow habitats than in deep demersal ecosystems (Gray 2001, White and Sommerville 2010). Shallow environments also contain a wide range of highly productive habitats commonly used by elasmobranchs (e.g. coral reefs, mangroves, estuaries, sea grass beds, rocky and soft bottoms) (Gratwicke and Speight 2005, White and Sommerville 2010).

Overfishing and habitat degradation have caused significant declines in the diversity and abundance of elasmobranchs (Dulvy *et al.* 2000, Stevens *et al.*2000, Ward and Myers 2005, Romanov *et al.*2010). Sharks and rays that inhabit continental shelves are a common component of the bottom trawling fisheries′ bycatch (Walker 2005). Although elasmobranchs have a wide range of life history strategies, many species exhibit slow growth rates, late maturity, low fecundity and therefore, a low resilience to intense fishing pressure (Casey and Myers 1998, Jennings *et al.* 1999, Dulvy 2002, Musick and Bonfil 2005). Despite this, elasmobranch bycatch is not regulated or even quantified in most tropical trawling fisheries (Kelleher 2005, Walker 2005).

Previous studies in Australia (Stevens *et al.*2000, Graham *et al.* 2001), the Gulf of Thailand (Stevens *et al.*2000) and the Gulf of Mexico (Shepherd and Myers 2005) have demonstrated that sustained trawling has the potential to drastically reduce elasmobranch abundance and thus, alter ecosystem biodiversity. In the Eastern Tropical Pacific (ETP), mid-term catch trends from the Colombian shrimp fishery have revealed significant changes in species composition and abundance of the demersal elasmobranch community (Mejia-Falla and Navia 2011). Though basic biological information on this taxonomic group has been generated in several countries, such as Mexico (López-Martínez *et al.* 2010), Guatemala (Ixquiac-Cabrera *et al.*2010) and Colombia (Puentes *et al.*2007, Mejia-Falla and Navia 2011), there is limited information available to determine the impact of shrimp trawling fisheries on the elasmobranch community in the Central American Pacific (Espinoza *et al.* 2012).

The Costa Rican shrimp trawling fishery operates exclusively on the Pacific coast, and recent studies reported bycatch rates of up to 93% of the total catch (Arana *et al.*in press). A shift in the demersal community structure was documented through a fishery monitoring program (2003-present, Wehrtmann and Nielsen–Muñoz 2009, Wehrtmann *et al.* 2012), though changes in elasmobranch species composition associated to this shift are not clear. Landing statistics and species-specific catch data of elasmobranchs associated with this fishery are not available. The lack of biological information and landing statistics has limited the development of better management practices and conservation strategies for elasmobranchs in Costa Rica. It is critical to incorporate ecological information of demersal elasmobranchs into management strategies for the Costa Rican shrimp fishery because this taxonomic group tends to be one of the most vulnerable to intense fishing levels within the bycatch (King and McFarlane 2003).

The present study examines the diversity and distribution patterns of the elasmobranch community associated to the trawling fishery along the Pacific continental platform of Costa Rica. Elasmobranch diversity is expected to adjust to general marine biodiversity patterns determined by depth and latitudinal gradients. While latitudinal gradients may not be detected due to the small local scale of the study area, depth gradients are expected to be an important factor structuring elasmobranch diversity along the Pacific coast of Costa Rica. Therefore, we hypothesized that: 1) species richness and abundance will be highest at shallower depths; 2) elasmobranch size will present a positive correlation with depth; 3) the proportion of females will be highest at shallower depths. This information was used to propose management measures that may ensure the long-term conservation of demersal elasmobranchs in Costa Rica.

METHODS

Study area

The Pacific coastline of Costa Rica is very irregular, with three large gulfs and an approximate length of 1254 km (Wehrtmann and Cortés 2009). The continental slope is steep and close to the coastline (Wehrtmann and Cortés 2009), resulting in a narrow continental shelf of 15,600 km^2 (Herrera-Ulloa *et al.* 2011). Costa Rica is located in a tropical region that presents a pronounced rainy (May-November) and dry season (December-April) (Fiedler and Talley 2006). Productivity increases in the rainy season as a consequence of nutrient input from the main rivers in the country. The northern region of Pacific Costa Rica presents seasonal upwelling between December and February (Jiménez 2001, Fiedler 2002). For analytical purposes, the Pacific coast was divided into four geographic areas (Area I-IV) and four depth levels (0-50 m, 50-100 m, 100-200 m, 200-350 m) (Fig. 1). Geographic areas were defined according to different oceanographic conditions: Area I is characterized by seasonal upwelling events (Jiménez 2001, Wehrtmann and Cortés 2009); Area II is defined by the influence of a large estuarine system, the Golfo de Nicoya (Wehrtmann and Cortés 2009); Area III is influenced by the second large estuarine system, the river mouth and associated mangrove area of the Térraba-Sierpe (Quesada-

Alpízar and Cortés 2006); Area IV represents the southern part of the country, adjacent to the Golfo Dulce, a tropical fjord (Quesada-Alpízar and Cortés 2006).

Sampling

Elasmobranch diversity and distribution were studied using samples collected from commercial shrimp trawlers (The Rainbow Jewels S.A., Costa Rica). Vessels were 22.5 m long, with 270 hp engine and two standard epibenthic nets (20.5 m long, mouth opening of 5.35 m x 0.85 m, mesh size, 4.45 cm, cod-end mesh size 3.0 cm). Sampling was carried out between March 2010 and September 2011 at a depth range of 25-350 m (Fig.1). Scientific sampling included monthly scientific surveys and annual latitudinal surveys. Monthly scientific surveys were conducted between April 2010 and September 2011. They consisted of one nocturnal and one diurnal set of three 20-minute trawls at depths of 100, 150, 200 and 220 m. Annual latitudinal surveys were carried out in March 2010 and February 2011. During each survey, 15-minute trawls were conducted along the entire Pacific coast of Costa Rica between depths of 150 and 350 m. Fishery-dependent sampling consisted of commercial surveys conducted during monthly field trips. Commercial trawls were mainly carried out in the Central Pacific (Areas II and III), within a 25-350 m depth range. Date, time, depth, and location (latitude/longitude) were recorded for each sampling station. Elasmobranchs caught during each trawl were identified, measured (total length – TL: distance between the tip of the snout to the posterior end of the caudal fin, disc width – DW: distance in a straight line between the widest portions of the pectoral fins), weighed (total wet weight – TW) and sexed onboard (Bussing and López 1993, Compagno *et al.* 2005). A photographic catalog of the elasmobranch species was created for identification purposes. Two specimens of each species were deposited in the Museo de Zoología of the Universidad de Costa Rica, in San José (Costa Rica).

Diversity and spatial distribution

General diversity and distribution patterns were examined among depths and geographic areas (Fig. 1). Preliminary analyses revealed that elasmobranch species richness, diversity, abundance and biomass did not vary between seasons (Clarke *et al.* unpubl. data). As a result, the season effect was excluded from the analysis.

Abundance and biomass data were standardized to catch per unit of effort (CPUE), as individuals per trawling hour (ind. × trawl h^{-1}) and kilograms per trawling hour (kg × trawl h^{-1}), respectively. The analysis of variance procedures were conducted using Kruskal-Wallis due to non-normal distributions, unequal sample sizes and variances (Zar 1999). These analyses examined the effect of area (independent variable) on each community metric: species richness, abundance and biomass (dependent variable). The hypothesis that species richness and abundance will be highest at shallower depths was tested using linear regressions (depth as the independent variable and species richness, abundance CPUE and biomass CPUE as dependent variables).

A linear regression was used to examine the relationship between body size and depth in order to test the hypothesis that elasmobranch size is positively correlated with depth. Linear relationships were assessed between: a) the average total length and the average depth of capture of each species; as well as b) the maximum total length and depth range of each species. The variables were normalized with a log-transformation. All analyses were conducted with R (R Core Team 2012).

Sexual segregation for each species was analyzed by detecting overall sex ratios that differed from 1:1 with a Pearson's chi-square test. Only species with at least ten individuals (five males and five females) were considered for the analysis. In order to test the hypothesis that a higher proportion of females will be found at shallower depths, spatial patterns in sex (male:female) ratios of the entire elasmobranch community were examined for each depth level and fishing area. Maturity ratios (immature:mature) of the elasmobranch community were also examined for each depth level and fishing area.

Community structure

The species composition of the elasmobranch community was examined using PRIMER v.6.2.1 (PRIMER-E, Ltd., Plymouth, UK). Rare species (caught once or twice during the study period) were excluded from these analyses. A matrix was constructed with the transformed species abundance in columns (log (ind × trawl h^{-1}+ 1)) and factors in rows (fishing area areas and depth levels). Differences in the elasmobranch species composition among factors were examined with an Analysis of Similarity (ANOSIM, Clarke and Warwick 1994). Significant differences were further evaluated with a Similarity Percentages analysis (SIMPER, Clarke and Warwick 1994) in order to identify the species that contributed to the greatest dissimilarities among factor levels. Elasmobranch species composition was also compared across geographic areas and depth levels using a non-parametric multi-dimension scaling (nMDS, Clarke and Warwick 1994) analysis, based on a Bray-Curtis similarity index (Clarke *et al.* 2006).Only the resulting plots with stress values of < 0.2 were selected for interpretation (Clarke 1993).

A canonical correspondence analysis (CCA) was used to examine the relationship between three environmental variables (depth, latitude and season) and the elasmobranch community (ter Braak and Verdonschot 1995). Depth (m) and latitude (degrees) were log-transformed and treated as continuous variables, year as a co-variable. The probability of the observed pattern being true due to chance was estimated with a Monte-Carlo randomization test (499 permutations). The results were displayed in a bi-plot ordination diagram for interpretation. These analyses were conducted using CANOCO v.4.5 software package (ter Braak andVerdonschot 1995).

RESULTS

A total of 217 trawls was analyzed (87 commercial, 78 scientific and 52 latitudinal) (Table 1). Commercial and scientific sampling effort was highest in the central Pacific region (Areas II and III). Overall, 36.8% of commercial trawls were conducted in Area II and 47.1% in Area III, while 53.8% of scientific trawls were conducted in Area II and 33.3% in Area III. Latitudinal trawls were distributed evenly across fishing area areas. Most commercial trawls occurred at shallow depths, while the majority of scientific and all latitudinal trawls were in deeper waters. Commercial trawls accounted for the highest number of species and over 90% of elasmobranch abundance. However, standardized abundance from commercial (7.8 ind. × trawl h^{-1}) and scientific surveys (7.7 ind. × trawl h^{-1}) were similar.

Diversity and spatial distribution

A total of 3283 elasmobranchs from 23 species, 14 families and 5 orders were captured as bycatch during the study period (Table 2). Eleven species were rare (<1% of total abundance), 8 species were common (1-5% of total abundance) and four species were very abundant (> 5% of total abundance). These included *Urotrygon aspidura,Raja velezi, Mustelus henlei* and *Zapteryx xyster,* which represented over 70% of the total abundance (Table 2).

Significant variations in species richness, abundance and biomass among geographic areas were not observed (Fig. 2). In agreement with the proposed hypothesis, species richness and abundance were higher at shallower depths. Negative linear relationships were detected between species richness and depth, as well as between abundance and depth, though not between biomass and depth (Fig. 3).

Body size for all elasmobranchs ranged from 8.8-138.0 cm TL (Table 2). There was a large number of species with small sizes (< 50 cm TL), mainly in the Narcinidae, Urotrygonidae and Rajidae families. *Mustelus lunulatus, Echinorhinus cookei, Squatina californica* and *Dasyatis longa* were the largest species. They were uncommon throughout the study period and collectively represented only 6.8% of the total elasmobranch abundance. Species with larger sizes were observed in deeper waters and exhibited wider depth ranges. In conformity with the proposed hypothesis, positive linear relationships were detected between average body size and average depth of capture (Fig. 4a), as well as between maximum body size and depth range (Fig. 4b).

Sex ratios for the entire elasmobranch community differed from 1:1 in all areas except for Area II (Table 3). As proposed in the last hypothesis, females were more abundant in shallower waters (<100 m, Table 3), while males dominated abundances at depths between 100-200 m. Most species presented even sex ratios (Table 2), however, sex ratios of the most abundant species were significantly uneven. A higher proportion of males were observed for *R. velezi* and *M. henlei*, while female *U. aspidura* and *Z. xyster* were captured in greater numbers(Table 2).

Maturity ratios for the entire elasmobranch community were biased in all areas, with overall higher percentages of mature individuals than neonates and juveniles (Table 3). A large number of mature elasmobranchs was also found in all depth levels except 50-100 m, where the maturity ratio was even (Table 3). Maturity percentages of each species elasmobranch varied widely. A higher percentage of mature individuals were caught in the remaining species, *U. aspidura, Raja velezi, M. henlei,* and *Z. xyster* presented larger numbers of mature individuals (Table 2). A higher percentage of immature individuals were caught in 10 species that represented 14.8% of total abundance (Table 2).

Community structure and composition

Elasmobranch species composition did not vary significantly among geographic areas (ANOSIM R = 0.274, p = 0.076, Supplement 1), however, differences were observed among depths (ANOSIM R = 0.63, p = 0.001). Species composition differed significantly among all depths, except at levels deeper than 100 m (Fig. 4, Table 4). The shallow-water elasmobranch community was characterized by 23 species, of which *U. aspidura* was clearly dominant (Table 5). The remaining 22 species were present in much lower abundances that ranged from 0.009 to 2.15 ind. × trawl h^{-1} (Table 4). In contrast, the deep-water community was characterized by six species with similar abundances (Table 5).

A SIMPER analysis revealed that species composition at the <50 m depth level was least similar to that of all other depth levels (Table 5). *Narcine entemedor*, *Dasyatis longa* and *U. aspidura* contributed more than 50% of the similarity between the <50 m and all other depths (Supplement 2). Similarities between the remaining depths ranged between 44.3% and 55.5%, and were mainly due to the presence of *R. velezi, M. henlei, Z. xyster* and *T. peruana* (Table 5).

Torpedo peruana presented the highest species contribution in both 100-200 m and >200 m (Table 5).

The CCA reinforces the strong association between depth and species composition (Fig. 6). Most species exhibited a negative association with depth, except for *R. velezi, M. henlei* and *T. peruana*. In contrast with the previously presented Kruskal-Wallis and ANOSIM results, the CCA indicates latitude is an importance factor in elasmobranch species composition, with most species associated with intermediate latitudes or Areas II and III (Fig. 6). The non-homogeneous sampling effort may have influenced this result, because a higher sampling effort was carried out in Areas II and III. Monte Carlo randomization tests showed that the observed patterns were not due to chance (p = 0.004).

DISCUSSION

Diversity and spatial distribution

The elasmobranch bycatch of the Costa Rican shrimp trawling fishery was comprised of 23 species, which represent over 35% of this taxon's diversity reported for the entire Pacific coast (Wehrtmann and Cortés 2009). Elasmobranch diversity associated with the Costa Rican shrimp fishery is in terms of species higher than that reported for the Pacific coast of Mexico (4-137 m, López-Martínez *et al.* 2010) and Guatemala (10-100 m, Ixquiac-Cabrera *et al.* 2010), but similar to that of Colombia (10-360 m, Puentes *et al.* 2007, Mejia-Falla and Navia 2011). The bycatch of these fisheries include 19 species of sharks and rays in the Gulf of California, Mexico (López-Martínez *et al.* 2010), 13 species of rays in Guatemala (Ixquiac-Cabrera *et al.* 2010), and

24 species in Colombia (Puentes *et al.* 2007, Mejia-Falla and Navia 2011). The lower diversity found in Guatemala is possibly due to the short sampling period (5 days).

The elasmobranch species composition associated with shrimp-trawling fisheries in the ETP region was expected to be similar due to the wide distribution range of these species (Compagno *et al.* 2005). Our results confirm this assumption as elasmobranch bycatch in Costa Rica shared eight species in common with the Gulf of California, Mexico (López-Martínez *et al.* 2010), 11 species with Guatemala (Ixquiac-Cabrera *et al.* 2010) and 14 species with Colombia (Puentes *et al.* 2007, Mejia-Falla and Navia 2011). The Gulf of California shared less species with Costa Rica, possibly due to differences in oceanographic conditions. According to Robertson and Cramer (2009), the Gulf of California belongs to the Cortez biogeographic province, characterized by the convergence of temperate, sub-tropical and tropical marine fish fauna (Mora and Robertson 2005, Rodríguez-Romero *et al.* 2008), while Costa Rica, Colombia and Guatemala belong to the Panamic biogeographic province that only encompass tropical marine fish species (Allen and Robertson 1994).

The CCA showed that latitude was important for elasmobranch distribution, however, this result should be interpreted with caution due to uneven sampling efforts across the different geographic areas. This limitation occurred as a consequence of the overall dependence on commercial fishing operations. Even though certain strategic areas and depths were chosen during scientific sampling, it was not possible to establish an experimental design with even sampling efforts among geographic areas. Overall, this study revealed that the entire Pacific coast of Costa Rica (approx. 1254 km of coastline) has a similar elasmobranch community structure. The observed similarity is not surprising since latitudinal gradients are apparent across wider latitudinal ranges than encompassed by the present study area (Hillebrand 2004). In addition, the widespread distributions and high mobility of many elasmobranchs may contribute to the observed homogeneity (Compagno *et al.* 2005, Knip *et al.* 2010, Mejia-Falla and Navia 2011).

Our findings suggest that depth is a major factor shaping the elasmobranch community structure along the Pacific of Costa Rica. Species richness and abundance peaked in shallow waters and decreased continuously along the depth gradient. This is a common feature in elasmobranchs and applies for both demersal and pelagic groups (Smith and Brown 2002, MacPherson 2003, Hillebrand 2004, Gouraguini *et al.* 2011). Depth has been identified as an important factor shaping elasmobranch communities in the ETP (Navia and Mejia-Falla 2011), Mediterranean (Massuti and Moranta 2003, Gouraguine *et al.* 2011), Australia, northeast Pacific rim (Smith and Brown 2002) and the South Atlantic (Menni *et al.* 2010).

Depth gradients are associated with changes in environmental variables such as temperature, oxygen, primary productivity, physical heterogeneity and seasonal patterns, which decrease rapidly with increasing depth (Levinton 2001, Smith and Brown 2002). In contrast, factors such as pressure and environmental stability increase with depth (Levinton 2001, Knip *et al.* 2010). The highly variable nearshore environments tend to concentrate species with smaller depth ranges, while deep-water environments tend to concentrate species with larger depth ranges (Stevens 1989, Smith and Brown 2002, Knip *et al.* 2010, Mejia-Falla and Navia 2011). Depth-related changes in environmental factors may partially explain the observed reduction in species richness and distribution. Temperature is considered as an important factor influencing species richness as it may affect speciation rates (Allen *et al.* 2002). Productivity is also known to influence species richness, since areas with a higher primary productivity tend to have species with high trophic levels, large body sizes and high energetic requirements (Smith and Brown

2002, Leathwick *et al.* 2006, Knip *et al.* 2010). Therefore, depths with high productivity levels would be able to sustain a larger abundance of sharks and rays (Priede *et al.* 2006).

A positive relationship between species body size and depth range was observed in the elasmobranch community of Costa Rica (Fig. 3). Species body size and morphometrics partially determine mobility and swimming speed, which in turn influences distribution (Mejia-Falla and Navia 2011). In Costa Rica, demersal batoids are typically small with narrow depth ranges, while larger demersal sharks presented wider depth distribution ranges(Mejia-Falla and Navia 2011). In addition, swimming speed partially determines catch probability in the shrimp-trawling fishery, which explains why elasmobranch bycatch was dominated by rays (17 ray species and 6 shark species). Large sharks (>1 m) are uncommon in shrimp fisheries because they typically swim faster and avoid trawling gear (Walker 2005). Consequently, *Sphyrna lewini* and *R. longurio* represented a very small percentage of the elasmobranch bycatch, and only as juveniles.

Sexual segregation in elasmobranchs has been widely reported (Strasburg 1958, Mollet 2002, Escobar-Sánchez *et al.* 2006). It tends to occur more often in adult populations, although is not restricted to these life stages (Carlisle *et al.* 2007, Wearmouth and Sims 2008). In this study, small rays that form large aggregations in shallow water habitats, such as *U. aspidura* and *U. rogersi,* presented a higher proportion of females. Sexual segregation may reduce intraspecific competition for prey (Carlisle *et al.* 2007, Espinoza *et al.* 2012). However, for some species like *M. henlei* males were more common than females. *Mustelus henlei* was distributed throughout a wide depth range, in which males occur in deeper habitats, while gravid females where more abundant in shallower coastal waters. Inhabiting areas with higher temperaturesmay give gravid females a reproductive advantage,as it would increase embryo growth rate (Hight and Lowe

2007, Pereyra *et al.* 2008, Speed *et al.* 2012). In the remaining species, sample size was insufficient to determine general or interspecific patterns of sexual segregation.

Community structure and composition

Composition of the standardized bycatch in the shrimp-trawling fishery is assumed to reflect the demersal elasmobranch community. However, it is important to consider some of the gear limitations. For example, shrimp trawlers operate on soft bottoms, consequently, species that prefer rocky substrates are likely to be underrepresented in samples (Williams *et al.* 2008). Larger and faster species inhabiting soft bottoms may have the capacity to avoid the gear or escape from the trawls, and thus, also be under-sampled. Conversely, pelagic or meso-pelagic species may be caught when sampling demersal habitats as the net descends or ascends through the water column. The elasmobranch bycatch associated with the Costa Rican shrimp fishery is characterized by the presence of a few dominant species (e.g. *R. velezi*, *U. aspidura*, *M. henlei*, *Z. xyster* and *T. peruana*), which accounted for more than 75% of the total abundance. This is typical of bycatch in other tropical shrimp fisheries (Campos 1986, Stobutzki *et al.*2001, López-Martínez *et al.* 2010).

Two well-defined elasmobranch assemblages are apparent along the Pacific of Costa Rica. The first assemblage was located on the shallow continental platform (<50 m depth range) and was composed of 22 species. This group was characterized by a majority of rare species (e.g. *R. longurio, S. lewini, G. marmorata, A. laticeps, R. cortezensis*). *Urotrygon aspidura* dominated the species composition at 0-50 m, with a maximum abundance of 139 individuals per trawling hour. In agreement with our observations, this species was also one of the most abundant species in Colombia (Mejia-Falla and Navia 2011). Shallow-water elasmobranch assemblages in Pacific

Guatemala and the Gulf of Mexico also included a high abundance of small ray species, such as *N. entemedor* and *N. vermiculatus* in Guatemala (Ixquiac-Cabrera *et al.* 2010) and *Urobatis halleri* in the Gulf of California (Rábago-Quiroz *et al.* 2011). *Narcine entemedor* and *N. vermiculatus* were moderately abundant in the shallow-water assemblage of Costa Rica, though not in the high relative abundance reported for Guatemala (Ixquiac-Cabrera *et al.* 2010).In the present study, *U. aspidura* and *Narcine* spp.exhibited patchy distributions and formed large aggregations. The existence of high-density sites could be associated with patches of favorable conditions such as high food availability (De Souza Vianna and Vooren 2009, Knip *et al.* 2010) or may be associated to reproductive behavior (De Souza Vianna and Vooren 2009).

The elasmobranch assemblage at 50-100 m, is not well-defined but serves as a transition between the shallow and deep-water assemblages. It was composed of 15 species, of which *Mustelus henlei* was the most abundant. This species presented considerable seasonal variations, large aggregations of male *M. henlei* (100 sharks caught in 15 minutes)were detected at93.5 m deepin September 2010. The observed seasonality pattern of *M. henlei* is supported by López-Garro *et al.* (2009), who also found aggregations of this species in shallow waters (>90 m) during September-October and January-February. This behavior has been associated with reproduction, as the majority of females found in shallow waters were gravid.

Elasmobranch bycatch associated to the shallow-water Costa Rican shrimp fishery (<100 m) in 1983-84 was described by Campos (1986). However, differences in sampling methods prevent a detailed comparison of the elasmobranch community structure between both studies, although general patterns can be discerned. The 1983-84 study revealed lower species richness (15 ray and five shark species) than the present study (17 ray and five shark species at the same depth). In 1983-84, *R. velezi* and *Z. xyster* were the two most abundant species with a total sample size of 30 and 22, respectively, while the remaining species presented sample sizes of eight individuals or less (Campos 1986). Changes in catch composition were evident as *M. henlei* and *U. aspidura* were very common species in 2010-11, but during 1983-84 *M. henlei* was absent, and only seven specimens of *U. aspidura* were caught. These results coincide with fishermen's traditional ecological knowledge assuring large aggregations of *U. aspidura* form part of recently observed shifts in demersal community structure. Conversely, *Nasolamia velox* and *Sphyrna corona* were caught in 1983-1984, but not in 2010-11. The lower abundance and diversity reported in Campos (1986) may be explained by differences in sample size (120 liters each trawl in 1983-84 vs. entire biomass in 2010-11) or actual changes in demersal elasmobranch diversity.

The second elasmobranch assemblage was located at depths between 100-350 m, and was composed of only six species. *Raja velezi*, *M. henlei* and *T. peruana* were the most abundant species throughout this depth range. *Mustelus lunulatus*, *S. californica* and *E. cookei* were rare at these depths, probably because it represents the deeper distribution limit of the two former species and the shallow distribution limit of the latter. *Echinorhinus cookei* isthe only true deep-water species in this assemblage and inhabits depths up to 1100 m (Compagno *et al.* 2005), with a wide geographic distribution (Compagno *et al.* 2005). Little is known about the deep-water elasmobranch assemblages, as only one previous study has been conducted within the ETP (Puentes *et al.* 2007). This study found eight species at depths between 72 and 360 m (Puentes *et al.* 2007). Additional studies are necessary to broaden our knowledge about deep-water elasmobranch communities along the ETP and their relation to physical and biological features.

Implications for management and conservation

From the entire bycatch, only two elasmobranch species are often retained due to their commercial value. *Mustelus lunulatus* is an important source of affordable protein in the local and national market of Costa Rica, while there is a growing market for *Dasyatis longa* in Mexico and Costa Rica (Rojas *et al.* 2000). In addition to being caught by shrimp trawlers, *M. lunulatus* and *D. longa* comprise 16.7% and 3.5% of elasmobranch landings in the artisanal fishery of Tárcoles, central Pacific of Costa Rica (2006-2007, López-Garro *et al.* 2009). Even though current records are insufficient to evaluate long-term trends in abundance within Costa Rica, catch data from Colombian artisanal and shrimp fisheries indicate that the abundances of *M. lunulatus* and *D. longa* have declined considerably since the 1990s, when they were two of the most abundant elasmobranchs on the Pacific coast (Navia and Mejia-Falla 2011). Therefore, it seems advisable to closely monitor the abundance of these two species along the Pacific coast of Costa Rica in order to avoid these resources from collapsing due to intense overfishing.

Resource competition between the shrimp trawling fishery and artisanal fishery is a pressing social and ecological issue (Beltrán 2001).For example, *Mustelus henlei, R. longurio* and *S. lewini* are targeted by the artisanal fishery and discarded by the shrimp fishery (Rojas *et al.* 2000). Moreover, *M. henlei* is one of the most abundant species in both artisanal landings (63.7% of the 2006 shark landings in Tárcoles, Pacific Costa Rica, López-Garro *et al.* 2009) and the shrimp fishery´s bycatch (18.3% of shark bycatch, Table 2).Although, in Costa Rica *S. lewini* was a rare component in the shrimp fishery bycatch, it is common in both the artisanal (López-Garro *et al.* 2009) and industrial longline fisheries (Arauz *et al.*2007, Whoriskey *et al.*2011), thus conservation efforts should also focus on this species.

Most sharks and rays caught by the Costa Rican shrimp fishery are discarded. Although survival rate estimates for these elasmobranchs are unavailable for Costa Rica, mortality is generally correlated with the codend weight (Enever *et al.* 2009), tow duration, handling time (Cedrola *et al.* 2005) and operating depth (Laptikhovsky 2004). In this fishery, codend weight and tow duration (between two and eight hours) tend to be high and operating depth tends to be shallow (<80 m). In the context of the precautionary principle, potentially high mortality of the group indicates that catch rates should be reduced (Stobutzki *et al.* 2002) through effort reductions and bycatch reduction devices (BRDs). According to Stobutzki *et al.* (2002), the survival rate for sharks and rays in northern Australia averaged 66%, however, these percentages may represent an overestimation, as species discarded in bad health conditions may be consumed by scavengers or predators before they are able to recuperate (Laptikhovsky 2004).

The high elasmobranch diversity and abundance in shallow areas along the Pacific of Costa Rica should be protected by at least partial spatial fishing closures. Moreover, the overall fishing effort should be reduced and not displaced because elasmobranchs inhabiting deeper areas tend to present larger body sizes, a trait associated with higher vulnerability towards high fishing mortality (King and McFarlane 2003). Enforcement of current fishing closures should also improve by implementing vessel monitoring systems and improving inspection efficiency. In addition to lowering fishing effort, long-term monitoring and observer programs should be established to assess general trends in the abundance of bycatch species, as population collapses and regional extinctions of elasmobranchs have been documented worldwide (Casey and Myers 1998, Dulvy *et al.*2000, Stevens *et al.*2000, White and Sommerville 2010).

Our results demonstrate that the shrimp trawling fishery of Costa Rica has a strong impact on demersal elasmobranchs, and thus on the overall marine biodiversity. Shifts in the demersal community structure associated with this shrimp fishery are occurring (Wehrtmann and Nielsen-Muñoz 2009), though the role of sharks and rays in these changes remains to be investigated (Espinoza *et al.* 2012, Espinoza *et al.* in press, Espinoza *et al.* unpublished data). Future studies on the ecological importance of these species in the trophic web along the Pacific continental platform of Costa Rica may provide an insight into these ecological changes.

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TABLES AND FIGURES

Table 1. Sampling effort along the Pacific of Costa Rica, Central America (2010-2011). Number of trawling minutes per geographic area and depth level.

Geographic areas	**Depth levels**											
	<50 m			50-100m			100-200m			>200m		
	Commercial	Scientific	Latitudinal	Commercial	Scientific	Latitudinal	Commercial	Scientific	Latitudinal	Commercial	Scientific	Latitudinal
I	221	0	0	1178	358	0	0	40	147	0	41	153
II	2265	40	0	3702	314	0	1584	600	109	545	190	154
III	3794		0	6151	127	0	436	295	0	535	121	62
IV	0	0	0		20	0	0	47	30	0	20	71

Table 2. Elasmobranch species captured as bycatch in the shrimp trawling fishery, Pacific of Costa Rica, Central America (2010-2011). Total number of individuals (N), percentage of abundance (%N), percentage of females (%♀), uneven sex ratios detected by a Pearson Chi-square test are underlined, % Mature individuals, minimum, mean and maximum total length (TL). Sizes for species indicated with an * are given in disc width.

Order	Family	Species	N	% N	%♀	% Mature	Males (TL, cm)			Females (TL, cm)		
							Min.	Mean	Max.	Min.	Mean	Max.
	Carcharhinidae	*Rhizoprionodon longurio*	6	0.19	50.0	0.0	32	33.9	34.9	31.3	37	42.9
	Sphyrnidae	*Sphyrna lewini*	2.0	0.1	50.0	0.0	53.5	53.5	53.5	49.5	49.5	49.5
	Triakidae	*Mustelus henlei*	427.0	13.0	31.2	60.4	21.8	44.1	56.8	23.2	37.8	66.5
		Mustelus lunulatus	119.0	3.6	47.1	5.4	31.1	53.6	100.0	39.2	56.1	138.0
Myliobatiformes	Dasyatidae	*Dasyatis longa**	19.0	0.6	68.4	0.0	40.2	71.8	98.7	35.9	67.4	107.7
	Myliobatidae	*Aetobatus laticeps**	2.0	0.1	50.0	50.0	39.5	39.5	39.5	98.0	98.0	98.0
		*Rhinoptera steindachneri**	30.0	0.9	13.8	100.0	73.6	79.9	94.2	88.0	89.6	91.5
Rajiformes	Gymnuridae	*Gymnura marmorata*	1.0	0.0	0.0	-	31.1	31.1	31.1			
	Rajidae	*Raja cortezensis*	1.0	0.0	100.0	0.0				10.2	10.2	10.2
		Raja equatorialis	68.0	2.1	69.1	83.8	13.6	34.6	42.7	14.0	38.3	48.6
		Raja velezi	685.0	20.9	45.6	57.5	13.2	49.2	85.6	13.8	49.7	76.9
Rhinobatiformes	Rhinobatidae	*Rhinobatos leucorhynchus*	40.0	1.2	62.5	32.5	19.6	41.9	63.6	19.2	37.4	76.6
		Zapteryx xyster	359.0	10.9	65.6	55.9	15.1	40.2	68.7	15.3	45.4	78.3
	Urotrygonidae	*Urotrygon aspidura*	937.0	28.5	61.6	59.5	13.5	28.4	50.5	12.7	28.0	56.0

		Urotygon chilensis	31.0	0.9	32.3	22.6	14.9	22.2	39.8	14.1	22.1	41.2
		Urotrygon rogersi	103.0	3.1	77.7	89.2	13.7	31.1	43.5	12.8	44.3	52.6
		Urotrygon nana	16.0	0.5	68.8	100.0	8.8	14.8	25.8	9.5	17.8	26.8
Squaliformes	Echinorhinidae	*Echinorhinus cookei*	11.0	0.3	100.0	0.0				63.0	73.1	95.1
Squatiniformes	Squatinidae	*Squatina californica*	52.0	1.6	57.7	44.2	29.8	65.9	92.1	31.0	56.6	94.5
Torpediniformes	Narcinidae	*Diplobatis ommata*	30.0	0.9	73.3	93.3	11.8	17.6	20.9	14.6	20.1	23.5
		Narcine entemedor	71.0	2.2	66.2	23.9	14.2	30.3	56.0	14.5	41.1	86.8
		Narcine vermiculatus	139.0	4.2	69.8	77.0	10.2	22.6	27.0	11.6	21.7	32.7
	Torpedinidae	*Torpedo peruana*	134.0	4.1	54.5	16.4	16.4	44.4	69.5	14.2	46.1	88.9

Table 3. Spatial distribution of elasmobranchs by geographic areas and depth levels, Pacific of Costa Rica, Central America (2010-2011). The p-value resulting from the corresponding Pearson Chi Square test is displayed.

	%♀	X^2	p-Value	% Mature	X^2	-Value
Geographic areas						
I	66.4	36.4	<0.0001	84.4	100.6	0.0001
II	51.9	1.6	0.20	71.9	198.9	0.0001
III	52.9	4.7	0.03	41.0	41.9	0.0001
IV	26.1	54.9	<0.0001	58.9	4.8	.028
Depth level						
<50m	64.1	81.0	<0.0001	60.3	42.2	0.0001
50-100m	47.3	4.5	0.03	51.9	1.9	.165
100-200m	36.0	27.9	<0.0001	65.0	12.4	0.0001
>200m	55.0	1.7	0.19	67.4	10.5	.001

Table 4. Summary information from the ANOSIM test comparing elasmobranch species composition among depth levels, Pacific of Costa Rica, Central America (2010-2011).

Depth levels (m)	ANOSIM R	p-Value
<50 vs. 50-100	1.000	0.037
<50 vs. 100-200	1.000	0.037
<50 vs. >200	1.000	0.037
50-100 vs. 100-200	0.745	0.037
50-100 vs. >200	0.663	0.037
100-200 vs. >200	0.250	0.333

Table 5. Average similarity and species contribution (%) to the SIMPER analysis among depth levels, Pacific of Costa Rica, Central America (2010-2011). Only elasmobranch species contributing up to 90% of the cumulative average similarity are included (ANOSIM R = 0.63 p = 0.001).

Species	**Av. Abundance**	**Similarity (mean ± SD)**	**Contribution (%)**	**Cumulative Contribution (%)**
< 50 m (Av. Similarity = 35.45)				
Narcine entemedor	1.23	8.31 ± 1.08	23.43	23.43
Dasyatis longa	0.90	6.61 ± 1.00	18.63	42.07
Urotrygon aspidura	2.09	4.86 ± 0.58	13.71	55.78
Narcine vermiculatus	1.42	4.29 ± 0.62	12.11	67.89
Zapteryx xyster	0.94	3.91 ± 0.58	11.02	78.91
Rhinobatos leucorhynchus	1.16	3.56 ± 0.79	10.05	88.96
Urotrygon chilensis	0.64	1.65 ± 0.38	4.65	93.61
50-100 m (Av. Similarity = 44.33)				
Raja velezi	2.52	23.72 ± 1.84	53.52	53.52
Zapteryx xyster	1.79	8.76 ± 1.11	19.77	73.29
Mustelus henlei	2.13	7.10 ± 0.85	16.02	89.31
Raja equatorialis	0.72	1.43 ± 0.6	3.22	92.53
100-200 m (Av. Similarity = 55.55)				
Torpedo peruana	2.88	35.77 ± 2.91	64.39	64.39
Raja velezi	2	11.57 ± 0.78	20.83	85.21
Mustelus henlei	1.61	8.21 ± 0.67	14.79	100.00
> 200 m (Av. Similarity = 52.72)				
Torpedo peruana	1.63	44.29 ± 1.58	84.01	84.01
Mustelus henlei	1.22	6.66 ± 0.48	12.63	96.64

FIGURE LEGENDS

Figure 1. Map of the geographic areas (a) and sampling locations (b), Pacific of Costa Rica, Central America (2010-2011). Lines represent the 50 m, 200 m and 500 m depth contours.

Figure 2. Mean values (± SE) for elasmobranchs species richness per tow (s), abundance (ind × trawl h^{-1}) and biomass (kg × trawl h^{-1}) across geographic areas, Pacific of Costa Rica, Central America (2010-2011).

Figure 3. Linear regressions between elasmobranch community metrics and the depth gradient along Costa Rican Pacific (2010-2011). a)Relationship between the number of elasmobranch species caught per tow and depth ($r^2 = 0.575$, $F = 37.815$, $p =<0.001$, $y = 2.512 - 0.933x$). b) Abundance (CPUE) of elasmobranchs along the 20-350m gradient ($r^2 = 0.370$, $F = 15.861$, $p =<0.001$, $y = 2.603 - 0.956x$). c) Biomass (CPUE) of elasmobranchs along the 20-350m gradient ($r^2 = 0.005$, $F = 0.146$, $p = 0.705$, $y = 0.0852 - 0.0153x$).

Figure 4. Linear regressions between body size and depth of elasmobranch species sampled along the Pacific of Costa Rica, Central America (2010-2011). a) Relationship between average total length and average depth ($r^2 = 0.505$, $F = 14.265$, $p = 0.002$, $y = 27.503 + 0.173x$). b) Relationship between maximum total length and depth range ($r^2 = 0.362$, $F = 7.373$, $p = 0.018$, $y = 44.992 + 0.202x$). Each symbol represents a single

species: (●) *Diplobatis ommata*, (●) *Echinorhinus cookei*, (□) *Mustelus henlei*, (◆) *Mustelus lunulatus*, (■) *Narcine entemedor*, (●) *Narcine vermiculatus*, (○) *Raja equatorialis*, (◇) *Raja velezi*, (■) *Rhinobatos leucorhynchus*, (◆) *Squatina californica*, (▲) *Torpedo peruana*, (△) *Urotrygon aspidura*, (▲) *Urotrygon chilensis*, (▼) *Urotrygon rogersi*, (▽) *Urotrygon nana*, (▼) *Zapteryx xyster*.

Figure 5. Elasmobranch species composition across depth levels, Pacific of Costa Rica, Central America (2010-2011). Depths: < 50 m (●), 50-100 m (◇), 100-200 m (▲), > 200 m (■). Dotted line indicates the 30% similarity contour.

Figure 6. Species and environmental biplot based on the canonical correspondence analysis. Environmental data: latitude, season and depth. Gray squares represent nominal variables and red arrows represent continuous variables (the length of the vector indicates the strength of the correlation and its direction indicates the relationship with the species). The species (blue solid triangles) are abbreviated as: *Dasyatis longa* (DLO), *Diplobatis ommata* (DOM), *Mustelus henlei* (MHE), *Mustelus lunulatus* (MLU), *Narcine entemedor* (NEM), *Narcine vermiculatus* (NVE), *Raja equatorialis* (REQ), *Raja velezi* (RVE), *Rhinobatus leucorhynus* (RLE), *Squatina californica* (SCA), *Torpedo peruana* (TPE), *Urotrygon aspidura* (UAS), *Urotrygon chilensis* (UCH*)*, *Zapteryx xyster* (ZXY)

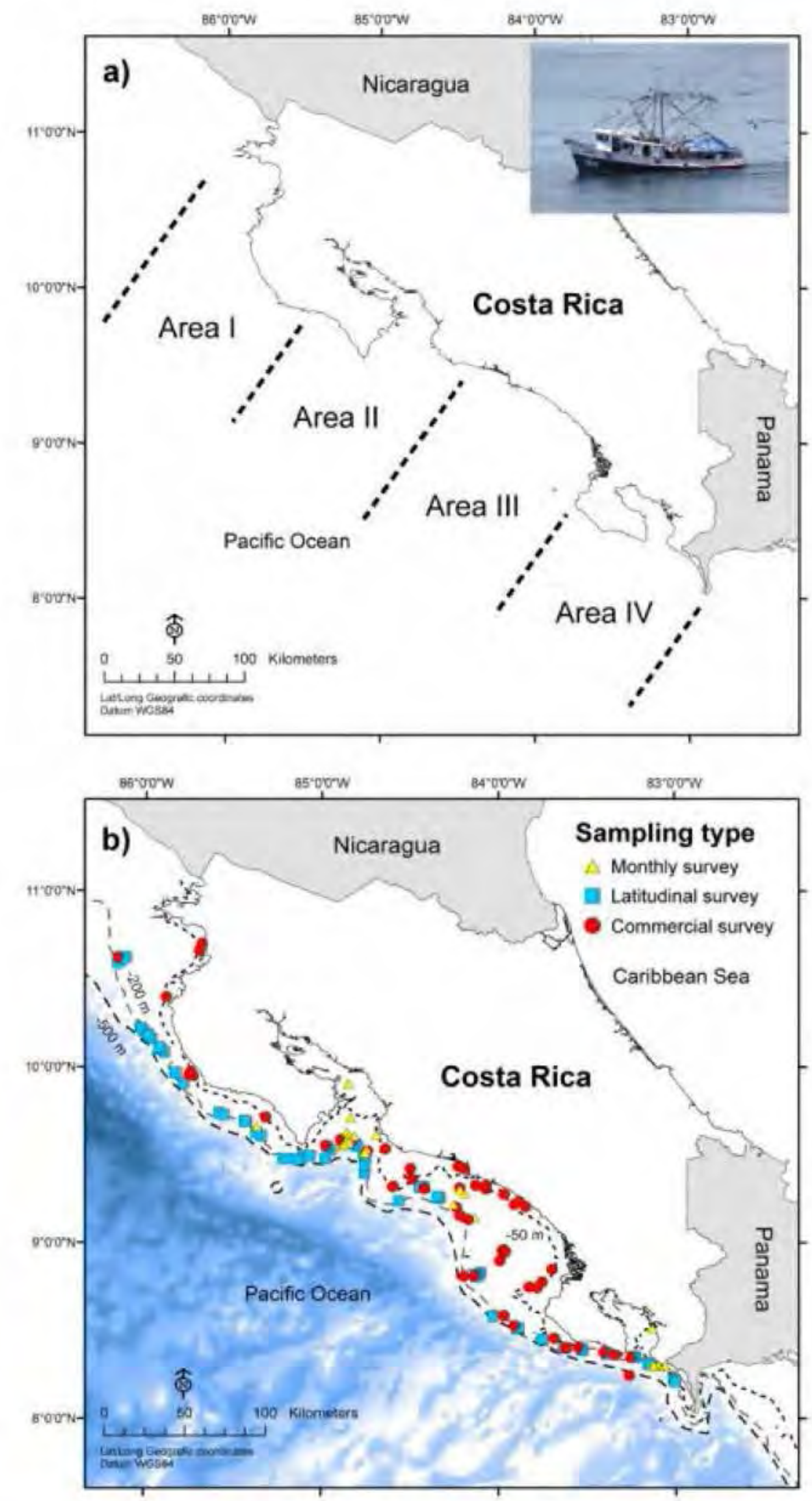

86°0'0"W
85°0'0"W
84°0'0"W
83°0'0"W
11°0'0"N
10°0'0"N
9°0'0"N
8°0'0"N
a)
Nicaragua
Costa Rica
Panama
Area I
Area II
Area III
Area IV
Pacific Ocean
0
50
100
Kilometers
Lat/Long Geografic coordinates
Datum WGS84
b)
Sampling type
Monthly survey
Latitudinal survey
Commercial survey
Caribbean Sea
-200 m
-500 m
-50 m

Figure. 1-

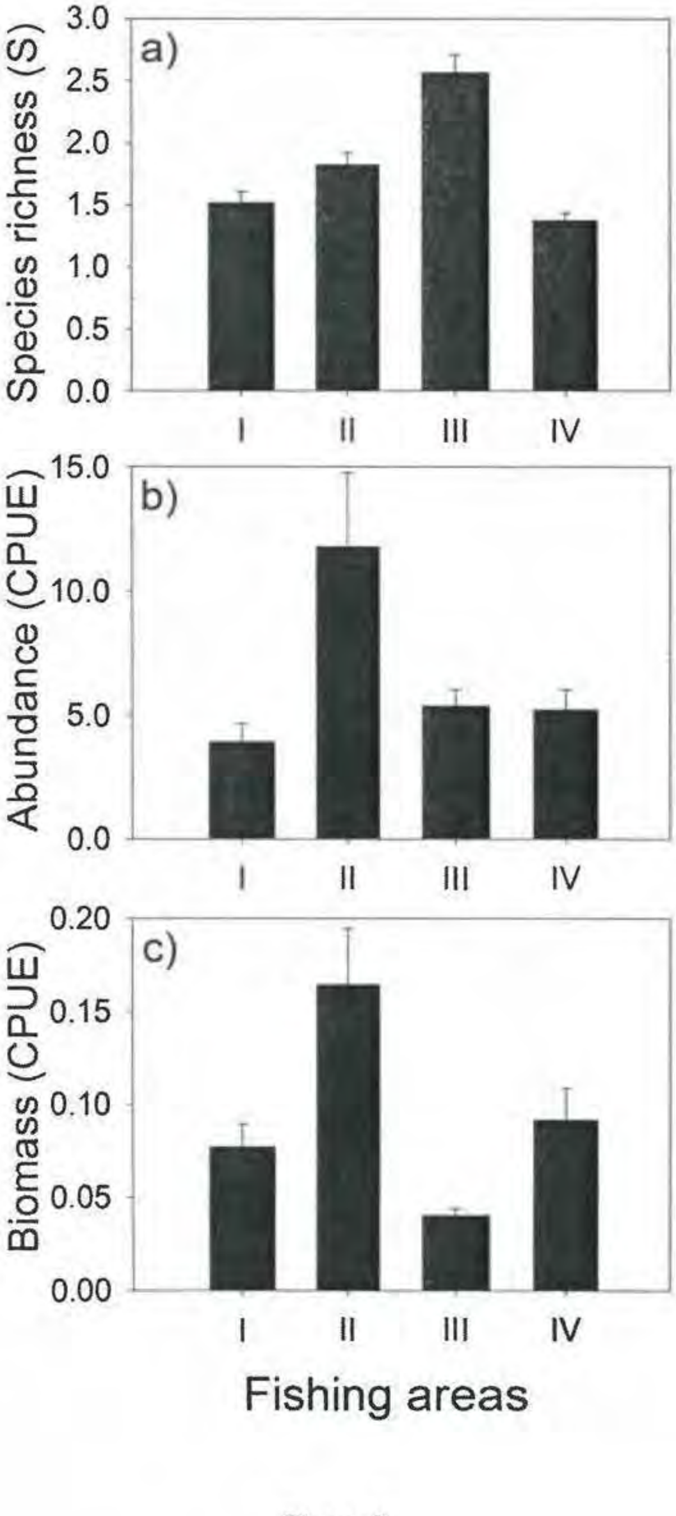

a)
Species richness (S)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
I
II
III
IV
b)
Abundance (CPUE)
15.0
10.0
5.0
0.0
I
II
III
IV
c)
Biomass (CPUE)
0.20
0.15
0.10
0.05
0.00
I
II
III
IV
Fishing areas

Figure 2.

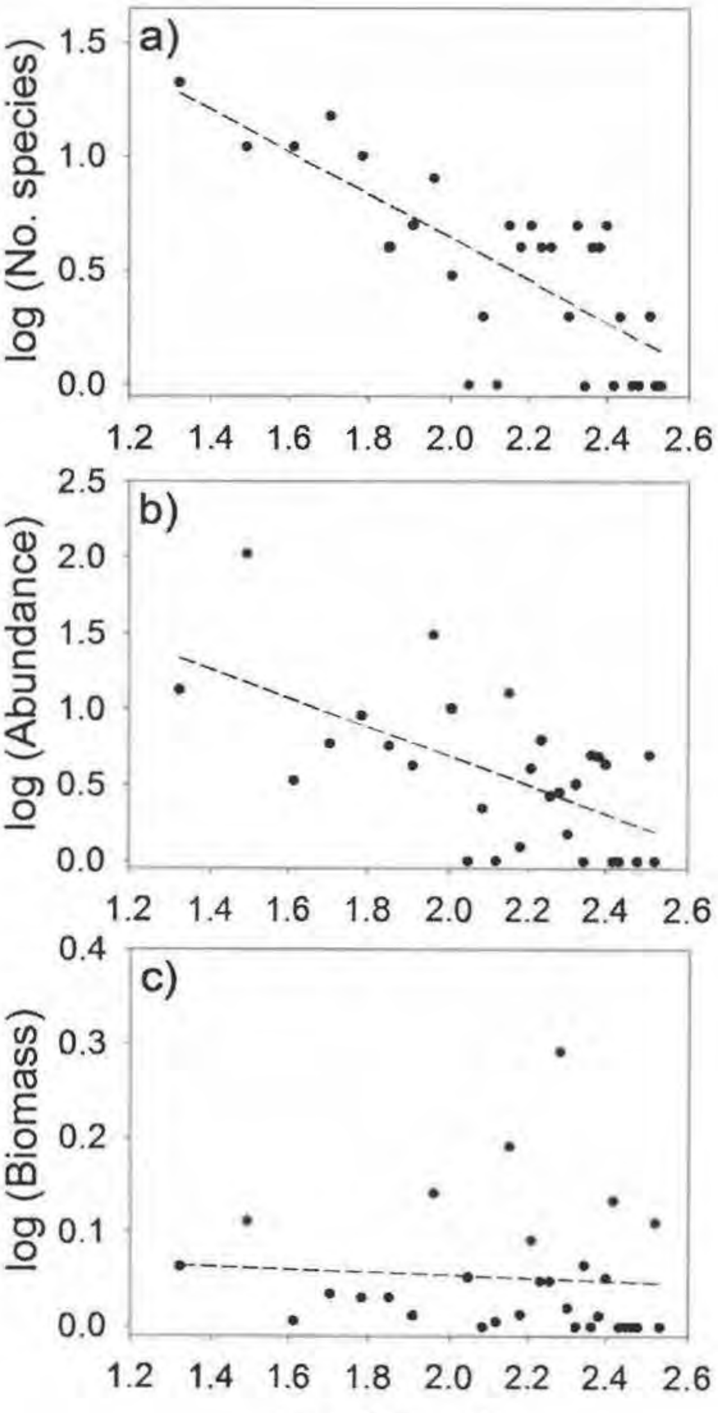

a)
log (No. species)
1.5
1.0
0.5
0.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
b)
log (Abundance)
2.5
2.0
1.5
1.0
0.5
0.0
c)
log (Biomass)
0.4
0.3
0.2
0.1
0.0
log (Depth)

Figure 3.

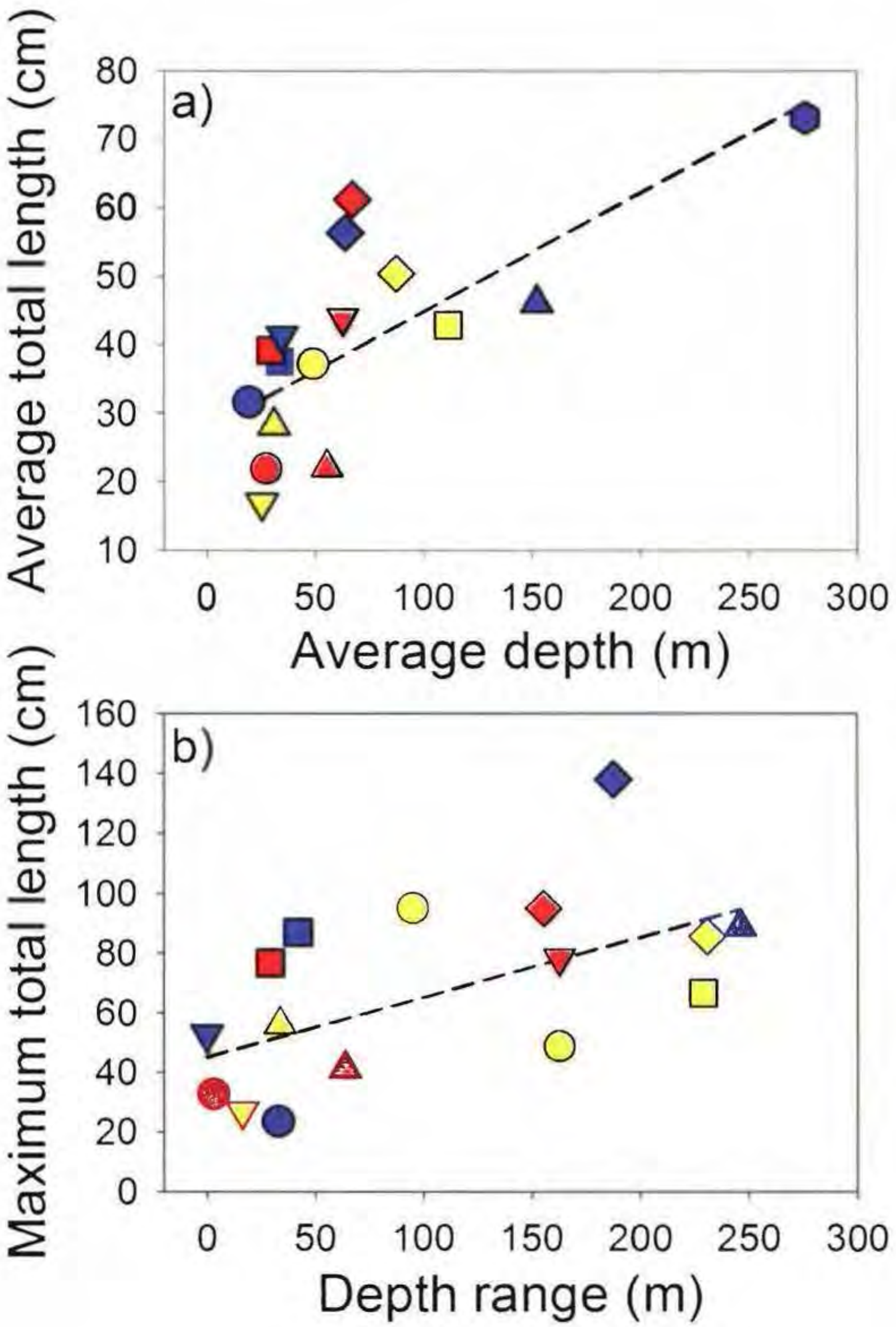
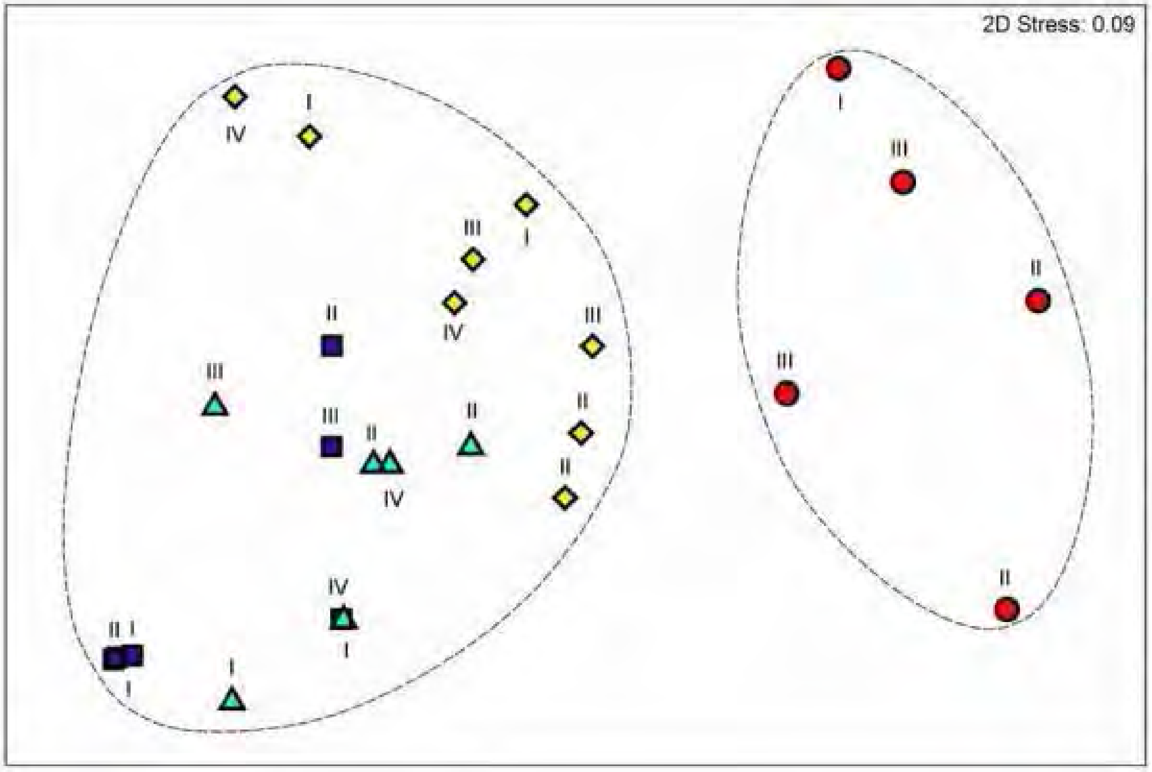

a)
Average total length (cm)
80
70
60
50
40
30
20
10
0
50
100
150
200
250
300
Average depth (m)
b)
Maximum total length (cm)
160
140
120
100
80
60
40
20
0
0
50
100
150
200
250
300
Depth range (m)

Figure 4.


2D Stress: 0.09
IV
I
I
III
I
IV
II
III
III
II
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II
II
IV
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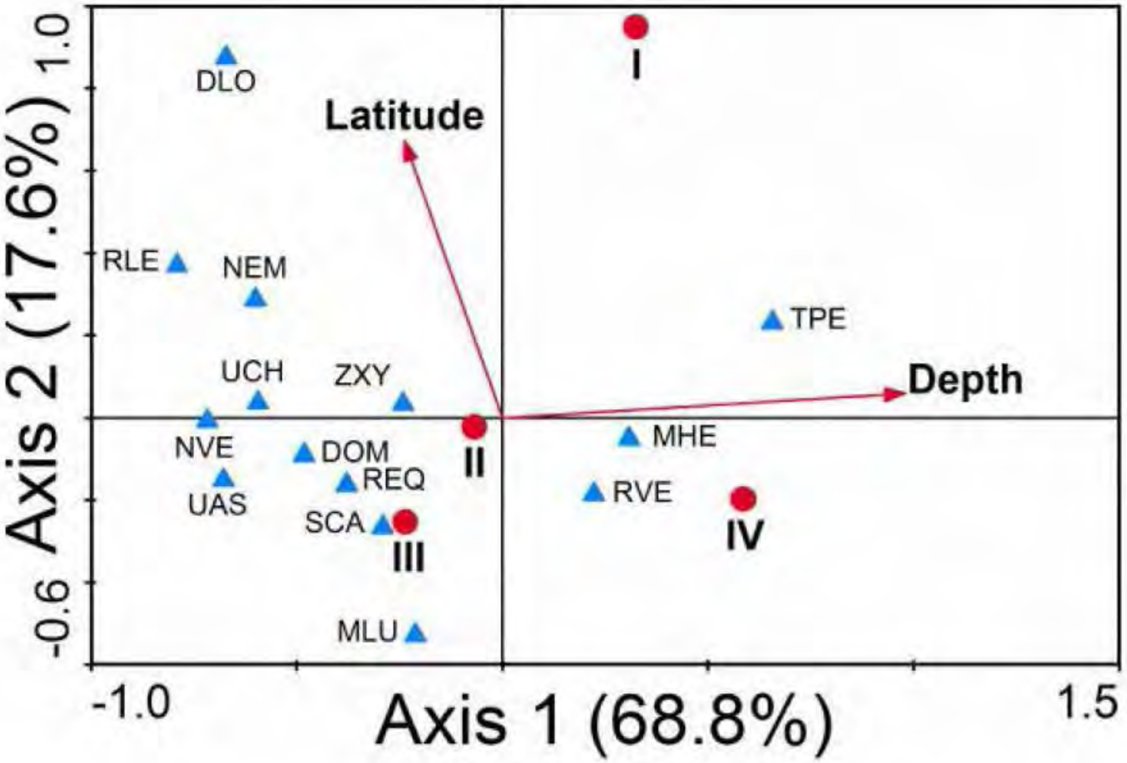
IV
I
II I
I
I
I
III
II
III
II

Figure 5.



Axis 2 (17.6%)
1.0
-0.6
Axis 1 (68.8%)
-1.0
1.5
I
II
III
IV
Latitude
Depth
DLO
RLE
NEM
TPE
UCH
ZXY
NVE
DOM
REQ
UAS
SCA
MHE
RVE
MLU

Figure 6.

Supplement 1. CPUE (mean ± SE) of elasmobranch abundance (ind × trawl h^{-1}) and biomass (kg × trawl h^{-1}) across geographic areas, Pacific of Costa Rica, Central America (2010-2011). Values are highlighted in bold for abundances higher than 0.3.

Species	**Area I**		**Area II**		**Area III**		**Area IV**	
	Abundance	**Biomass**	**Abundance**	**Biomass**	**Abundance**	**Biomass**	**Abundance**	**Biomass**
Rhizoprionodon longurio	-	-	0.024±0.101	0.000±0.001	0.003±0.023	0.000±0.000	-	-
Sphyrna lewini	-	-	-	-	0.009±0.052	-	-	-
Mustelus henlei	**0.305±1.441**	**0.002±0.003**	**4.247±3.011**	**0.023±0.017**	**2.205±0.433**	**0.011±0.002**	**1.794±0.595**	**0.009±0.003**
Mustelus lunulatus	0.018±0.059	0.001±0.002	0.058±0.083	0.001±0.002	0.206±0.064	0.002±0.000	-	-
Dasyatis longa	0.145±0.245	0.000±0.000	0.038±0.182	0.013±0.72	0.021±0.032	0.000±0.000	-	-
Aetobatus laticeps	-	-	-	-	0.006±0.033	-	-	-
Rhinoptera steindachneri	-	-	-	-	0.066±0.031	0.005±0.003	-	-
Gymnura marmorata	-	-	-	-	0.003±0.023	0.000±0.000	-	-
Raja cortezensis	-	-	0.003±0.026	0.000±0.000	-	-	-	-
Raja equatorialis	0.024±0.053	0.000±0.000	0.174±0.173	0.001±0.000	0.092±0.048	0.000±0.000	-	-
Raja velezi	**0.361±0.161**	**0.010±0.005**	**1.475±0.284**	**0.034±0.008**	**0.885±0.147**	**0.009±0.001**	**2.224±0.877**	**0.055±0.020**
Rhinobatus leucorhynchus	-	-	0.208±0.507	0.004±0.011	0.083±0.101	0.000±0.000	-	-
Zapteryx xyster	0.277±0.181	0.004±0.003	**0.855±0.219**	**0.009±0.003**	**0.352±0.065**	**0.003±0.001**	0.165±0.165	0.000±0.000
Urotrygon aspidura	0.005±0.030	0.000±0.000	**2.075±0.559**	**0.005±0.001**	**0.593±0.193**	**0.001±0.000**	-	-
Urotygon chilensis	-	-	0.111±0.111	0.000±0.000	0.003±0.024	0.000±0.000	-	-
Urotrygon rogersi	**1.595±0.875**	**0.004±0.002**	-	-	-	-	-	-
Urotrygon nana	-	-	0.251±0.551	0.000±0.000	-	-	-	-
Urotrygon sp.	-	-	0.002±0.020	0.000±0.000	-	-	-	-
Echinorhinus cookei	-	-	**0.462±1.017**	**0.014±0.031**	-	-	-	-
Squatina californica	-	-	0.114±0.312	0.003±0.006	0.075±0.044	0.003±0.002	0.055±0.095	0.001±0.002
Diplobatis ommata	-	-	0.053±0.121	0.000±0.000	0.061±0.105	0.000±0.000	-	-

Narcine entemedor	0.099±0.195	0.001±0.002	0.052±0.080	0.001±0.001	0.121±0.064	0.000±0.000	-	-
Narcine vermiculatus	-	-	0.08±0.185	0.000±0.000	**0.401±0.161**	**0.001±0.000**	-	-
Torpedo peruana	**1.077±0.842**	**0.054±0.057**	**1.496±0.663**	**0.056±0.25**	0.193±0.158	0.006±0.005	**0.976±0.693**	**0.026±0.020**

Supplement 2. CPUE (mean ± SE) of elasmobranch abundance (ind × trawl h^{-1}) and biomass (kg × trawl h^{-1}) across depth levels, Pacific of Costa Rica, Central America (2010-2011). Values are highlighted in bold for abundances higher than 0.3.

Species	**< 50 m**		**50-100 m**		**100-200 m**		**> 200 m**	
	Abundance	**Biomass**	**Abundance**	**Biomass**	**Abundance**	**Biomass**	**Abundance**	**Biomass**
Rhizoprionodon longurio	0.102±0.183	0.000±0.000	-	-	-	-	-	-
Sphyrna lewini	0.027±0.091	0.000±0.000	-	-	-	-	-	-
Mustelus henlei	0.095±0.087	0.001±0.000	**8.659±2.344**	**0.047±0.0133**	**0.781±0.390**	**0.004±0.002**	**0.66 ±0.735**	**0.002±0.002**
Mustelus lunulatus	0.043±0.059	0.000±0.000	**0.336±0.074**	**0.003±0.001**	-	-	0.006±0.047	0.001±0.004
Dasyatis longa	**0.400±0.249**	**0.053±0.058**	0.003±0.025	0.000±0.000	-	-	-	-
Aetobatus laticeps	0.017±0.590	0.000±0.000	-	-	-	-	-	-
Rhinoptera steindachneri	0.025±0.069	0.000±0.000	0.072±0.034	0.006±0.003	-	-	-	-
Gymnura marmorata	0.009±0.041	0.000±0.000	-	-	-	-	-	-
Raja cortezensis	0.011±0.052	0.000±0.000	-	-	-	-	-	-
Raja equatorialis	0.245±0.077	0.000±0.000	**0.306±0.189**	**0.001±0.001**	-	-	-	-
Raja velezi	0.009±0.041	0.000±0.000	**2.565±0.213**	**0.046±0.005**	**1.243±0.490**	**0.030±0.011**	**0.326±0.299**	**0.008±0.008**
Rhinobatus leucorhychus	**1.073±0.518**	**0.017±0.011**	0.003±0.019	0.000±0.000	-	-	-	-
Zapteryx xyster	0.565±0.124	0.004±0.001	**1.531±0.178**	**0.015±0.002**	0.195±0.764	0.002±0.010	-	-
Urotrygon aspidura	**10.039±0.969**	**0.024±0.002**	0.003±0.022	0.000±0.000	-	-	-	-
Urotygon chilensis	0.320±0.233	0.001±0.001	0.05±0.115	0.000±0.000	-	-	-	-
Urotrygon rogersi	**2.15 ±1.016**	**0.006±0.003**	-	-	-	-	-	-
Urotrygon nana	**0.992±1.093**	**0.001±0.002**	-	-	-	-	-	-
Urotrygon sp.	0.008±0.040	0.000±0.000	-	-	-	-	-	-
Echinorhinus cookei	-	-	-	-	-	-	0.700±1.250	0.020±0.038
Squatina californica	0.130±0.626	0.004±0.019	0.238±0.133	0.006±0.002	0.006±0.039	0.000±0.003	0.000±0.000	0.000±0.000
Diplobatis ommata	0.230±0.173	0.000±0.000	0.068±0.203	0.000±0.001	-	-	-	-
Narcine entemedor	0.642±0.132	0.003±0.001	0.028±0.033	0.001±0.001	-	-	-	-
Narcine vermiculatus	**1.556±0.275**	**0.002±0.001**	-	-	-	-	-	-

Torpedo peruana	0.035±0.049	0.000±0.000	**0.335±0.164**	**0.007±0.004**	**2.044±0.845**	**0.083±0.033**	**0.489±0.252**	**0.017±0.010**

CHAPTER II

CHAPTER II

Reproductive ecology of *Raja velezi, Mustelus henlei, Zapteryx xyster* and *Torpedo peruana* associated with the shrimp-trawling fishery along the Pacific coast of Costa Rica

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ABSTRACT

The elasmobranch bycatch of the shrimp trawling fishery operating along the Pacific coast of Costa Rica is composed of 23 species. In data-deficient fisheries such as this one, knowledge of the life history strategies can be used as a valuable tool to identify vulnerable species and apply precautionary measures that could ensure their long-term conservation. We studied the reproductive ecology of *Raja velezi*, *Mustelus henlei*, *Zapteryx xyster* and *Torpedo peruana* associated with the Costa Rican trawling fleet. A total of 217 trawls were analyzed at a depth of 25-350 m from March 2010 to September 2011. During this period, a sample size of 751 *R. velezi*, 569 *M. henlei*, 394 *Z. xyster* and 157 *T. peruana* was obtained. The size at sexual maturity was estimated as: 52-56 cm TL for *R. velezi*, 39-43 cm TL for *M. henlei*, 45-47 cm LT for *Z. xyster,* and 54-65 cm LT for *T. peruana*. Fecundity was found to increase with female length. Litter size varied between 1 and 12 embryos in *M. henlei*, and between 1 and 9 embryos in *Z. xyster*. Size and sexual segregation was observed in all species, mainly related to depth. Most gravid females were found in depths >50 m along the Pacific coast. However, shallow coastal waters near the Golfo de Nicoya, the Quepos-Manuel Antonio wetlands and the Humedal Nacional Térraba-Sierpe (HNTS) presented larger aggregations of gravid females and immature individuals and may function as part of the essential habitats for these elasmobranchs species. Management strategies should be oriented towards the reduction of the fishing effort, and should implement measures to protect these essential shark and ray habitats.

KEYWORDS: *Life history strategies, Eastern Tropical Pacific,* elasmobranchs, segregation, aggregation

INTRODUCTION

Life history strategies partially determine the response of a population to fishing pressure (King and McFarlane 2003). Life history traits such as size at maturity, fecundity and longevity influence the intrinsic growth rate of a population (King and McFarlane 2003), which in turn is associated with the proportion of the population that may be sustainably removed by a fishery. In general, elasmobranchs tend to present slow growing life history strategies (Stevens *et al.* 2000). However, there is a wide range of population growth rates within the elasmobranch group, which influences the fishing intensity they can sustain (Prince 2005).

Other reproductive aspects, such as segregation and aggregation patterns characteristic of some elasmobranchs can increase the impact a fishery has on a species (Wearmouth and Sims 2008, Mucientes *et al.* 2009). Sex and size segregation can result in the differential exploitation of a certain sex or maturity stage (Wearmouth and Sims 2008, Noriega *et al.* 2011). A fishery that removes a larger fraction of vulnerable stages, such as neonates, juveniles or gravid females, can cause disproportionate effects (Wearmouth and Sims 2008). Aggregation patterns may also increase overall removal rates if there is a high overlap between aggregation sites and fishing grounds (Jacoby *et al.* 2011). Consequently, information on segregation and aggregation patterns displayed by a species should be incorporated in fishery management strategies.

Many elasmobranch species are a common component of the bycatch in deepwater bottom trawling fisheries (Stevens *et al.* 2000). In many countries, species-specific catch records of elasmobranchs associated with bottom trawling fisheries are unavailable (Casey and Myers, 1998, Stevens *et al.* 2000), and therefore, long-term catch trends cannot be used to identify species with declining populations. In cases like this, information on the life history and segregation may be used as a valuable management tool (Musick and Bonfil 2005).

The Costa Rican shrimp fishery operating along the Pacific coast of the country is an example of a data poor fishery (Wehrtmann and Nielsen-Muñoz 2009, Herrera-Ulloa 2011, Trujillo *et al.* 2012), where bycatch can reach up to 93% of total catch and mainly discarded (Arana *et al.* 2012, Trujillo *et al.* 2012). The bycatch of this fishery includes 23 species of sharks and rays, which corresponds to over 36% of elasmobranchs reported for the area (Wehrtmann and Cortés, 2009, Clarke *et al.* 2011). Three of the most abundant species within the bycatch are *Raja velezi*, *Mustelus henlei* and *Zapteryx xyster* (Clarke *et al.* 2011). These species have wide depth distribution ranges (approx. 25-300 m) and are caught by both the shallow and deep water shrimp fisheries. Although *Torpedo peruana* is not a very abundant species within the bycatch, it shares the same wide depth range and biological information on this species is extremely scarce. (Clarke *et al.*2011). The former three species are relatively small (< 1 m total length) and exhibit demersal habits (Bussing and López 1993, Compagno *et al.* 2005, Clarke *et al.* 2011), while *T. peruana* is an epipelagic species that has been poorly studied (Lamilla and Romero 2006). Generally, small, slow moving demersal species are the most susceptible to being caught and therefore further attention is required (Walker 2005).

Information on the reproductive ecology of elasmobranchs along the Pacific coast of Costa Rica is scarce (Zanella *et al.* 2009), which hampers the development of appropriate management strategies for this taxonomic group. The Pacific coastline of Costa Rica is very irregular, with many gulfs, wetlands and estuaries that are thought to play an important role in the reproduction of elasmobranch species (Rojas *et al.* 2000, Espinoza 2006, Arauz *et al.* 2007, Zanella *et al.* 2009). Typically, immature life stages are small and slow, which make them most vulnerable to intense fishing pressure from bottom trawling fisheries.

In the present study, we analyze how life history traits and segregation patterns determines the susceptibility of elasmobranchs to high fishing pressures. We focused on *M.*

henlei, R. velezi, Z. xyster and *T. peruana* and (i) estimated the size at maturity; (ii) fecundity; (iii) spatial sex and size segregation patterns, which were used to identify essential habitats and recommend management measures for elasmobranchs in Costa Rica.

METHODS

Study area

Costa Rica is located in a tropical region with pronounced rainy and dry seasons which drastically influence the amount of sediment, nutrients and water that flow into the ocean (Wehrtmann and Cortés 2009, Fig. 1). The northern Pacific region (Area I) is defined by a seasonal upwelling that occurs between December and April (Wehrtmann and Cortés 2009). The central Pacific (Areas II and III) is bordered by two large estuarine systems, the Golfo de Nicoya (north) and the Humedal Nacional Térraba-Sierpe (south), the southern Pacific region (Area IV) is adjacent to the Golfo Dulce, a tropical fjord. To facilitate further analysis, the Pacific coast of Costa Rica was divided into three geographic areas (Areas I-IV) and four depth levels (<50m, 50-100m, 100-200m, >200m) (Fig. 1B)

Sampling methods

Fieldwork was conducted onboard commercial shrimp trawlers from The Rainbow Jewels S.A. (Puntarenas, Costa Rica). Each vessel is 22.5 m long, equipped with a 270 hp engine and two standard epibenthic nets (20.5 m long, mouth opening of 5.35 m x 0.85 m, mesh size, 4.45 cm, cod-end mesh size 3.0 cm), the towing speed was 0.8-1.2 nm. Scientific and fishery dependent sampling was conducted along the entire Pacific coast at depths between 25 and 350 m. Scientific trawls were carried out in monthly scientific surveys (May 2010-September 2011) and annual latitudinal surveys (August 2008, May 2009, March 2010, February 2011), while fishery dependent trawls were conducted every month between May 2010 and September 2011 (Fig. 1). Elasmobranchs were identified (Bussing and López 1993, Allen and Robertson 1994, Compagno *et al.* 2005), sexed, measured (total length - TL, cm, pre-caudal length - PCL, cm, fork length - FL, cm, disc width - DW, cm) and weighed (total weight –TW, g, eviscerated weight - EW, g) onboard. A representative sample, (of approximately 30 individuals of each species), was taken to the laboratory for further analysis.

Size at maturity

The reproductive tract of each individual was visually inspected and maturity status was assessed based on microscopic criteria (Conrath 2005). In males, the length of the right inner clasper was measured (point of insertion to the distal end, mm) and its calcification stage was determined. Males were classified as immature (I) when claspers were not calcified and as mature adults (M) when claspers were calcified. Additionally, wet gonad mass (g) was weighed to corroborate maturity status. Females were classified as: immature (I) when small, translucent eggs were present in the ovary, oviduct and shell gland uterus were undeveloped and uteri was thin and with no venation; mature adults (M), when well-developed yolky eggs were present in the ovary, oviduct had expanded and detached from the body, shell gland was approximately the same size of the largest egg and uteri were developed and venated; gravid (G), when egg capsules or embryo were developing (Conrath 2005).

There is no standardized accepted indicator of sexual maturity in elasmobranchs. In general, a variety of indicators is used and compared (Powter and Gladstone 2008, McPhie and Campana 2009). Corroboration of maturity status was accomplished by weighing uterus width (mm) and wet ovary mass (g). In gravid females, the number of embryos, their length (mm), weight (g) and sex were also recorded (Conrath 2005). In addition, wet liver mass was weighed in both males and females.

The size at first maturity was calculated for both males and females using a logistic curve (Conrath 2005). The proportion of mature individuals in every 2 cm class interval was fitted to the curve represented by the following equation: $\% \, Mature = 1\sqrt{1 - e^{a+b \times TL}}$, where *% Mature* was the percentage of mature individuals, *TL* was the total length, *a* was the intercept and *b* was the slope. The size at first maturity was estimated as *-a/b* (Conrath 2005).

Additional estimates for maturity sizes were obtained by plotting the relationship between the size of male and female reproductive organs and total length (McPhie and Campana 2009). Gonad and liver weight, the length of claspers in males and uterus width in females uterus was also used to estimate size at maturity. Differences in liver and gonad growth between males and females were detected by applying a t-test to slope values.

In order to assess the relationship between gravid female size and litter size, a simple linear regression was carried out for each species, in which litter size was the dependent variable and gravid female total length was the independent variable. To comply with the analysis assumptions, all variables were normalized with log (x+1) transformations.

The average standardized abundance (catch per unit of effort, CPUE, ind. × trawl h^{-1}) of each species was plotted for each geographic area, depth level and month to examine distribution patterns. Due to the non-normal distributions and unequal variances, a Kruskal-Wallis analysis was conducted to evaluate monthly differences in the abundance of each study species (Zar 1999). All analyses were conducted with SYSTAT v.13 (Systat Software, Inc., Point Richmond, California).

Sex and maturity ratios (immature:mature ratio pooling both sexes) of the four study species were examined. A Pearson's Chi-square test was used to evaluate the evenness of sex and maturity ratios in four depth categories (0-50 m, 50-100 m, 100-200 m, 200-350 m). The evenness of sex ratios in two maturity stages (mature, immature) was also examined using a Pearson's Chi-square test. The spatial distribution of males/females and mature/immature among geographic areas were examined using ArcMap 9.2® (ESRI, Redlands, California).

Areas with a high percentage of gravid females and immature individuals were considered to be important for reproduction. The total number of gravid females, the proportion of gravid females for each species (gravid females / mature females) and the proportion of immature individuals (immature individuals / total number of individuals) were plotted using ArcMap 9.2® (ESRI, Redlands, California) to identify potential essential habitats for elasmobranchs.

Segregation by sex and size was examined with a canonical correspondence analysis (CCA) (ter Braak andVerdonschot 1995). Abundance (CPUE) values of each species-maturity stage were used as dependent variables, depth, latitude, longitude and season (rainy and dry season) were independent variables, years were co-variables. A weighting procedure was used to down-weigh rare species-maturity stage combinations, and all continuous variables (CPUE, depth, latitude, longitude, year) were log-transformed. The probability of the observed pattern being true due to chance was estimated by a Monte-Carlo randomization test (499 permutations, ter Braak andVerdonschot 1995). The results were displayed in a bi-plot ordination diagram. These analyses were conducted using CANOCO v.4.5 software package (ter Braak andVerdonschot 1995).

RESULTS

A total of 217 trawls equaling 385.5 towing hours were analyzed during the 2010-2011 study period (Table 1). Duration per tow ranged from 0.2 to 8.1 hours, with an overall average of 1.8 hours, 184.2 trawling hours were carried out during the day and 201.4 trawling hours during the night. The fishing area with the highest sampling effort was Area II, which presented the highest number of trawls and trawling hours. The depth level with the highest sampling effort was 50-100 m, which presented the largest number of trawling hours, though a higher number of trawls were conducted at the 100-200 m and 200-350 m (Table 1).

The fishing area and depth level where most sharks and rays were caught was Area II and 50-200 m. *Raja velezi* was the most abundant species in trawl catches, followed by *M. henlei*, *Z. xyster,* and *T. peruana* (Table 1). All these speciesform part of the shrimp fishery's bycatch throughout a wide size range. The minimum size of these species varied between 13.2 cm TL and 21.8 cm TL, the smallest species caught was *R. velezi.* The maximum observed sizes of all species remained under 1 m and ranged between 63.7 cm TL - 88.9 cm TL (Table 1). *Torpedo peruana* reached the largest size with 88.9 cm TLfollowed by *R. velezi* with 85.6 cm TL (Table 1).

Size at maturity

The majority of *R. velezi* specimens obtained along the Pacific of Costa Rica were neonates (n = 208) and adults (n = 442), whereas juveniles were less common (n = 100, Fig. 2). Overall, 55% of female and 59% of male *R. velezi* were classified as mature (Fig. 2A-B). Females matured at 52.2 cm TL (Fig. 2A), uterus width increased at 60.0-70.0 cm TL (Fig. 2E). Males matured at 56.0 cm TL (Fig. 2B), clasper length increased rapidly from 60.0 to 70.0 cm

TL (Fig. 2F). Both liver (t = -14.225, p < 0.0001) and gonad size (t = 20.783, p < 0.0001) were significantly larger in females than males (Fig. 2C-D).

In *M. henlei,* 31% of all females and 78% of all males were mature (Fig. 3A, 3B). Females matured at 42.8 cm TL (Fig.3A), and uterus width increased between 40.0 and 50.0 cm TL (Fig. 3E). Males matured at 39.1 cm TL (Fig. 3B), clasper size increased rapidly from 38.0-50.0 cm TL (Fig. 3F). *Mustelus henlei* exhibited sexual dimorphism in liver (t = -21.562, p < 0.000) and gonad size (t = 17.733, p < 0.0001), as the liver was larger in females, but gonads were larger in males (Fig. 3C, 3D).

In *Z. xyster,* most females were mature (55%), while most males were immature (65%) (Fig. 4A,-B). Females matured at 45.4 cm TL (Fig. 4A), and uterus width increased between 50.0 and 65.0 cm TL (Fig. 4E). Males matured at 46.9 cm TL (Fig.4B), calcified claspers were observed between 50.0 and 65.0 cm TL (Fig. 4F). *Zapteryx xyster* displayed sexual dimorphism in liver (t=-11.147, p=0.000) and gonad size (t = 2.6584, p = 0.0084), as both attained a greater size in females (Fig. 4C-D).

The majority of female (89%) and male (75%) *T. peruana* obtained by the shrimp fishery were immature (Fig. 5A, 5B). Females matured at 69.8 cm TL (Fig. 5A), uterus width began to grow at a faster rate from 63 to 80 cm TL (Fig. 5E). Males matured at 50.4 cm TL (Fig. 5B), and clasper size increased from 55.0-70.0 cm TL (Fig. 5F). A sexual dimorphism in liver (t = 3.9983, p = 0.0001) and gonad size (t = 15.179, p < 0.0001) was also found in *T. peruana*, in which both organs developed to larger sizes in females (Fig. 5C-D).

Gravid females of *R. velezi* (N = 16) ranged 60.6-76.9 cm TL, with up to two egg capsules per female. Gravid females of *M. henlei* (N = 33) measured between 46.5 and 66.5 cm TL, with litter sizes of 1-12 embryos (Fig. 6A). Finally, gravid females of *Z. xyster* (N = 5) ranged between 39.6 and 64.0 cm TL, with litter sizes that varied between one and eight embryos

(Fig. 6B). A linear relationship was found between female size and litter size in both *M. henlei* and *Z. xyster* (Fig. 6A-B).

Segregation patterns

The monthly abundance patterns of *R. velezi* were statistically significant (H = 20.876, d.f = 10, p = 0.022). Two cycles in the abundance of this ray was observed, with peaks in May and September (Fig 7a). *Raja velezi* was significantly more abundant in Area IV (Fig. 8a). *Raja velezi* was not present in the 0-50 m depth range: its abundance was highest at 50-100 m and decreased in deeper levels (Fig. 8b).

Monthly variations in the abundance of *M. henlei* were statistically significant (H = 23.248, d.f = 10, p = 0.010). This shark's abundance peaked in September (Fig. 7b). The abundance of *M. henlei* presented no discernable patterns throughout geographic areas (Fig. 8c). This shark was most abundant at the 50-100 m depth level (Fig. 8d).

The abundance of *Z. xyster* varied significantly across months (H = 36.689, d.f = 10, p = <0.001) and peaked during May and August (Fig. 7c). A higher abundance of *Z. xyster* was detected in Area II (Fig. 8e). *Zapteryx xyster* was not present in the 200-350 m depth trawls, but it rather peaked at 50-100 m (Fig. 8f).

The abundance of *T. peruana* did not vary significantly across months (H = 15.246, d.f = 10, p = 0.123), though it was slightly higher during June (Fig. 7d). Abundance of *T. peruana* was similar in all geographic areas, with the exception of Area III, where abundance was lowest (Fig. 8g). This ray was most abundant at the 100-200 m depth level (Fig. 8h).

Sex ratios for R. velezi differed significantly from a 1:1 ratio (X^2 = 4.63, df = 1, p = 0.031, 1:1.17, F:M), though it was even in both mature and immature stages (Table 3). Males were more abundant than females in 50-100 m and 200-350 m (Table 3). This skate's maturity ratio did not differ from 1:1 at 50-100, contrary to 100-200 m and 250-350 m, where mature individuals were more abundant (Table 3). Neonate *R. velezi* were more common in shallow waters (<50 m), as were egg capsules (Fig. 9). Juveniles and adult male *R. velezi* occurred at intermediate depths in the central Pacific region (Fig. 9). Gravid and adult female *R. velezi* were associated with deeper waters, with greater abundance of gravid females in the Central (Areas II and III) and South Pacific region (Area IV) (Fig. 9, Fig. 10b).

Male *M. henlei* were more common than females (1:2.45 ratio), and sex ratio differed from an equal proportion ($X^2 = 5.78$, d.f = 1, p = 0.02, Table 3). While sex ratio was even in immature individuals (Table 3), males dominated mature stages (Table 3). *Mustelus henlei* presented an even sex ratio at the 50-100 m depth level, but it was male biased at 100-200 m, where 20 females and 102 males were observed (Table 3). Mature *M. henlei* were more common than immature specimens at 0-50 m, 50-100 m and 100-200 m (Table 3). Juveniles and adults were found at similar depths (Fig. 3). Gravid females and neonates were found in very shallow waters, particularly in the Central Pacific region (Fig. 9, 10c). Neonates were associated with lower latitudes, males with intermediate latitudes andfemales and juveniles with higher latitudes (Fig. 9).

Zapteryx xyster showed a female biased sex ratio of 1:0.54 (F:M) ($X^2 = 35.340$, d.f = 1, p < 0.0001). Uneven sex ratios were also observed across maturity stages and depth levels, where females also dominated in both immature and mature stages (Table 3) as well as in the 50-100 m depth level (Table 3). Sex ratio was even at all other depth levels. A larger proportion of immature individuals was present in 0-50 m (Table 3). Neonates and gravid females of *Z. xyster* occurred in shallow waters, and gravid females were more associated with lower latitudes, while neonates were more associated with higher latitudes (Fig. 9-10). Juveniles, adult males and females presented similar correlations with depth, latitude and longitude.

Overall, *T. peruana* presented an even sex ratio ($X^2 = 0.52$, d.f = 1, p = 0.47). Females were significantly more abundant in immature stages ($X^2 = 6.125$, d.f = 1, p = 0.013), while males were more abundant in mature stages ($X^2 = 12.448$, d.f = 1, $p < 0.0001$) (Table 3). Additionally, sex ratios did not differ from an equal proportion at any of the sampled depth levels (Table 3). The proportion of immature individuals was higher in all depth levels (Table 3). Neonate *T. peruana* were associated with shallow waters, while juveniles, adult males and adult females occurred in a similar range of the depth gradient. Adult females were more abundant in Area I (north Pacific), particularly during the dry season. Adult males were more abundant in the central and south Pacific during the rainy season (Fig. 9). Gravid females of *T. peruana* were not found during the study period.

Identification of reproductive areas

Most gravid females of all elasmobranch species obtained during the study were found at depths < 100m along the coastline. Some coastal areas such as the Golfo de Nicoya, the Quepos-Manuel Antonio wetlands and the Humedal Nacional Térraba-Sierpe (HNTS) presented larger aggregations of gravid females (Fig. 10). The highest number of gravid females (up to 8 individuals per hour) was found in the HNTS during the October 2010 survey. Other specific locations were of a great ecological importance to certain species, such as the Puerto Coyote mangroves (Area I), HNTS (Area III) and Golfo Dulce (Area IV) in the case of *M. henlei*, and HNTS (Area III) for *Z. xyster*. On the other hand, gravid *R. velezi* were found in small numbers along the entire coastline, with higher densities observed along the Central Pacific (Areas II and III, Fig. 10). In addition, a large number of *R. velezi* egg capsules were found in Area III, near HNTS at a depth of 65 m, uncovering a possible hatchery for this species.

Areas with a high abundance of immature individuals and females were also considered to be important for reproduction (Fig. 11-12). The HNTS and the wetlands of Quepos-Manuel Antonio (Area III) showed greater abundances of immature *R. velezi, M. henlei* and *Z. xyster* than other shallow coastal areas (Fig. 12A-C), although immature individuals of *Z. xyster* were also common outside Golfo Dulce (Area IV) (Fig. 12C).High percentages of immature *T. peruana* were found along the entire Pacific coast (Fig. 12D).

DISCUSSION

Raja velezi, M. henlei, Z. xyster and *T. peruana* were abundant species within the bycatch of the shrimp fishery, mainly between 50 m and 200 m deep. They were associated with this fishery throughout all their life stages and most of their depth range along the Pacific coast of Costa Rica and probably Central America. These elasmobranchs are relatively small, as their maximum sizes were less than 1 m TL.

Size at maturity

This study provides the first estimates of size at maturity for *Raja velezi*, *Mustelus henlei.*, *Zapteryx xyster* and *Torpedo peruana.* The former threematured at similar sizes, within the 39-56 cm TL range. These maturity sizes were intermediate, when compared to species in the *Raja* (Dulvy *et al.* 2000, Stevens *et al.* 2000, Romanelli *et al.* 2007, Ebert *et al.* 2008), *Mustelus* (Compagno *et al.* 2005, Oddone *et al.* 2007, Tavares *et al.* 2007, Pereyra *et al.* 2008, Farrel *et al.* 2010, Pérez-Jiménez and Sosa-Nishisaki 2010) and*Zapteryx* (Abilhoa *et al.* 2007, Blanco-Parra *et al.* 2009, Colonello *et al.* 2011) genera. *Torpedo peruana* was the largest of the studied species, and its observed maximum size (88.9 cm max. TL) was much larger than previously reported for the Eastern Pacific region (50 cm TL) (Mejia-Falla and Navía 2011). However, sample size for mature individuals was relatively low and thus, its maximum size might be even larger than reported in this study. Our estimate for size at maturity of *T. peruana* (50.4 cm TL for males and 69.8 cm TL for females) places it among one of the larger *Torpedo* species, with sizes at maturity similar to *T. nobiliana* (55.0 cm TL males, 90.0 cm TL females: Capape *et al.* 2006) and *T. californica* (60.0 cm TL in males, 84.0 cm TL in females: Neer 1998).

Raja velezi, M. henlei, Z. xyster and *T. peruana* matured between 58% and 79% of their maximum total sizes. This range is consistent with what has been reported for other elasmobranchs, which tend to mature between 60% and 90% of their maximum size (Ebert *et al.* 2008, McPhie and Campana 2009). Elasmobranchs present a strong correlation between these two parameters (Powter and Gladstone 2008) because after attaining maturity they tend to invest most of their energy in reproduction and therefore, growth rates significantly decrease (Ebert *et al.* 2008).

Sexual dimorphism in maximum size and size at maturity occurred in all of the studied species. Females matured at larger sizes than males in *M. henlei* and *T. peruana*, while maturity estimates for *Z. xyster* and *R. velezi* were higher for males than females. Larger maturity size estimates for females rather than males has been widely reported for elasmobranchs (Capape *et al.* 2006, Consalvo *et al.* 2007, Pereyra *et al.* 2008, Blanco-Parra *et al.* 2009, Pérez-Jiménez and Sosa-Nishisaki 2010). Sexual dimorphism in size is mainly caused by the larger energy investment required of females during reproduction (Consalvo *et al.* 2007, Ebert *et al.* 2008). Larger females typically have larger litter sizes and are able to provide more nutrients to their offspring (Consalvo *et al.* 2007). Growth slows down after maturity, which causes population structures to be comprised of higher proportions of large females than large males (Consalvo *et al.* 2007).

The difference between maturity sizes of male and female *T. peruana* was of 19.4 cm TL. The large disparity between female and male maturity sizes was also reported for *T. californica* (see Neer 1998),*T. nobiliana* (see Capape *et al.* 2006)and *T. marmorata* (see Consalvo *et al.* 2007). This implies that considerable differences in sizes at maturity are characteristic of some *Torpedo* species. Presumably, it is caused by the higher energy requirements of gestation in female *T. peruana* in comparison to females of other species with a less pronounced sexual dimorphism in maturity size (Consalvo *et al.* 2007).

Although sexual dimorphism in the maturity size of *Z. xyster* was inconspicuous, males did mature at slightly larger sizes than females (Fig. 4). The size segregation displayed by this species throughout the study area could have affected the sample composition and as a consequence, the maturity size estimates. This effect has also been reported by Ebert *et al.* (2008). It is probable that females matured at larger sizes than males in this species, consistently with what occurs in *Z. exasperata* (Blanco-Parra *et al.* 2009) and *Z. brevisrostris* (Colonello *et al.* 2011).

In contrast with *M. henlei, T. peruana* and *Z. xyster*, male *R. velezi* matured at larger sizes than females. An increasing number of studies have demonstrated that females do not necessarily mature at larger sizes than males in oviparous species such as skates (Cortés 2000, Ebert *et al.* 2008, McPhie and Campana 2009). Selection towards larger females in oviparous species may not be advantageous because size is not positively correlated with fecundity, as they can only deposit two eggs at a time (Ebert *et al.* 2008). Sexual selection may actually favor large sized male skates due to their higher probability of controlling and mating with females (Ebert *et al.* 2008).

Our data revealed sexual dimorphism of liver size in the four studied species, which is in agreement with similar studies with elasmobranchs. Female elasmobranchs tend to present larger livers as a consequence of their higher reproductive energy requirements (Lucifora *et al.* 2002, Mabragaña *et al.* 2002). In females, lipid reserves stored in the liver are used during vitellogenesis and gestation in species that do not feed during pregnancy (Lucifora *et al.* 2002).

Fecundity

Fecundity was not estimated for *R. velezi*, the only oviparous species in this study, nor for *T. peruana* because gravid females were not observed during the study period. Future studies should concentrate on estimating fecundity for these species, as it is an important indicator of a population's rate of increase (King and McFarlane 2003). Although it is presumed that *R. velezi* presents a high fecundity like the majority of oviparous species (Gatica and Acuña 2008),fecundity of *T. peruana* could be very low, as suggested by other life history traits, such as large maximum size and conspicuous sexual dimorphism of maturity size. It is probable that fecundities are comparable to similar sized *Torpedo* species such as *T californica,* which presented 17 embryos (Neer 1998) and *T. torpedo* with a litter size of 5-28 in the Eastern Tropical Atlantic (Capape 2000).

Embryo production of *Mustelus henlei* and fecundity ranged between 1 and 12 embryos, which were born approximately at 22.0 cm TL. *Zapteryx xyster* presented from 1 to 8 embryos. This is higher than average fecundity reported for *Z. brevirostris* in southern Brazil, of mean annual fecundity of one to two embryos*(*Abilhoa *et al.* 2007, Colonello *et al.* 2011). Fecundity of *Z. exasperata* varies from 2 to 13 embryos per year (Blanco-Parra *et al.* 2009).

In *M. henlei* and *Z. xyster*, fecundity increased with increasing female length, which is a general trait of the elasmobranch group (Consalvo *et al.* 2007, Gatica and Acuña 2008, Farrel *et al.* 2010). The reported absence of senescence in sharks suggests that larger females produce more embryos (Powter and Gladstone 2008). This positive correlation between female size and fecundity has important management implications, as even moderate fishing efforts can remove enough large females to affect abundance (García *et al.* 2012).

Segregation patterns

Raja velezi, M. henlei., *Z. xyster* and *T. peruana* occurred over relatively wide depth ranges and were distributed from 0 to 125-350 m deep along the continental platform. However, the results of this study indicate that *R. velezi, M. henlei* and *Z. xyster* do have an optimal depth range at 50-100 m, where they occur in higher abundances. This depth range presents favorable conditions, as it is located within the photic zone (0-100 m) characterized by elevated productivity and temperature, yet has a higher environmental stability than at 0-50 m (Smith and Brown 2002, Knip *et al.* 2010).

Elasmobranchs are known to segregate by size and sex (Ebert *et al.* 2008) due to resource partitioning, social behavior, reproductive strategies or thermal factors, though few theories have been proven (Klimley 1987, Economakis and Lobel 1998, Carlisle *et al.* 2007, Hight and Lowe 2007, Ebert *et al.* 2008, Pereyra *et al.* 2008, Wearmouth and Sims 2008, Wearmouth and Sims 2010). In our study, *Mustelus henlei* showed a strong segregation by sex and size, while the rest of the studied species mostly segregated by size. Although females of *Z. xyster* were more abundant, sex segregation was not evident in Costa Rica or Colombia (Mejia-Falla *et al.* 2006). In contrast, *Z. exasperata* in the Gulf of California exhibited a strong segregation by sex, as males and females only occupied the same habitat during mating season (Blanco-Parra *et al.* 2009).

Depth is the main factor that influences size segregation in *R. velezi, M. henlei*, *Z. xyster* and *T. peruana* along the Costa Rican Pacific continental platform.This type of segregation, in which smaller size classes are associated with shallow waters, while larger individuals are associated with deeper waters has also been reported for skates (Henderson *et al.* 2005, Romanelli *et al.* 2007), *Mustelus* spp. (Pereyra *et al.* 2008) and *Torpedo*spp.(Consalvo *et al.* 2007). Shallow waters with high temperatures, food availability and complex habitats may provide a favorable environment for juveniles, in which they can attain fast and constant growth rates with reduced predation pressure (Heupel *et al.* 2007). In contrast, deeper environments are more favorable to larger elasmobranchs because energy requirements are lower due to lower temperatures (Carlson *et al.* 2004).

The sexual and size segregation displayed by *M. henlei*may be related to reproductive migrations. Adult males and gravid females of this species formed reproductive aggregations in January-February and September-October. However, adult males were associated with deeper (>90 m), while gravid females were associated with shallower (<90 m), waters (Arauz *et al.* 2007, Clarke *et al.* 2011). Therefore, females are presumed to gestate and give birth in shallow coastal areas, after which they return to deeper waters. It may be advantageous for gravid females to remain in shallow habitats because high temperatures increase embryo growth rate (Economakis and Lobel 1998, Hight and Lowe 2007). Neonates may stay in these coastal areas and then move to deeper waters as juveniles (Pereyra *et al.* 2008).

Torpedo peruana exhibited a strong segregation by size class, illustrated by the high percentage of immature *T. peruana* (83%) caught by the shrimp fishery. Adult females were associated with the northern coast of Costa Rica during the dry season, when seasonal upwelling occurs (Wehrtmann and Cortés 2009). A similar segregation pattern was observed in *T. torpedo* in the Mediterranean, where immature individuals inhabited coastal areas while adult females only approached the coast during the breeding period (Consalvo *et al.* 2007). The small percentage of adult *T. peruana* may also be due to their lower catchability, they possibly inhabit demersal habitat at depths out of this study range or epipelagic waters, like *T. californica* (Ebert 2003).

Exploitation of sharks that segregate sexually can contribute to drastic population declines, such as the case of *Squalus acanthias* in the English Channel (Wearmouth and Sims 2008). This appears to occur in *M. henlei* were females inhabiting shallow waters are subjected to higher fishing pressures from both the shallow water shrimp fishery and the artisanal fishery (Álvarez and Ross-Salazar 2009, López-Garro *et al.* 2009). To the contrary, males, which inhabit deeper water environments, are subjected to lower fishing intensities from the shrimp fishery. Further attention should be paid to this species, in order to determine long-term catch trends and evaluate the stock status.

Identification of areas of reproductive importance

An *R. velezi*hatchery was found in Area III, near HNTS at a depth of 65 m. Our study indicates that this species deposits its egg capsules in shallow environments, including bays and estuaries. Such a behavior in *R. velezi*contrasts with other skate species (Love *et al.* 2008, Hoff 2010, Truede *et al.* 2011), which use deeper waters (148-380 m) (Hoff 2010), but is similar to other skate species such as *Sympterygia bonapartii* (Mabragaña et al. 2002) that also deposits its egg cases in shallow waters. Juvenile *R. velezi* did not inhabit the same area as the hatchery but occurred in deeper waters. This has been observed in other skate hatcheries, where juveniles occupy different habitats to reduce predation risk (Hoff 2010).

*Mustelus henlei*and *Z. xyster* presented discrete areas with a high abundance of neonates and gravid females, which may act as pupping or nursery grounds. Immature *T. peruana*were present along the coast, however no gravid females or possible nursery areas were found. The use of pupping sites is a well-known behavior in other species of the *Mustelus*(*M. canis*:

Rountree and Able 1996, *M. henlei*, *M. lunulatus*: Salomon-Aguilar *et al.* 2009)and *Zapteryx* genera (*Z. brevirostris*:Abilhoa *et al.*2007, *Z. exasperata*, Blanco-Parra *et al.*2009) genera.

Pupping grounds, with high abundances of young of the year and gravid females, occurred in shallow habitats along the Pacific coast of Costa Rica, near coastal wetlands such as estuaries, bays or mangroves, specifically in the Golfo de Nicoya, the Quepos-Manuel Antonio wetlands, the Humedal Nacional Térraba-Sierpe (HNTS), and the mangroves of Coyote-Tamarindo (Fig. 9). Proposed reasons for the existence of pupping areas in the vicinity of coastal wetlands have been high food availability, low predation rates, and constant temperatures that contribute to high growth rates (Salomon-Aguilar *et al.* 2009). Here, presumed pupping sites seem to conform to these assumptions, since they are very productive and diverse zones (Wehrtmann and Cortés 2009). Moreover, these areas provide physically heterogeneous habitats (e.g. mangroves, gulfs, bays and estuaries) that may act as refuges. However, the exact importance of these habitats for the life cycle of elasmobranchs in Pacific Costa Rica is unknown. The duration and design of this study did not allow us to identify shark nursery areas as defined by Heupel *et al.*(2007). Constant sampling was not carried out in these coastal wetlands throughout the two year study period and therefore temporal abundance patterns of immature individuals and gravid females could not be evaluated. Additional studies on the subject are needed to define areas that may function as nurseries for elasmobranchs along the Pacific coast of Costa Rica.

Implications for management

The shrimp trawling fishery of the Pacific coast of Costa Rica is currently operating at highly unsustainable levels (FIINPESCA 2007, Herrera-Ulloa *et al.* 2011) that have resulted in (1) diminishing catches of traditional target species (*Heterocarpus vicarius* and *Solenocera* *agassizii*), (2) increasing catches of some bycatch groups (e.g. stomatopods and smaller demersal teleost fishes), and (3) the reduction of the bycatch's average trophic level in Costa Rica, and possibly in the Central American region (Álvarez and Ross-Salazar 2010, Wehrtmann and Nielsen-Muñoz 2009, Wehrtmann *et al.* 2012). Fisheries that target fast growing species, such as tropical shrimps, generally operate at high intensities that are likely to cause a population collapse of slow-growing species, such as sharks and rays (King and Macfarlane 2003). The management strategies for these fisheries should take slow-growing species into account and apply the precautionary principle.

The importance of the HNTS should be considered in the management and conservation strategies for elasmobranchs. Based on our results, the creation of a biological corridor between the Marino Ballena National Park, HNTS and Reserva Biológica Isla del Caño is recommended. The corridor should be delimited by the 50 m depth contour, where majority large proportion of neonates and gravid females occurr (McPhie and Campana 2009). Additional fishing closures should be established along the Central Pacific coast. However, fishing pressure on all maturity stages needs to be minimized in order to assure long-term conservation of entire elasmobranch populations (Kinney *et al.* 2009). A long-term monitoring program should be implemented to examine catch trends and possible variations in life history traits such as size at maturity and fecundity (Sosebee 2005, Lowerre-Barbieri *et al.* 2011).

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TABLES AND FIGURES

Table 1. Sampling effort, abundance and size (minimum, maximum and mean total length (TL - cm)) of *Raja velezi, Mustelus henlei, Zapteryx xyster* and *Torpedo peruana* along the Pacific coast of Costa Rica (2010-2011).

	Area			Depth level			
	Area I	Area II	Area III	0-50 m	50-100 m	100-200 m	200-350 m
Trawling minutes	2135.0	19594.0	1403.0	5447.0	12139.0	3593.0	1953.0
Number of trawls	31.0	168.0	24.0	23.0	57.0	77.0	60.0
Average duration	68.9	116.6	58.5	236.8	213.0	46.7	32.6
Maximum duration	360.0	485.0	364.0	408.0	485.0	250.0	210.0
Minimum duration	14.0	12.0	11.0	20.0	15.0	15.0	11.0
R. velezi							
N	46.0	565.0	74.0	1.0	545.0	95.0	44.0
Minimum TL (cm)	29.3	13.2	19.5	65.8	13.2	24.7	44.2
Average TL (cm)	66.9	46.1	64.1	65.8	45.1	64.8	68.7
Maximum TL (cm)	76.9	85.6	74.6	65.8	85.6	76.4	75.9
M. henlei							
N	6.0	390.0	31.0	10.0	359.0	38.0	20.0
Minimum TL (cm)	43.4	21.8	26.3	42.7	21.8	26.3	25.5
Average TL (cm)	50.8	41.8	44.6	48.3	41.5	45.9	42.3
Maximum TL (cm)	56.5	66.5	63.6	52.3	66.5	63.6	52.2
Z. xyster							
N	37.0	298.0	24.0	60.0	294.0	5.0	0.0
Minimum TL (cm)	19.2	15.3	15.1	15.6	15.1	41.8	0.0
Average TL (cm)	58.3	43.6	21.3	32.0	45.8	52.8	0.0
Maximum TL (cm)	78.3	70.7	43.1	78.3	70.7	66.2	0.0
T. peruana							
N	10.0	110.0	14.0	4.0	40.0	69.0	21.0
Minimum TL (cm)	21.6	14.2	16.4	18.3	14.2	21.6	35.5
Average TL (cm)	49.2	46.1	36.4	35.3	39.6	48.3	48.5

Maximum TL (cm)	88.9	80.3	52.9	55.9	69.5	88.9	73.2

Table 2. Information on maturity curves for males and females of *Mustelus henlei, Raja velezi, Torpedo peruana,* and*Zapteryx xyster.* Size at first maturity, R square (R^2) constant (a), slope (b), and the percentage of the maximum total length at which species attain maturity (% mature) and litter size (fecundity).

	R. velezi		*M. henlei*		*Z. xyster*		*T. peruana*	
	Male (N = 371)	Female (N = 311)	Male (N = 293)	Female (N = 133)	Male (N = 123)	Female (N = 235)	Male (N = 61)	Female (N = 73)
Size at maturity (cm)	56	52.2	39.1	42.8	46.9	45.4	50.4	69.8
a	-0.5352	-0.238	-0.5405	-0.1399	-0.3555	-0.1586	-0.4277	-0.1099
b	29.9445	12.4963	21.1332	5.9817	17.9848	7.2065	21.6091	7.675
% mature	59	55	78	31	35	55	25	11
Fecundity				1 to 12		1 to 8		

Table 3. Number of males and females in the 0-50 m, 50-100 m, 100-200 m and 200-350 m depth levels of *Mustelus henlei, Raja velezi, Torpedo peruana* and *Zapteryx xyster*. The p values are shown for each Pearson chi square test and significant results are underlined.

	Sample size	**Proportion of females**	**X^2**	**p-Value**	**Sample size**	**Proportion of mature**	**X^2**	**p-Value**
Raja velezi								
0-50 m	1	1			1	0		
50-100 m	542	0.426199262	**10.098**	0.001	529	0.483931947	0.546	0.46
100-200 m	95	0.473684211	**0.191**	0.608	84	0.821428571	34.714	0
200-350 m	44	0.772727273	**9.83**	0	44	0.954545455	36.364	0
Mustelus henlei	0							
0-50 m	10	0			10	0.9	6.4	0.011
50-100 m	358	0.335195531	**1.18**	0	358	0.561452514	5.641	0.018
100-200 m	38	0.157894737	**55.115**	0	38	0.815789474	15.158	0
200-350 m	20	0.35	**6.811**	0.18	20	0.6	0.8	0.371
Zapteryx xyster	0							
0-50 m	60	0.6	2.4	0.121	59	0.220338983	18.458	0
50-100 m	293	0.672354949	**16.071**	0	218	0.513761468	0.165	0.684
100-200 m	5	0.4	0.2	0.655	5	0.6	0.2	0.655
200-350 m	0				0			
Torpedo peruana	0							
0-50 m	4	0.75	1	0.317	4	0		
50-100 m	40	0.575	1.195	0.343	39	0.128205128	21.564	0
100-200 m	69	0.47826087	0.054	0.718	69	0.202898551	24.362	0
200-350 m	21	0.666666667	0.105	0.127	21	0.047619048	17.19	0

Table 4. Number of males and females in immature and mature stages of *Mustelus henlei, Raja velezi, Torpedo peruana* and *Zapteryx xyster*. The p values (p-Values) are shown for each Pearson chi square test and significant results are underlined.

	Sample size	**Proportion of females**	**X^2**	**p-Value**
Raja velezi				
Immature	291	0.47766323	0.205	0.446
Mature	390	0.43846154	0.948	0.015
Mustelus henlei				
Immature	168	0.57738095	2.531	0.045
Mature	260	0.13846154		<0.0001
Zapteryx xyster				
Immature	158	0.58860759	4.612	0.026
Mature	200	0.71	36.161	<0.0001
Torpedo peruana				
Immature	112	0.61607143	6.125	0.014
Mature	22	0.18181818	12.448	0.003

FIGURE LEGENDS

Figure 1. Map of the geographic areas (A) and trawling locations (B) along the Pacific of Costa Rica, Central America (March 2010 – September 2011). The number of trawls are shown in parentheses.

Figure 2. Estimated size at first maturity for *Raja velezi.* Sexual maturity curves of females (A) and males (B). Red represents females and blue represents males. Correlations between liver weight (C) / gonad weight (D) and total length for both males and females. Correlations between uterus width and total length for females (E) and correlation between clasper size and total length for males (F).

Figure 3. Estimated size at first maturity for *Mustelus henlei.* Sexual maturity curves of females (A) and males (B). Red represents females and blue represents males. Correlations between liver weight (C) / gonad weight (D) and total length for both males and females. Correlations between uterus width and total length for females (E) and correlation between clasper size and total length for males (F).

Figure 4. Estimated size at first maturity for *Zapteryx xyster.* Sexual maturity curves of females (A) and males (B).. Red represents females and blue represents males. Correlations between liver weight (C) / gonad weight (D) and total length for both males and females. Correlations between uterus width and total length for females (E) and correlation between clasper size and total length for males (F).

Figure 5. Estimated size at first maturity for *Torpedo peruana.* Sexual maturity curves of females (A) and males (B). Red represents females and blue represents males. Correlations between liver weight (C) / gonad weight (D) and total length for both males and females. Correlations between uterus width and total length for females (E) and correlation between clasper size and total length for males (F).

Figure 6. Relationship between the number of embryos and the total length of the females and litter size of *Mustelus henlei* (A, R^2=0.7951, y=-19.8058+0.4630x), *Zapteryx xyster* (B, R^2=0.9040, y=-9.5569+0.2564x). All variables are log-transformed.

Figure 7. Mean abundance ± SE (CPUE, ind./hour) of *Raja velezi, Mustelus henlei, Zapteryx xyster* and *Torpedo peruana* along the Pacific coast of Costa Rica each month(2010-2011).

Figure 8. Mean abundance ± SE (CPUE, ind./hour) of *Raja velezi, Mustelus henlei, Zapteryx xyster* and *Torpedo peruana* in every geographic area and depth level along the Pacific coast of Costa Rica (2010-2011).

Figure 9. Biplot resulting from a canonical correspondence analysis, of the relationship between five CPUE (ind./hour) of five maturity-sex stages of *Raja velezi* (RVE), *Mustelus henlei* (MHE), *Zaptery xyster* (ZXY) and *Torpedo peruana* (TPE) on the Pacific coast of Costa Rica (2010-2011) and environmental factors. Latitude, longitude, dry season, rainy season and depth acted as independent variables and species abundance were dependent variables. Arrows indicate continuous variables squares indicate nominal variables and triangles represent each maturity

stage-species combination. N: neonate, J: juvenile, M: adult male, F: adult females, G: gravid female

Figure 10. Location of gravid females along the Pacific coast of Costa Rica. Bubble sizes indicate the number of gravid females found (A). Proportion of gravid females for *Raja velezi* (B) *Mustelus henlei (*C), and *Zapteryx xyster* (D)along the Pacific coast of Costa Rica. Red represents gravid females and blue represents mature females.

Figure 11. Relative abundance (CPUE – individuals h^{-1}) of mature and immature individuals along the Pacific coast of Costa Rica for *Raja velezi* (A), *Mustelus henlei* (B), *Zapteryx xyster* (C), *Torpedo peruana* (D). Each pie graph represents relative abundance in the established geographic areas. Blue represents the mature stages and yellow represents the immature stages.

Figure 12. Relative abundance (CPUE – individuals h^{-1}) of femlaes and males along the Pacific coast of Costa Rica for *Raja velezi* (A), *Mustelus henlei* (B), *Zapteryx xyster* (C), *Torpedo peruana* (D). Each pie graph represents relative abundance in the established geographic areas. Blue represents the mature stages and yellow represents the immature stages.

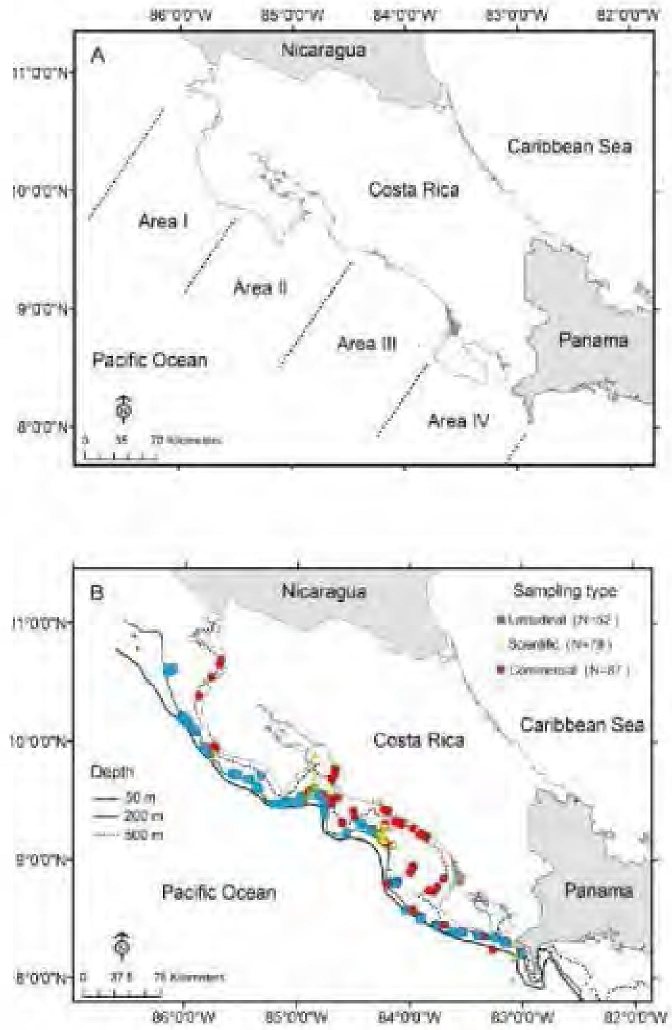

86°0'0"W
85°0'0"W
84°0'0"W
83°0'0"W
82°0'0"W
11°0'0"N
10°0'0"N
9°0'0"N
8°0'0"N
A
Nicaragua
Caribbean Sea
Costa Rica
Area I
Area II
Area III
Area IV
Panama
Pacific Ocean
0 35 70 Kilometers
B
Nicaragua
Sampling type
Longitudinal (N=62)
Scientific (N=78)
Commercial (N=87)
Caribbean Sea
Costa Rica
Depth
50 m
200 m
500 m
Pacific Ocean
Panama
0 37.5 75 Kilometers

Figure 1.

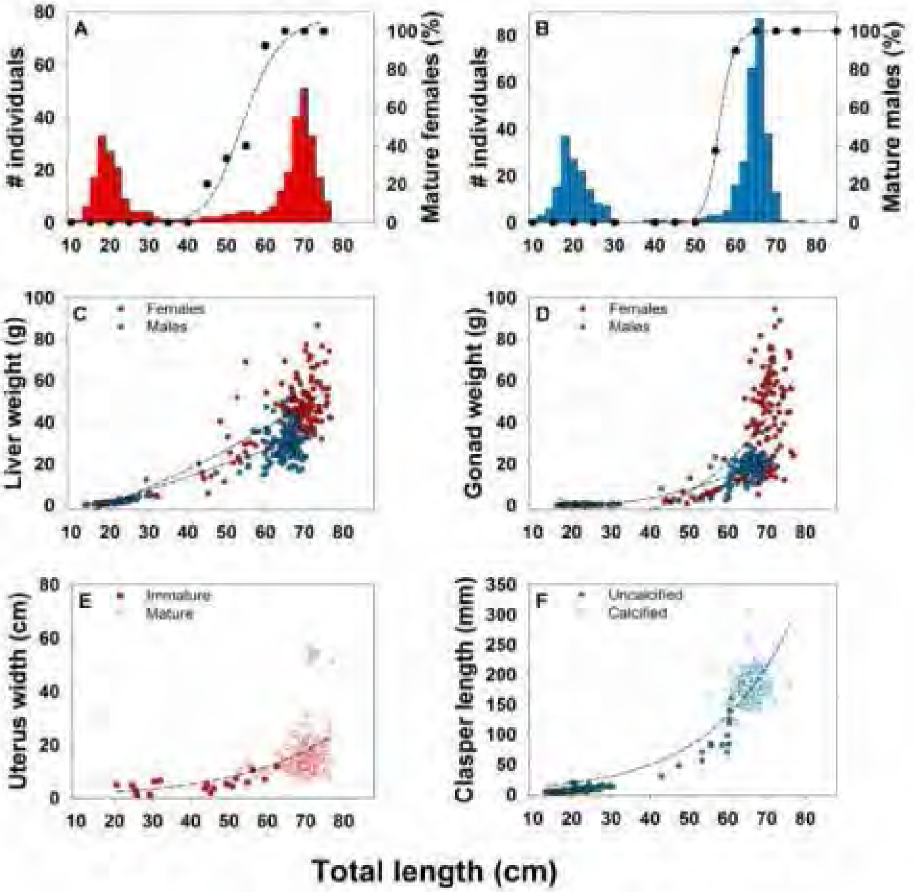

A
B
C
D
E
F
individuals
Mature females (%)
Mature males (%)
Liver weight (g)
Gonad weight (g)
Uterus width (cm)
Clasper length (mm)
Females
Males
Immature
Mature
Uncalcified
Calcified
Total length (cm)

Figure 2

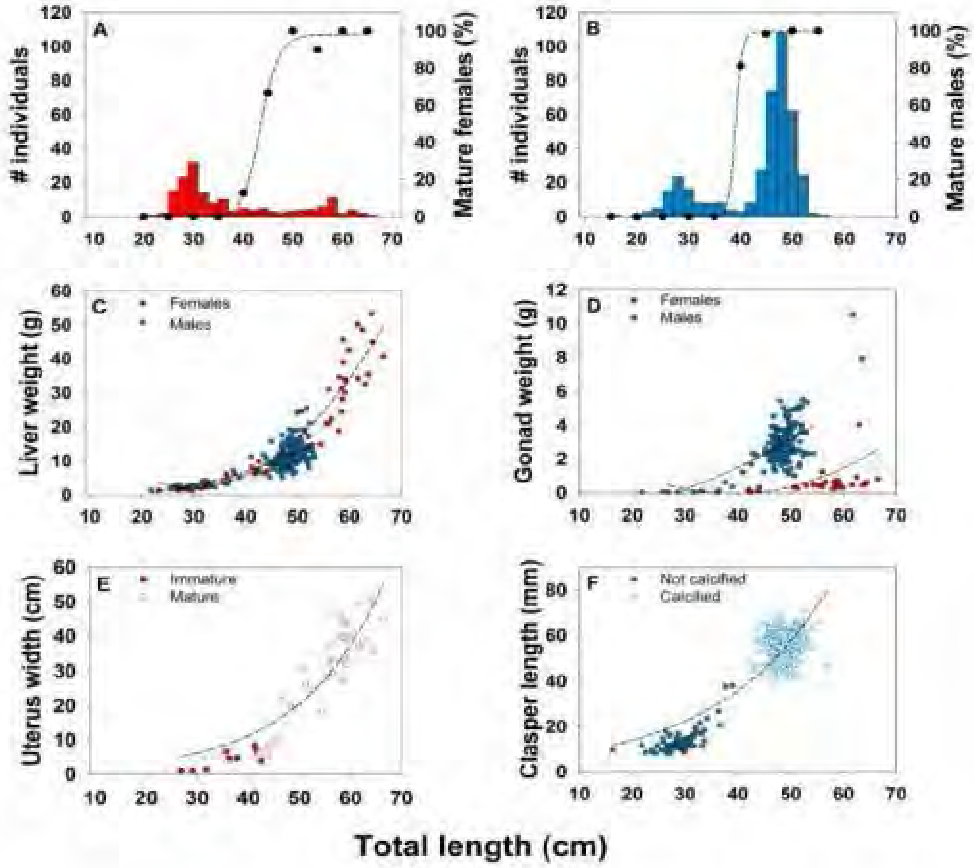

A
B
C
D
E
F
individuals
Mature females (%)
Mature males (%)
Liver weight (g)
Gonad weight (g)
Uterus width (cm)
Clasper length (mm)
Females
Males
Immature
Mature
Not calcified
Calcified
0
20
40
60
80
100
120
0
2
4
6
8
10
12
10
20
30
40
50
60
70
Total length (cm)

Figure 3

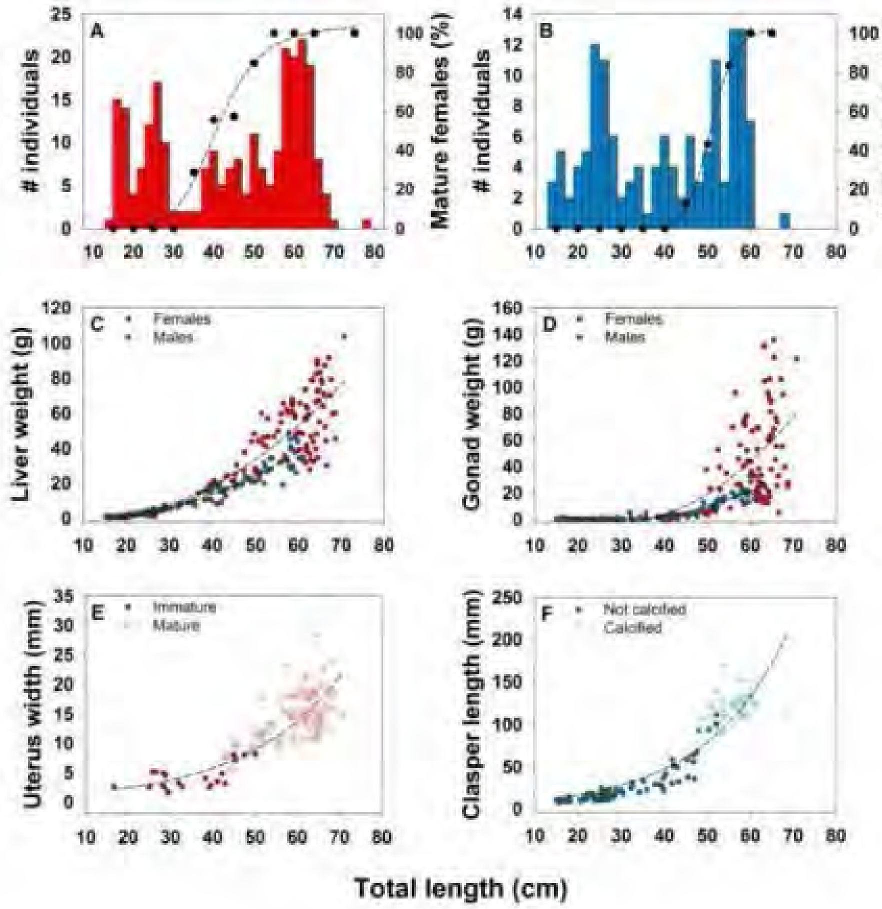
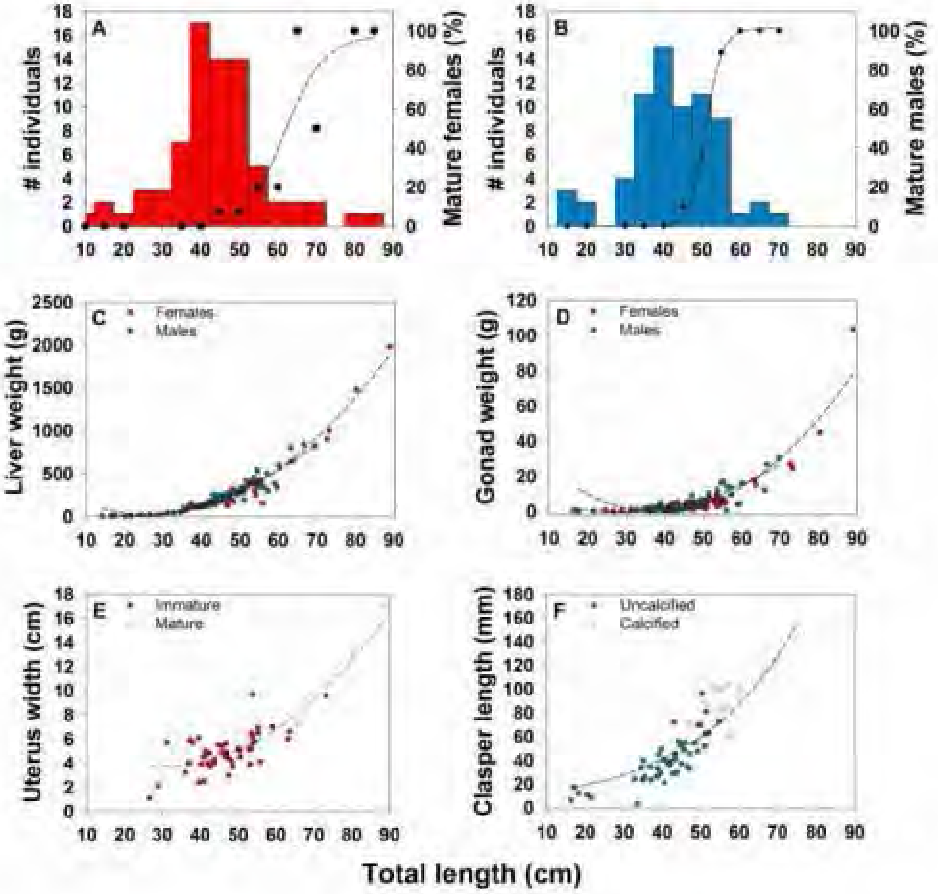

A
B
C
D
E
F
individuals
Mature females (%)
Mature males (%)
Liver weight (g)
Gonad weight (g)
Uterus width (mm)
Clasper length (mm)
Females
Males
Immature
Mature
Not calcified
Calcified
Total length (cm)
10
20
30
40
50
60
70
80

Figure 4.



A
B
individuals
Mature females (%)
Mature males (%)
0
2
4
6
8
10
12
14
16
18
0
20
40
60
80
100
10
20
30
40
50
60
70
80
90
C
Females
Males
Liver weight (g)
0
500
1000
1500
2000
2500
D
Females
Males
Gonad weight (g)
0
20
40
60
80
100
120
E
Immature
Mature
Uterus width (cm)
F
Uncalcified
Calcified
Clasper length (mm)
0
20
40
60
80
100
120
140
160
180
Total length (cm)

Figure 5.

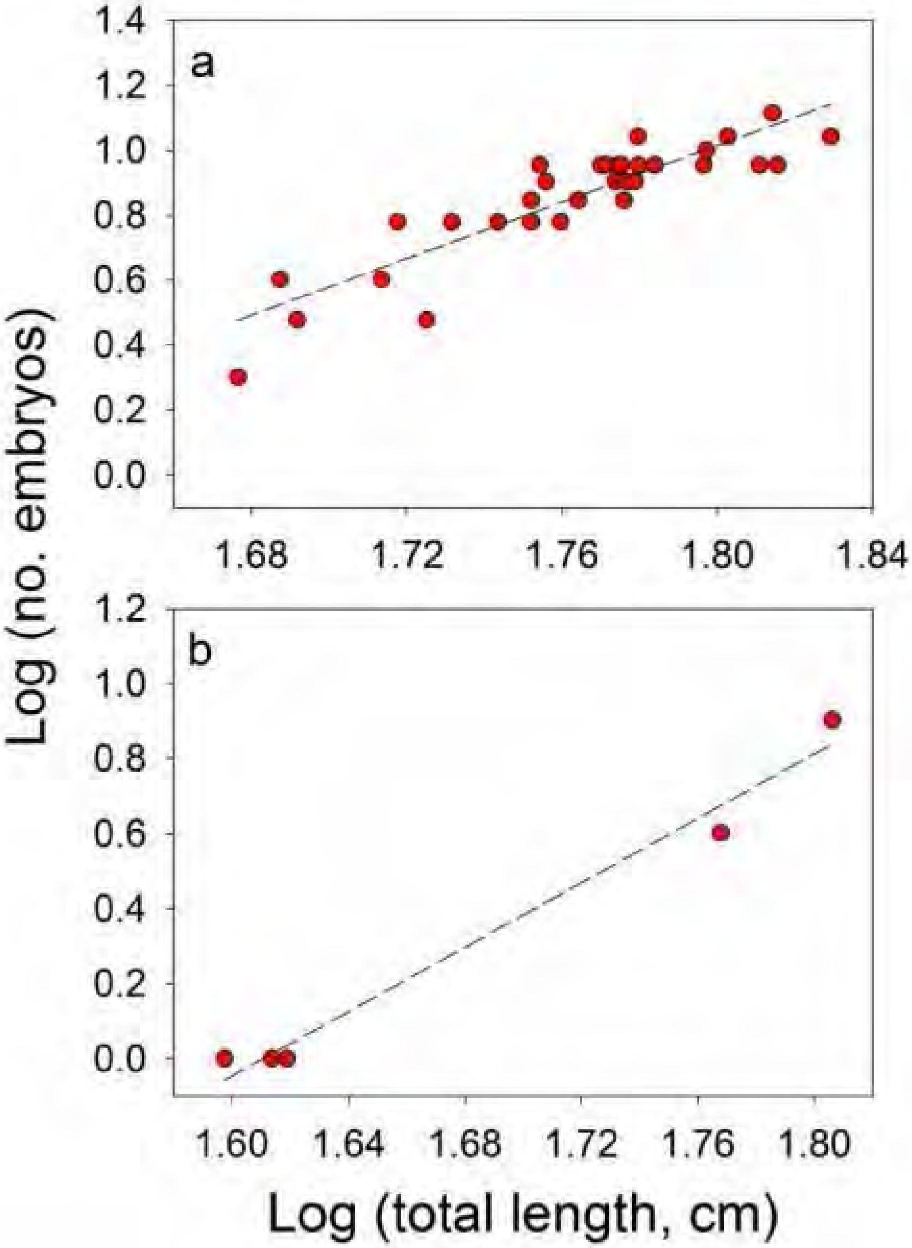
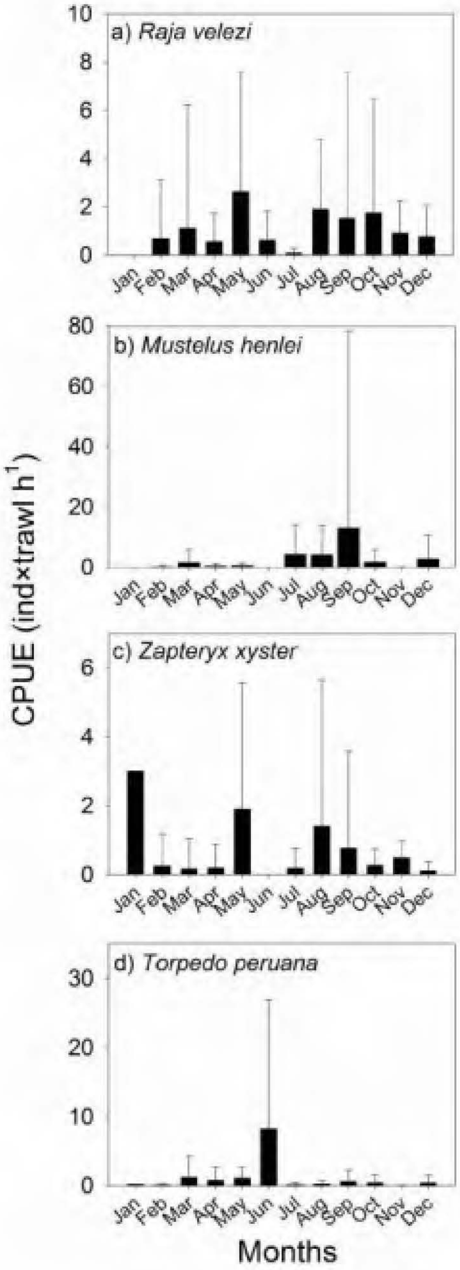

a
b
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1.68
1.72
1.76
1.80
1.84
1.60
1.64
Log (no. embryos)
Log (total length, cm)

Figure 6.



a) Raja velezi
b) Mustelus henlei
c) Zapteryx xyster
d) Torpedo peruana
CPUE (ind×trawl h^{1})
Months
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
0
2
4
6
8
10
0
20
40
60
80
0
2
4
6
0
10
20
30

Figure 7.

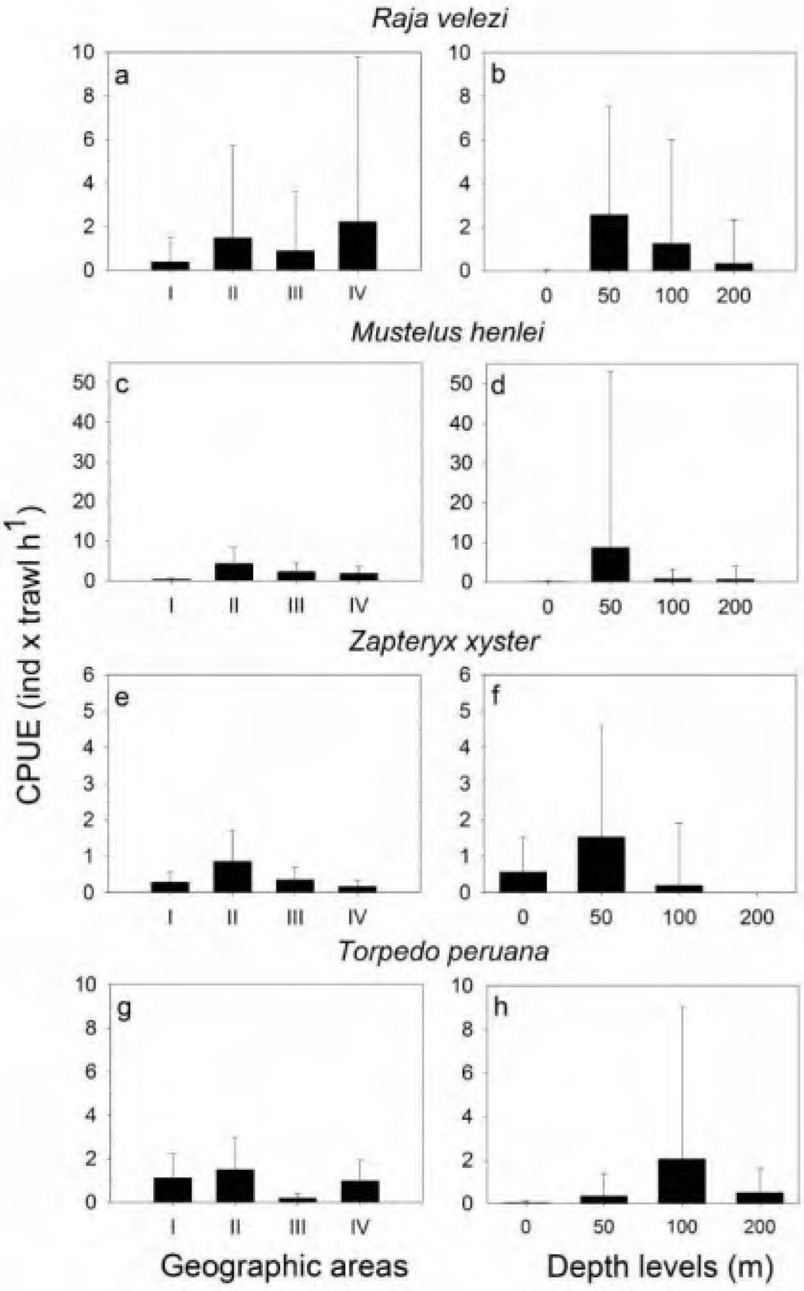

Raja velezi
a
b
0
2
4
6
8
10
I
II
III
IV
0
50
100
200
Mustelus henlei
c
d
0
10
20
30
40
50
Zapteryx xyster
e
f
0
1
2
3
4
5
6
Torpedo peruana
g
h
CPUE (ind x trawl h-1)
Geographic areas
Depth levels (m)

Figure 8.

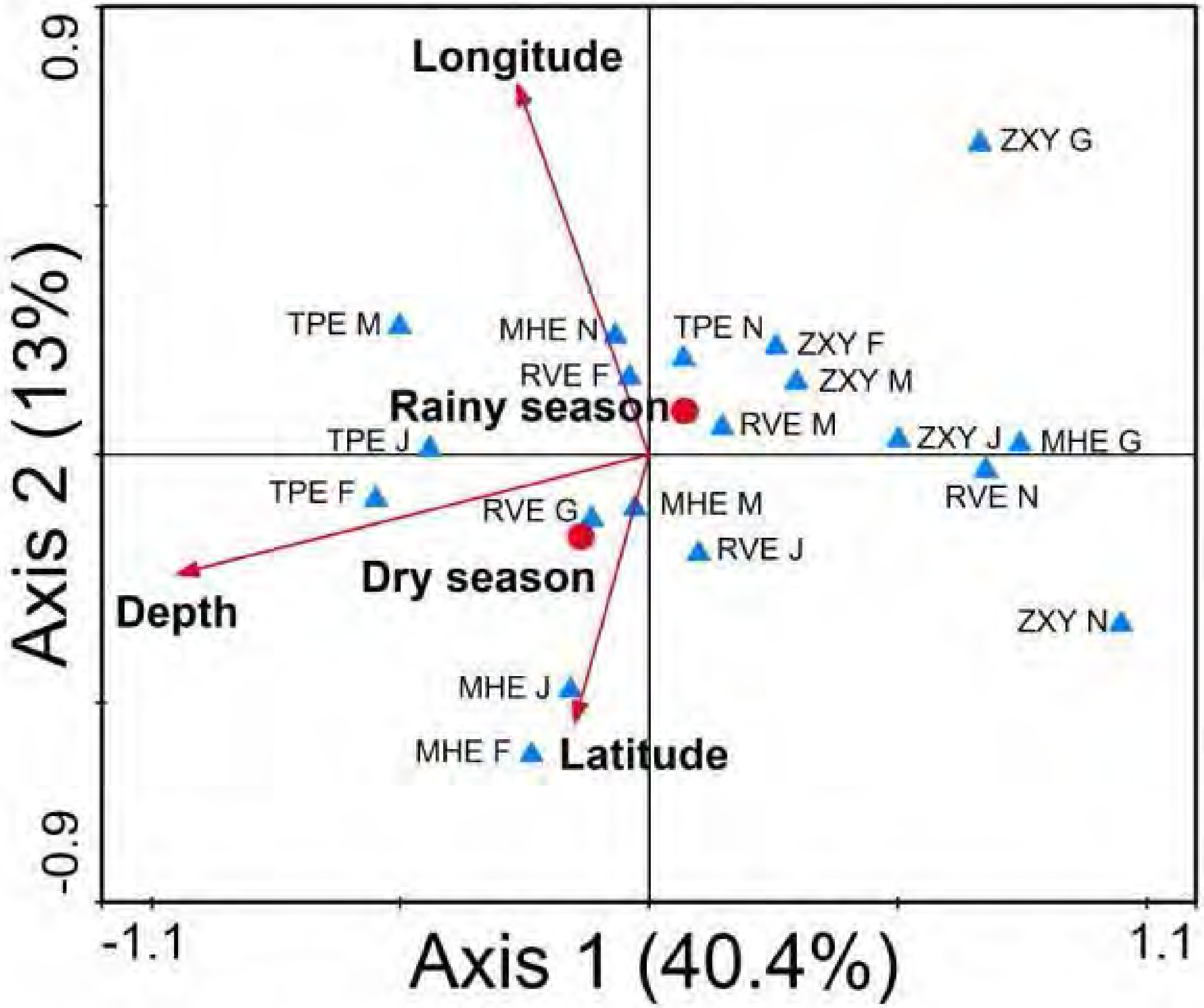

Longitude
ZXY G
TPE M
MHE N
TPE N
ZXY F
RVE F
ZXY M
Rainy season
RVE M
TPE J
ZXY J
MHE G
RVE N
TPE F
RVE G
MHE M
RVE J
Dry season
Depth
ZXY N
MHE J
MHE F
Latitude
0.9
-0.9
Axis 2 (13%)
-1.1
1.1
Axis 1 (40.4%)

Figure 9.

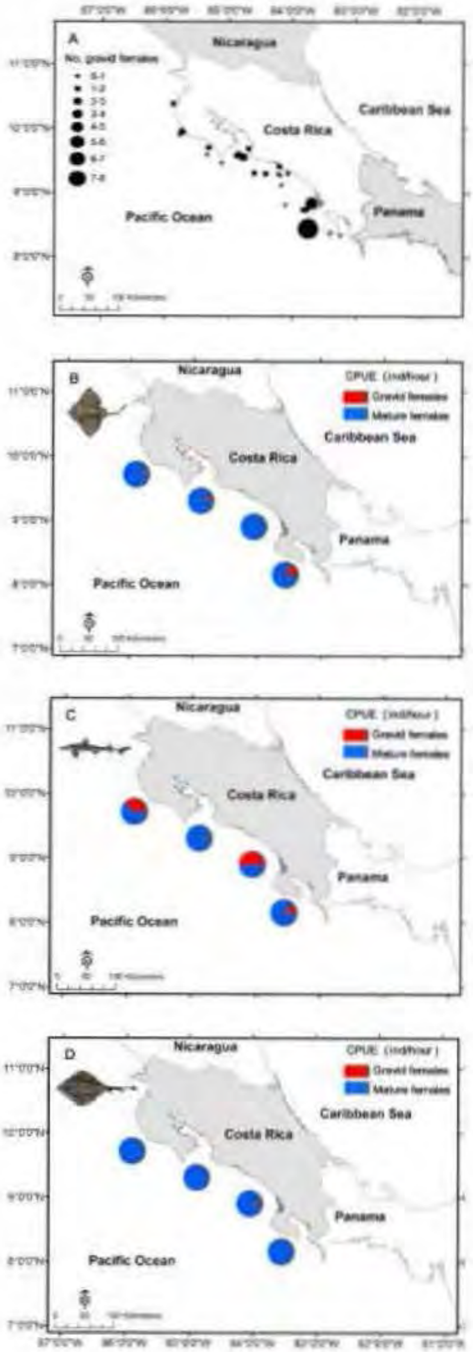

A
No. gravid females
Nicaragua
Costa Rica
Caribbean Sea
Panama
Pacific Ocean
B
C
D
CPUE (ind/hour)
Gravid females
Mature females
11°0'0"N
10°0'0"N
9°0'0"N
8°0'0"N
7°0'0"N

Figure 10 .

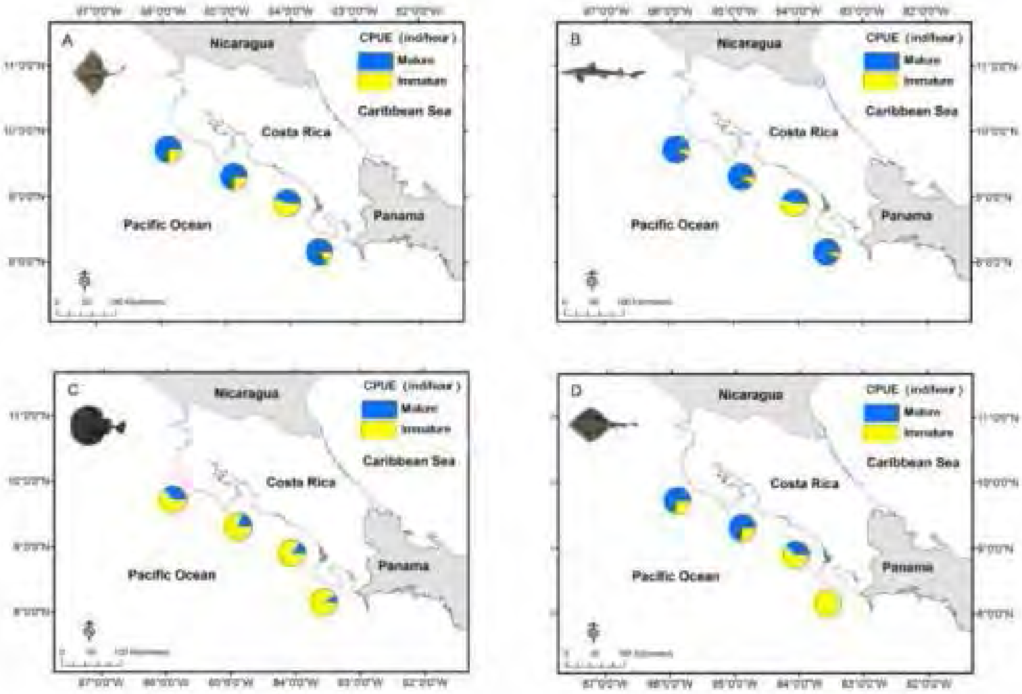

A
B
C
D
Nicaragua
Costa Rica
Panama
Caribbean Sea
Pacific Ocean
CPUE (ind/hour)
Mature
Immature
87°0'0"W
86°0'0"W
85°0'0"W
84°0'0"W
83°0'0"W
82°0'0"W
11°0'0"N
10°0'0"N
9°0'0"N
8°0'0"N
0 50 100 Kilometers

Figure 11.

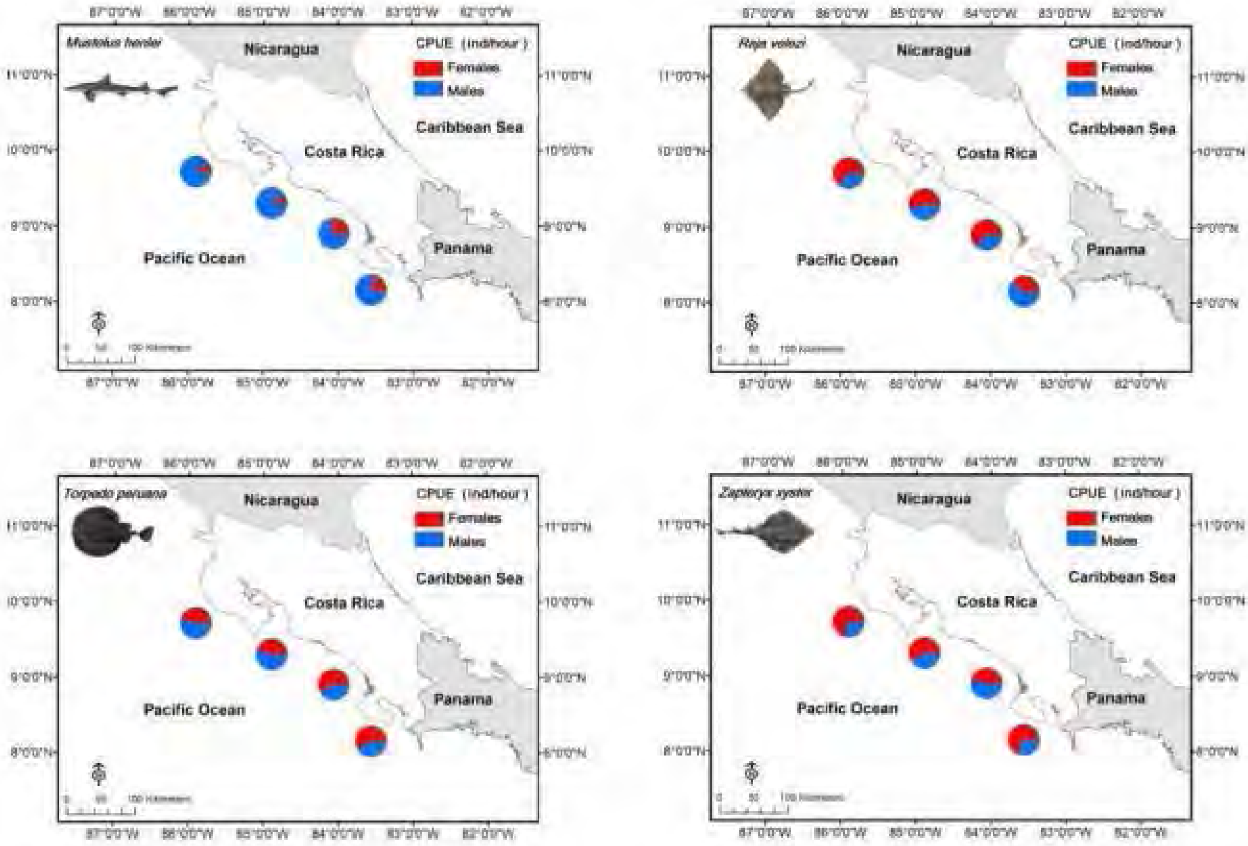

Mustelus henlei
Raja velezi
Torpedo peruana
Zapteryx xyster
Nicaragua
Costa Rica
Panama
Caribbean Sea
Pacific Ocean
CPUE (ind/hour)
Females
Males
87°0'0"W
86°0'0"W
85°0'0"W
84°0'0"W
83°0'0"W
82°0'0"W
11°0'0"N
10°0'0"N
9°0'0"N
8°0'0"N
0
50
100 Kilometers

Figure 12.

CHAPTER III

CHAPTER III

Sharks and rays as bycatch in tropical shrimp-trawling fisheries: review of the current research situation and management measures for the Pacific coast of Costa Rica and Central America

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ABSTRACT

Here we formulate management recommendations based on anreview of the regional management framework for elasmobranch bycatch on the shrimp fishery and the biological information generated in a research program conducted in Costa Rica. Current management strategies that benefit sharks and rays are oriented towards the reduction of fishing effort, regulation of fishing gear, management of fisheries data and research. However, specific regulations on bycatch within the shrimp fishery are extremely rare, and regulations for elasmobranch bycatch are non-existent in Central America. The review of the shrimp fishery's management framework in Central America and ecological research conducted in the region indicate that three main issues should be addressed in order to improve elasmobranch conservation: (1) Reduction of the fishery trawling impact on the environment, (2) Long-term conservation of sharks and rays, (3) Assessment of species vulnerability towards current shrimp fishing pressure. In conclusion, the most vulnerable species from Pacific Costa Rica are *Sphyrna lewini, Mustelus henlei, M. lunulatus, Dasyatis longa, Raja velezi, Zapteryx xyster, Echinorhinus cookei, Squatina californica, Narcine entemedor*and *Torpedo peruana.* Shrimp trawl fisheries in Central America are very similar and therefore a solution should be regional.

KEYWORDS: *elasmobranchs, Eastern Tropical Pacific, management framework*

INTRODUCTION

Elasmobranchs provide valuable ecosystem services, which stem from their role as top predators in aquatic food webs(Cortés 1999). They are a fundamental factor in the population dynamics of their prey and regulate the densities of certain populations (Heithaus 2004).Not all elasmobranchs are keystone predators, but those who prey on species with slow growth rates or that play an important role in structuring and regulating communities have a higher importance within marine ecosystems (Heithaus 2004). Additionally, sharks and rays have an impact onecosystem structure by influencing the behaviour of many species (Heithaus 2004) and by transferring biomass and energy between ecosystems (Beamish*et al.* 2005).

Elasmobranchs also provide a wide variety of consumptive and non-consumptive uses (Walker 2005). Meat, fins, liver and skin are by far the most commonly utilizedproducts. Shark meat has been an important source of protein forcoastal communitiesfor more than 5000 years. However, in recent decades, fins have been the highest valued shark product, which has lead to the unsustainable practice of finning (Lack and Sant 2009). Shark skin, bile, cartilage and liver have also been very important in traditional and non-traditional medicine (García-Núñez 2008).Some less common uses for sharks include: liver extracts for hidrocarbons, oil, agriculture, textile industry, cosmetics; jaws, teeth, preserved sharks and sawfish rostra as curios; bait; dissections; fishmeal; fertilizer (Musick 2005).Non consumptive uses include education, recreational diving and catch and release sportfishing (Camhi *et al.* 2009). As elasmobranchs provide both valuable ecosystem services and human uses, these two benefits must be balanced. However, this sustainability has not been attained and intense fishing pressure caused a phenomena coined “fishing down marine food webs” (Pauly *et al.* 1998, Pauly & Palomares

2005). The reduction in elasmobranch abundance described by this phenomenon has caused trophic cascades due to predator release and competitive release (Stevens *et al.* 2000). Several cases have been documented in the Gulf of Mexico (Sheperd & Myers 2005) in which the functional extinction of sharks has caused changes in the trophic structure of has caused trophic cascades. This has caused negative ecological and economic impacts produced by changes in predator prey relationships.

Most elasmobranch worldwide catches occurby incidental fisheries, e.g. bottom trawling (Barker and Schluessel 2005). Although some of the catch is landed and reported, estimates indicate that 200 000 MT are discarded every year and therefore remains unreported (Barker and Schluessel 2005, Kelleher 2005). The high vulnerability of elasmobranchs to fishing pressure coupled with the lack of catch records may result in an unnoticed, yet drastic reduction of population sizes (Casey and Myers 1998, Dulvy *et al.* 2000, Stevens *et al.* 2000, Dulvy and Forest 2010). Declines in demersal shark and ray populations caused by trawling fisheries have been documented in Australia (Graham *et al.* 2001), the Mediterannean Sea, Irish Sea, the North Sea, the Gulf of Thailand, North West Atlantic (Stevens *et al.* 2000) and the northeast Atlantic (Dulvy and Forrest 2010).

Recuperation periods for most shark and ray species are extensive and therefore, the precautionary principle should be applied to the management of elasmobranch fisheries(FAO 2000, King and McFarlane 2003, Walker 2005). Elasmobranch bycatch reduction should be established as a priority (Musick 2000). However, current efforts concentrate on pelagic fisheries, with little concrete efforts to manage demersal fisheries (Barker and Schluessel 2005). The management of elasmobranch fisheries in general is deficient or absent in developing countries, where 60% of all reported shark catches occur (Barker and Schluessel 2005).

The shrimp-trawling fishery along the Pacific coast of Central America is currently operating at an unsustainable level that has led to the overexploitation of most target species (Arrivillaga 2003, Fuentes 2007, FIINPESCA 2007, Arauz 2008, López-Mendoza 2009, Herrera-Ulloa *et al.* 2011). Total shrimp and bycatch landings in Costa Rica have decreased since 1987 (Trujillo *et al.* 2012). Overfishing in the region has also caused both a decline in the average trophic level of bycatchand a shift in the demersal community structure (López-Mendoza 2009, Wehrtmann and Nielsen-Muñoz 2009, Álvarez and Ross-Salazar 2010). However, the impact of this bottom-trawl fishery on elasmobranch populations has not been examined yet.

The Pacific shrimp-trawling fisheries in Central America are comparable in terms of fleet sizes, vessel traits, target species, resource status and bycatch levels (FIINPESCA 2007), as well asthe species composition of the elasmobranch bycatch (Ixquiac-Cabrera *et al.* 2010, López-Martínez *et al.* 2010, Clarke *et al.* 2011). Therefore, a proposed management framework should have a regional approach (FIINPESCA 2007). Current approaches to tropical shrimp fishery management are typically focused on target species, despite the impacts on the entire ecosystem (Herrera-Ulloa*et al.* 2011). Currently, many studies support community ecology based management strategies, which consider the fishery's impact on vulnerable bycatch groups (e.g. sharks and rays) (King and McFarlane 2003, Mangel and Levin 2005, Herrera-Ulloa *et al.* 2011).

The objectives of this study are to analyze the current management framework for elasmobranch bycatch in the shrimp fishery along the Pacific coast of Central America and identify gaps. In addition, we review the biological information available for the elasmobranch bycatch in this fishery. The overall goal is to formulate management strategies and assess species vulnerability based on the analysis of the current framework and available information on elasmobranch bycatch in the shrimp fishery.

METHODS

Study area

Costa Rica, like the rest of the Central American isthmus, is bordered by the Eastern Tropical Pacific Ocean on the west. Its Pacific coast is approximately 1254 km long and very irregular, with three large gulfs,many bays, coves and a large delta (Wehrtmann and Cortés 2009, Fig. 1). The Pacific continental platform of Costa Rica comprises15 600 km^2, with a continental slope that is generally steep and close to the coastline. There are four major geographic areas defined by oceanographic conditions (see Wehrtmann and Cortés 2009): (1) Area I: north Pacific, with seasonal upwelling occurring between November and April; (2) Area II: Central Pacific, influenced by a large estuarine system,Golfo de Nicoya; (3) Area III: central Pacific influenced by a large estuarine mangrove system, the Humedal Nacional Térraba-Sierpe (HNTS); and (4) Area IV: southern Pacific, which includes the Golfo Dulce, a tropical fjord (Wehrtmann and Cortés 2009).

Management measures

Recommendations for the management of elasmobranch bycatch associated with the shrimp fishery in the Costa Rican Pacific are presented based on ecological criteria (c.f Chapters 1 and 2).In addition, a review of management measures in Central America provides the basis for an analysis at the regional scale.

Ecological studies in Costa Rica

Ecological information on elasmobranch bycatch of the shrimp fishery was obtained from the following projects of the Unidad de Investigación Pesquera y Acuicultura (Fisheries and Aquaculture Research Unit; UNIP) of the Centro de Investigación en Ciencias del Mar y Limnología (Marine Science and Limnology Research Center; CIMAR)of the Universidad de Costa Rica (University of Costa Rica; UCR): (1) "Deepwater carcinofauna and its sustainable use in Costa Rica: a regional initiative" (UCR-VI project N° 808-A9-537); (2) "Development of standards for the sustainable development of the camello shrimp (*Heterocarpus vicarius*)" (UCR-VI project N° VI 111-A4-508); (3) "Demersal sharks and rays of the Pacific continental platform of Costa Rica: identification of reproduction sites and the elaboration of recommendations for their sustainable management" (UCR-VI project N° 808-B0-536), and (4) "Shark and ray parasites (UCR-VI project N° 808-B1-537). All these projects were supported by the company The Rainbow Jewels S.A. (Puntarenas), which facilitated the use of their shrimp vessels for research. Samples were collected from a monthly scientific monitoring program between May 2010 and September 2011, and an annual scientific survey carried out from 2008 to 2011 (for more details on field work see Wehrtmann and Nielsen-Muñoz 2009; Clarke *et al.* 2011; for details on laboratory and data analysis see Clarke *et al.* 2011; Espinoza *et al.* 2012). The aim of these research activities was to generate information on the biology and ecology (e.g., diversity, distribution, life history traits, feeding habits,parasites) of sharks and rays, which would eventually help develop management strategies for sharks and rays in the shrimp fishery.

The management measures proposed below are also supported by a review of management techniques for shark and ray bycatch in Central American shrimp fisheries. Given that the management of trans-boundary stocks such as elasmobranchs,this review focused on Central America. Legislation on shrimp fishery and elasmobranch management for each country in the region was examined.

RESULTS AND DISCUSSION

During this revision, over 80 technical reports, official management documents and scientific articles were consulted. Main topics were bycatch in shrimp fisheries; description, management and legislation of shrimp fisheries in Central America; case studies on the successful implementation of management measures and fisheries science.Current management strategies for the shrimp trawling fisheries in Central America that may benefit sharks and rays are oriented towards the reduction of fishing effort, regulation of fishing gear, management of fisheries data and research (Table 1). Regulations on bycatch within the shrimp fishery are extremely rare, and regulations for elasmobranch bycatch are non-existent in Central America. The review of the shrimp fishery's management framework in Central America and ecological research conducted in the region indicate that three major issues should be addressed in order to improve elasmobranch conservation: (1) Reduction of the bottom trawling impact on the environment; (2) Long-term conservation strategies for sharks and rays; (3) Assessment of species vulnerability under current shrimp fishing pressure.

▶ISSUE 1: *Reduction of trawling fishery's environmental impact*

Ecological overview

An increasing number of studies have demonstrated the negative effect of trawling on marine demersal ecosystems (Jennings *et al.*1999, Thrush *et al.* 2002, Althaus *et al.* 2009, Munga *et al.* 2012). Trawling alters species diversity and community structure through habitat destruction, high mortality and by providing excess food for scavengers (Kaiser and Spencer 1994). As a consequence, bottom trawling impacts sharks and rays not only by fishing mortality, but by habitat destruction as well.

The management strategies presented in this section are oriented towards reducing the shrimp fishery's impact on the demersal ecosystem by improving gear selectivity and implementing catch restrictions. The Costa Rican shrimp fishery presents high bycatch rates (Wehrtmann and Nielsen-Muñoz 2009, Arana et al., in press.), especially in shallow, coastal areas (0-100 m depth range) (Clarke *et al.* 2011, Trujillo *et al.* 2012). Average discard rate estimates were of 50% of the bycatch in the shallow water shrimp fishery and 100% of the bycatch in the deepwater shrimp fishery (Clarke *et al.* 2011, Trujillo *et al.* 2012, Wehrtmann *et al.* 2012). Discards include 23 elasmobranch, 67 fish, 32 crustacean and 25 mollusk species (Wehrtmann and Echeverría-Sáenz 2007, Clarke *et al.* 2011, Arana *et al.* in press.). Approximately 50% of the bycatch in the shallow-water shrimp fishery and 100% of the bycatch in the deepwater shrimp fishery is not commercialized and thus, discarded (Gutierrez 2001, Marín 2001, Trujillo *et al.* 2012).

Twenty-nine commercial trawls conducted in shallow waters (10 - 60 m deep) during 2010 and 2011 (cf. Chapter 1) revealed that 90% of the catch at this depth level consisted of commercial and non-commercial fish, including 20 species of sharks and rays. The December-April period is known for its high commercial fish abundance and therefore, fishermen mainly target commercial fish during that season (R. Villalobos, The Rainbow Jewels S.A., pers.

comm.). Though they do not have the same seasonal patterns as bony fish, adult longtail stingrays (*Dasyatis longa*) and sicklefin smooth-hounds (*Mustelus lunulatus*) were also landed and sold for human consumption in Costa Rica (López-Garro *et al.* 2009, F. Villalobos pers. com., J. Picado pers. comm., Clarke *et al.* in prep).

Management strategies in Central America

*Gear selectivity.*Measures to increase gear selectivity have been implemented in the form of mandatory Bycatch Reduction Devices (BRDs) and net mesh size regulations. All Central American countries legally require the use of Turtle Excluder Devices (TEDs) in shallow-water shrimp operations (Table 1; Cajiao-Jiménez 2003, FAO 2004b, d, Fuentes 2007, Lopez-Mendoza 2009).

Panama, Costa Rica and El Salvador have studied the efficiency of additional BRDs in their trawling fisheries with positive results; however, these BRDs are not currently implemented in their fisheries management plans (García *et al.* 2008, Marchena-Sanabria *et al.* 2008, López-Mendoza 2009). All Central American countries also regulate mesh sizes, though regulations are not consistent throughout the region (Table 1) (FIINPESCA 2007).

Bycatch restrictions. In contrast, only two Central American countries have established catch limits (Table 1). Nicaragua considers shrimp resources fully exploited and therefore manages it through a limited access regime, with annual global quotas (FAO 2004b). However, regulations do not exist for bycatch landings, and enforcement of existent regulations remains weak (FAO 2004b) (Table 1).

Recommendations

In order to reduce the amount of bycatch, we recommend the implementation of additional BRDs in the shrimp fishery and the establishment of limitsfor landed non-target products (Table 2). The high diversity of elasmobranchs, bony fish, crustaceans and mollusks that comprise the trawling bycatch is a challenge to the development and implementation of effective BRDs (Stobutzki *et al.* 2001). However, experimental research on the design and implementation of BRDs in the Gulf of Mexico, Gulf of California, Mexico, Panama, Colombia, Chile and Australia have yielded positive results concerning overall bycatch, especially for large (>1 m) individuals, such as elasmobranchs (Quevedo-Heredia 2001). Quevedo-Heredia (2001) indicated that rigid TEDs with guiding funnels coupled with a square mesh window resulted in the highest fish exclusion and lowest shrimp loss. Additionally, the efficiency of modified nets that successfully reduced bycatch in Chile`s *Heterocarpus reedi* fishery should be tested in the Costa Rican deep water *Heterocarpus vicarius* fishery, as they operate at similar depths and present similar catch compositions (Queirolo *et al.* 2011a,b, Arana *et al.* in press).

Three common requirements for the successful implementation of BRDs are (Cox *et al.* 2007): (1) long-standing collaborations between the fishery, scientific and management sectors, (2) fishery monitoring programs that cover the time period before and after BRD implementation, and (3) appropriate enforcement. The success of BRD implementation in Queensland, Australia, was partially due to the involvement of the fishery sector, which designed BRDs to suit catch composition in their fishing grounds (Robins *et al.* 1999). In contrast, fishermen in Costa Rica often have a negative attitude towards the use of BRDs because bycatch is considered an opportunity, not a problem (Herrera-Ulloa 2001). When shrimp abundance is low, they target high-value fish to supplement their income. The proper implementation of TEDs does not occur due to the desire to minimize loss of large commercial fish (Marín 2001, Stobutzki *et al.* 2002, T. Clarke obs. pers.). This aspect should be improved, as the correct use of TEDs can reduce the catch of large fish, such as sharks and rays (Table 2).

According to the Costa Rican fishery law, licenses granted to trawlers legally allow them to only target shrimp, not fish (Ley 8436 Costa Rica, 2005). Although approximately 50% of the bycatch in the shallow-water shrimp fishery is landed these landings are not recorded by the fisheries authorities. It is estimated that 451,000 MT of bycatch have been landed between 1950 and 2008 (Trujillo *et al.* 2012). To prevent this situation, we recommend that a maximum of 25% of landing weight may be of bycatch destined for human consumption, all of which must be included in national fishery statistics. The remaining bycatch must be discarded, or used as fishmeal. To encourage the release of live specimens, we also suggest that landing sharks and rays should be prohibited, due to their vulnerability (Table 2). Many of the elasmobranchs are alive when caught, and survival may be high if discarded immediately (Stobutzki *et al.* 2002, Laptikhovsky 2004, Cedrola *et al.* 2005, Enever *et al.* 2009). There is a high degree of overlap between fish species targeted by the shrimp trawlers and coastal artisanal fisheries. Therefore, the above-mentioned measures are designed to deter shrimpers from targeting fish in order to reduce competition with the artisanal fishery. An additional action to enforce this measure is to close the trawling fishery when shrimp abundance is low, between December and April of each year (Table 2).

▶*ISSUE 2: Conservation of sharks and rays*

Ecological overview

The low rate of population increase that is characteristic of elasmobranchs, implies that a low percentage of the population should be extracted to ensure the maintenance of a sustainable fishery (Walker 2005). This measure has not been applied in most fisheries and therefore, a large number of species have suffered from drastic population reductions (Camhi *et al.* 1998). In data poor situations, it has been suggested that shark fisheries should be managed as K-selected species rather than teleost or invertebrate fisheries (Walker 2005). As a consequence, the management measures proposed in this section are aimed towards improving fishery data collection and management and the reduction of fishing effort (e.g. fishing closures, license restrictions).

The elasmobranch bycatch of the Costa Rican shrimp fishery is composed of23 species with only adults of two species (*M. lunulatus* and *D. longa*) being retained (Clarke *et al.* 2011). Additional fishing pressure is exerted by coastal artisanal or longline fisheries on several species (*D. longa, M. henlei*, *M. lunulatus,Rhizoprionodon longurio* and *Sphyrna lewini*) (Porras *et al.* 1993, Proambiente 1999, Arauz *et al.* 2004, Lopez-Garro *et al.* 2009, Zanella *et al.* 2009, Clarke *et al.* 2011, Whorisky *et al.* 2011). As a consequence of the wide distribution ranges (Table X), these species are also subjected to fishing pressures from both national and neighboring fleets (Allen and Robertson 1994, Proambiente 1999, Mejía-Falla and Navia 2012), making a regional approach to fishery management necessary.

Information on elasmobranch diversity, distribution, reproductive ecology and feeding habits were used herein to detect highly priority areas for elasmobranch conservation. The results highlight the importance of shallow areas along the Central Pacific coast of Costa Rica (Clarke *et al.* 2011). These areas were characterized by: (1) the highest shark and ray diversity; (2) pupping areas with high proportions of immature individuals and gravid females (Clarke *et al.* 2011); (3) a high overlap in target resources between juvenile elasmobranchs and the shrimp fishery (immature individuals consumed higher proportions of crustaceans while adults consumed larger proportions of fish) (Espinoza *et al.* in press, Espinoza *et al.* 2012).

Pupping areas were located mainly in shallow waters (<50 m) surrounding coastal wetlands, such as Quepos-Manuel Antonio, and the Humedal Nacional Térraba-Sierpe (HNTS). Although they may be nursery areas, further studies are needed to corroborate this by assessing seasonal patterns of habitat use and confirming long-term occupation by neonates and pregnant females (Heupel *et al.* 2007). The wetland with the highest abundance of gravid females and neonates was the HNTS (Clarke *et al.* 2011). The importance of HNTS for elasmobranch and other ecological groups justifies the creation of a biological corridor between the Marino Ballena National Park, HNTS and Reserva Biológica Isla del Caño, delimited by the 50 m depth contour (Table 3, Fig. 2) (Quesada-Alpízar and Cortés 2006, Clarke *et al.* 2011). However, more studies are needed to identify areas that may function as nurseries along the Pacific coast of Costa Rica, especially HNTS.

Although shallow waters are undeniably important, deeper waters are important as well, because they contain a smaller number of larger, slower growing species that tend to be more vulnerable. Therefore, fishing effort should not be displaced, it should be reduced.In addition to the protection of nursery and pupping areas, regulations (e.g. reduction of fishing effort) must protect adults to avoid drastic population declines (Kinney *et al.* 2009).

Management measures in Central America

*Data collection.*Onboard observer programs for the shrimp fishery do not exist in Central America. However, information on elasmobranch bycatch has been generated in Guatemala and Costa Rica (Table 1).

Fishing closures. All Central American countries have established a series of Marine Protected Areas (MPA) closed to fishing that aid in the recuperation and conservation of marine ecosystems (Rodríguez and Windevoxhel 1998, Alvarado *et al.* 2012). Although they do not protect the 10% of their EEZs recommended for the conservation of marine biodiversity (IUCN), they are an essential component in the management of every fishery (FAO 2000, Rodrigues *et al.* 2004, Walker 2005). Several countries in the region, such as Guatemala, Nicaragua and Costa Rica, are in the process of creating new MPAs (UICN 1998, Quesada-Alpízar 2006).

Seasonal fishing closures (SFC) are applied by all Central American countries with the exception of Guatemala (FAO 2004a) (Table 1). Guatemala eliminated its previously established SFC due to pressure from the shrimp fishing sector, in exchange for larger net mesh sizes. However, the fishing sector has not upheld its side of the deal (FAO 2004a). El Salvador established a permanent closure for the shrimp fishery along the first three miles off the coast, as well as SFCs ranging from one to two months (López-Mendoza 2009, Rivera 2011). Nicaragua initially applied fishing closures in the Pacific (FAO 2004a), and closed the industrial shrimp fishery for a one-year period in response to drastic declines in shrimp landings. During this period, the government stimulated the development of economic alternatives such as a fishery for unconventional resources (e.g., the squat lobster *Pleuronchodes planipes*) and aquacultural production of shrimp (FIINPESCA 2007). In Costa Rica, permanent fishing closures protect several estuarine environments and productive coastal wetlands, such as the internal zone of the Golfo de Nicoya (A.J.D.I.P Nº 221-2009 from 30 July 2009), the internal zone of Golfo Dulce, and all estuaries(Artículo 46, Ley de Pesca de Costa Rica, Acuerdo de Junta Directiva del INCOPESCA Nº 051-1995 from 23 March 1995) (Cajiao-Jiménez *et al.* 2003). In addition, SFCs in Costa Rica are set in estuarine systems of reproductive importance for shrimps such as the external region of Golfo de Nicoya (Acuerdo de Junta Directiva del INCOPESCA Nº 051-1995 from 23 March 1995,A.J.D.I.P Nº 221-2009 from 30 July 2009) (FAO 2004c). Panama established permanent fishing closures in nursery areas, estuaries, set a 70-day SFC from February to April, and restricted fishing days to 19 per month from September to February (FAO 2004d). These fishing closures have been established primarily as a management measure to protect shrimp resources; they may, however, also help to protect shark and ray essential habitats (FAO 2000).

Although it is assumed that neighboring countries share shrimp stocks, fishing closures are not coordinated on a regional level (FIINPESCA 2007). While fishing closures in most countries are set during the reproductive season of the target species, in other countries they are set during the lowest catch seasons (FIINPESCA 2007).

License restrictions. License restrictions are also a very common management tool used to decrease fishing effort (Table 1). All countries except Costa Rica do not grant new licenses to enter the shrimp fishery (Table 1). Maximum fleet sizes have been set at 90 in El Salvador (López-Mendoza 2009), and at 232 in Panama (FAO 2004d). Panama also prohibits new vessels from entering the fishery with the goal of gradually reducing the fleet size (Arauz 2008). Major reductions in the number of actively operating vessels are also occurring in the region because the fishery has reached economically unsustainable levels. Though Costa Rica does not restrict fleet size, not all shrimp vessels with licenses are currently active because of low economic returns (Álvarez and Ross-Salazar 2010). In 2009, 44 of 63 shallow-water licenses and 2 of 10 deepwater licenses were active (Álvarez and Ross-Salazar 2010).

Discussion

The impact of fishing pressure on elasmobranchs should be monitored by onboard observer programs and long-term catch tendencies should be examined (Table 3). Onboard observer programs have been successfully implemented in Canada (Benoit and Allard 2009), Greenland (Vesteergard 1996), the United States (Richards 2006) and Australia (MacBeth *et al.* 2009). The following information should be registered per fishing trip: vessel name, captain`s name, trawling speed, net size, fishing days, geographic areas, number of individuals of each species caught in each depth category, number and weight of commercialized specimens per species (Table 3).

*Fishing closures.*Closures for the trawling fishery along the Central Pacific in areas <50 m would reduce fishing pressure in areas with the highest diversity of sharks and rays (Table 3). However, parallel to creating new fishing closures, the enforcement of current fishing closures needs to be improved.True fishing closures are likely to have positive effects (Gillet 2008, Lamilla *et al.* 2008), though resistance from the industry tends to hinder the effective implementation of such measures (Patterson and Tudman 2009). Closures must be combined with other effort reduction strategies to minimize effort displacement towards deeper waters, where species tend to have slower life cycles (Morato *et al.* 2006, Patterson and Tudman 2009).

Fishing closures for the shrimp fishery have been successfully applied in the United States, Australia, New Zealand, Scotia and Italy, where large sections of the coast are closed off to trawling fisheries (Lamilla *et al.* 2008). Other countries such as Venezuela, Palaos, Oman and Indonesia have taken an extra step and have decided to eliminate completely the shrimp-trawling fishery (Lamilla *et al.* 2008). Documented benefits from applying this measure in Indonesia have been increased profitability in the artisanal fishery (Gillet 2008).

▶ *ISSUE 3: Identification of the most vulnerable species (IUCN categories)*

Ecological Overview

This section examines the vulnerability of the 23 elasmobranch bycatch species, considering both their interaction with fisheries in the region and life history traits. The degree of interaction with the shrimp fishery is associated with species habitat and distribution (depth and latitude). Highest overlaps occur in demersal, shallow-water habitats, as more semi-industrial shrimping licenses are granted for shallow waters than for deep waters (Álvarez and Ross-Salazar 2010). The number of sharks and rays caught by the shrimp fishery is assumed to be an indicator of their degree of interaction with the fishery. Due to the lack of historical catch records, traditional ecological knowledge (TEK) was used to assess mid-term catch trends (Poizat and Baran 1997, Aswani and Lauer 2006, Rasalato *et al.* 2010).

Life history strategies also determine the response of a population to fishing pressures (Dulvy *et al.* 2000, King and McFarlane 2003, Shepherd and Myers 2005). In general, species with large maximum sizes, late maturity and low fecundity have low intrinsic rates of increase and consequently are less resilient to high fishing mortality (Denney *et al.* 2002, Dulvey *et al.* 2008). Maximum size is correlated with all these parameters and therefore can be considered as a good indicator of a species' vulnerability to fishing (Denney *et al.* 2002). Maximum size is also positively correlated with trophic level (Cortés 1999, Espinoza *et al.* in prep.). The elasmobranch species considered to be most vulnerable are subjected to high fishing pressures and present decreasing trends of abundance, comparatively large sizes, low fecundity and high trophic levels (Dulvy and Forest 2010).

Typical behavior displayed by sharks and rays associated to the Costa Rican shrimp fishery, such as aggregation, sex and size segregation can increase the negative impact of the fishery on these species. As a consequence, trawlers can affect one life-cycle stage of the population more than others. Theoretically, the proportion of immature individuals caught by the fishery is positively correlated with the fishery's impact on the population.

In conclusion, the most vulnerable species from Pacific Costa Rica are *Raja velezi, Mustelus henlei, Mustelus lunulatus,Dasyatis longa, Zapteryx xyster, Sphyrna lewini, Echinorhinus cookei, Squatina californica* and *Torpedo peruana.* Special attention should be paid to *D. longa*and*M. lunulatus* as they are commercially exploited. Although these two species are not commonly caught in the shrimp fishery, they may become a target species, because they are commercialized for meat. *Dasyatis longa* and *M. lunulatus* are mainly alive when caught, so survival may be high if discarded and handling practices are improved. Though long-term catch trends are not available for Costa Rica, abundance of *M. lunulatus* and *D. longa* has been drastically reduced in Colombia since the early 1990s, when they were important commercial species (Mejia-Falla and Navia 2012). It is probable that similar trends are occurring in Costa Rica and neighboring countries due to the high fishing pressure from the artisanal and shrimp trawling fisheries (López-Garro *et al.* 2009); however, the lack of available data prevents reaching solid conclusions.

Discussion

Raja velezi.Raja velezi is one of the most abundant species and occupies a depth range of 30-300 m, though it is most abundant between 50 and 100 m deep. This skate is not commercially utilized and 100% of all catches are discarded. *Raja velezi* is overall one of the largest species within the bycatch, with a maximum size of 85.6 cm TL and a maturity size of 52.2 cm TL in females and 56 cm TL in males (Clarke *et al.* 2011). The relatively large sizes at which skates mature in proportion to their maximum size make them particularly sensitive to fishing pressure and overexploitation (Henderson *et al.* 2005). However, the biological and physiological requirements of oviparous elasmobranchs may be different from those of viviparous species, such that egg layers do not need to grow after attaining sexual maturity (Ebert *et al.* 2008). Further informationis needed to complete reproductive information of *R. velezi*.

All life stages of *Raja velezi* are caught by the shrimp-trawling fishery. This species segregates by size, with smaller skates found in shallower waters, where high fishing pressure is exerted by the shrimp fishery. A higher abundance of neonates is found in discrete reproductively important locations such as the HNTS. *Raja velezi* occupies amid-level trophic position and undergoes ontogenetic dietary shifts. Its diet overlaps very little with *M. henlei*,the second most common elasmobranch inhabiting the same depth level. The diet of *R. velezi* consists mainly of shrimp, which overlaps with the shrimp fishery's target resource (Espinoza *et al.* in prep.).

*Mustelus henlei.*This species is the elasmobranch with one of the highest catches in both the Costa Rican shrimp fishery and the artisanal fishery. It is distributed mainly from 0-250 m, and is most abundant between 50 and 100 m deep. *Mustelus henlei* is landed by artisanal fisheries, but generally discarded in shrimp fisheries due to its small size. This shark can reach up to 66.5 cm TL, with maturity sizes of 42.8 cm TL in females and 39.1 cm TL in males. It is a viviparous species with small litter sizes, which implies that they have very small population doubling potential.

Mustelus henlei is caught by the shrimp fishery throughout its entire life cycle. The species segregates by sex and size. *Mustelus henlei* has discrete pupping areas in shallow waters, mainly in HNTS and the mangroves of Playa Coyote (Clarke *et al.* in prep.). They form reproductive aggregations in areas known to fishermen during September-October and February-March, which allow them to capture large numbers of sharks (200 sharks in one night) (PROAMBIENTE 1999). TEK indicates that the abundance of this shark has decreased in the past decades. Female brown smooth-hounds (*M. henlei*) are in general less abundant than males. This is possibly because female aggregations are formed in shallow waters, where higher fishing efforts are exerted by both the trawling and artisanal fisheries (Rojas *et al.* 2000, Álvarez and Ross-Salazar 2009, López-Garro *et al.* 2009).

Mustelus lunulatus.Mustelus lunulatus is not a common component of the shrimp fishery bycatch. It inhabits depths up to 100 m, but is more abundant between 50 and 100 m deep. When caught in the shrimp fishery, large specimens are landed. In addition, the species is targeted by artisanal fisheries. *Mustelus lunulatus* is relatively large (up to 170 cm TL), and its size at maturity has not yet been estimated.

Mustelus lunulatus forms aggregations and segregates by size and sex. The majority of sharks caught by the shrimp fishery are immature males. Though long-term catch trends do not exist for Costa Rica, TEK suggests that the population size has decreased in the past decades. Decreasing trends have also been observed in Colombia since the early 1990s, when it was one of the most important commercial species (Mejía-Falla and Navía 2011). It is probable that similar trends are occurring in Costa Rica due to high fishing pressure from the artisanal fishery (Golfo Dulce, Golfo de Nicoya: Misión Tiburón). The trophic level of *Mustelus lunulatus* is relatively high and mainly feeds on crustaceans and fish.

*Dasyatis longa.*This species is a large demersal species that inhabits depths up to 70 m, and is more common below 50 m. Though it is not a frequent component of the shrimp fishery's bycatch, it may become targeted, as its meat is commercialized. It is also caught and landed by the artisanal fisheries in the Costa Rican Pacific. This ray reaches a maximum size of 260 cm TL, with an average size at maturity of 110 cm TL (Villavicencion-Garayzar *et al.* 1994). It is ovoviviparous with small brood sizes (Villavicencio-Garayzar *et al.* 1994), and therefore has a low reproductive potential. The TEK indicates that the abundance of *D. longa* has declined in the past decades.The species is potentially vulnerable to the current fishing pressure, due to its large size, small litter sizes and the high fishing pressure applied by shrimp and artisanal fisheries.

Sphyrna lewini.Althoughthe bonnet-head shark (*S. lewini*) was a very common component of the shrimp fishery's bycatch in the 1990s, only two immature individuals of this species were caught during the 2010-2011 study period (Clarke *et al.* 2011). Heavy fishing pressure may have caused population declines, as the species is caught and landed by both the artisanal and long-line pelagic fisheries in the Eastern Tropical Pacific (Campos 1986, Zanella *et al.* 2009, Whorisky *et al.* 2011, R. Villalobos comm. pers. 2012). The bonnet-head shark is discarded in the shrimp fishery because they are caught only as small juveniles.This species displays a strong segregation by size, in which small juveniles inhabit discrete areas close to the coast, while adults move away from the coast and towards oceanic habitats. Large females seasonally approach the coast to give birth. Due to size segregation patterns and fast swimming speeds, only juvenile *S. lewini* are captured by the shrimp and artisanal fisheries (Zanella *et al.* 2009).

Echinorhinus cookei.This shark is currently not a very common species in the shrimp fishery. It inhabits depths between 11 and 1100 m (Rojas 2006), within the shrimp fishery's range highest abundances were observed between 200 and 350 m, though it may be more abundant in deeper waters and is associated with cold temperatures. Only immature females were caught, probably because we only sampled the shallowest end of the shark's distribution range. It has the highest trophic level and maximum size of all species in the shrimp fishery's bycatch (Espinoza *et al.* in prep.).A decline in the abundance of *E. cookei* was observed by the fishery's monitoring program over a relatively short sampling period (2008-2012) (Clarke *et al.* in prep.). This may reflect population sizes, as this species seems to be a large top predator, vulnerable to shrimp fisheries due to its low mobility.

Zapteryx xyster.This guitarfishis one of the most common elasmobranch species in the bycatch of the shrimp fishery and inhabits a depth range of 0-150 m. The species has been misidentified as *Z. exasperata* in some studies carried out in the Eastern Tropical Pacific region (Espinoza *et al.* in press). It is not targeted or caught incidentally by other fisheries. *Zapteryx xyster* can reach up to 90 cm TL, though maximum sizes caught in Costa Rica were of 78.3 cm TL. The speciespresents a strong segregation by maturity stages, where gravid females and neonates are found in shallow habitats. The *Z. xyster* diet consists mainly of shrimp (Espinoza *et al.* in press), overlapping with the shrimp fishery's target resource, which make the species more vulnerable.

Squatina californica.This speciesoccurs in demersal habitats from 3 – 205 m and is most abundant between 50-100 m. It is one of the largest elasmobranchs (up to 95 cm TL) and has one of the highest trophic levels. Though it was relatively abundant in 2010, very few specimens were caught during 2011. Most individuals of this species that were caught were mature.

Torpedo peruana.There is very little information available for *T. peruana*. Its depth range is unknown and we collected the species between 30 and 285 m. *Torpedo peruana* presents a maximum size of 90 cm TL. While the *Torpedo* genus presents a wide variety of life history traits, species such as *T. peruana* appear to be adjusted to deeper habitats, with lower fecundities and larger sizes at first maturity (Consalvo *et al.* 2007). It is ovoviviparous and matures at the relatively large size of 69.8 cm TL in females. *Torpedo peruana* displays a strong size segregation pattern, as only 16% of all caught torpedos were mature. Further information on the habitat occupied by adults, the reproductive cycle and fecundity is required in order to assess its potential vulnerability to shrimp fishery.*Torpedo peruana* has one of the highest trophic levels of the elasmobranch community and mainly feeds on fish.

Although *Urotrygon aspidura* also forms large aggregations and is one of the most abundant species in the overall bycatch in shallow waters (Clarke *et al.* 2011), it is not listed as a vulnerable species because of its life history traits. The fast reproductive and growth rate of this species allows it to withstand intense fishing pressures, like *U. rogersi* in Colombia (Mejía-Falla *et al.* 2012). Additionally, the decreasing abundance of other demersal elasmobranchs and increased food availability caused by discards may have lowered competition and favored their population expanses (Dulvy *et al.* 2000, Heithaus 2004, Mejía-Falla *et al.* 2012). All these factors have enabled these ray´s populations to grow and maintain large sizes.

CONCLUSIONS

There is an established international and regional management framework that could be used to incorporate specific management strategies for elasmobranch bycatch in shrimp fisheries, which includes several international agreements, Regional Fisheries Management Organization (RFMOs) and national initiatives to write National Plan of Action for the Conservation and Management of Sharks (NPOA-Sharks). Shark management worldwide has been promoted by international conventions and organizations such as the FAO, and Central America is not the exception.In 1994, CITES adopted the Resolution Conf. 9.17 entitled “Situation of the international trade of shark species”, where it recognizes the need for conservation of sharks and urges the FAO to address and promote the issue at an international level. After consulting with experts worldwide, the FAO approved the International Plan of Action for Sharks (IPOA-Sharks) in 1999, which encouraged every State with a shark fishery to adopt a National Plan of Action for Sharks (NPOA-Sharks) (OLDEPESCA 2011), which provides a management guideline. IPOA-Sharks main objective is to guarantee the long-term conservation and sustainable management of sharks and rays. It has three main principles: (1) the participation of member states that contribute towards shark mortality; (2) achieve population sustainability through management and conservation strategies, and (3) the precautionary principle should be maintained (OLDEPESCA 2011).

However, by 2001, no significant developments had been accomplished, and few countrieshad adopted their own NPOA-Sharks. CITES insisted that all its member States adopt their own NPOA-Sharks in2002, carry out research and compile data on shark fishery and trade; it also encouraged RFMOs to support the process (Lamilla *et al.* 2008). The FAO, Comisión Permanente del Pacífico Sur (CPPS), Organización Latinoamericana para el Desarrollo Pesquero (OLDESPESCA) and OSPESCA have supported the creation of NPOAs and RPOAs through a process that began in 2008 and continues in 2012 (OLDEPESCA 2011).

The following countries have approved NPOA-Sharks: Ecuador (1999), Mexico (2004), Chile (2007), Guatemala (UNIPESCA –MAGA 2008), El Salvador (CENDEPESCA 2008), Costa Rica (2009, Comisión Nacional para la Conservación y Ordenación de los Tiburones 2010), Colombia (2010), Panama (OLDEPESCA 2011), Perú (2011-2012), Honduras y Nicaragua. Fishery administrators of Chile, Costa Rica, Colombia, Ecuador, Guatemala, Mexico and El Salvador have implemented their NPOA-Sharks to a certain degree (OLDEPESCA 2011). Though several goals include monitoring and long-term conservation of bycatch species in fisheries such as the shrimp trawling fisheries, immediate attention is being turned towards the problem that attracts more of the public's attention, such as pelagic shark fisheries and finning.

An overlying issue is the single-species management approach applied to the shrimp fishery, although the fishery impacts the entire ecosystem. It is necessary to begin making management decisions for the shrimp fishery based on community ecology instead of shrimp production (Herrera-Ulloa *et al.* 2011). Information on vulnerable species, such as sharks and rays should be taken incorporated into management strategies.

Although there is an active research group that focuses on sharks and rays in Costa Rica, important information for management on the biology and ecology of elasmobranchs is still missing. Some research priorities should be the identification of nursery areas, description of reproductive cycles, evaluation of reproduction and feeding habits of shallow-water species and the creation of a monitoring program that will generate long-term abundance data.

Enforcement. High bycatch rates and the overexploitation of shrimp resources in Central American fisheries have been raised as management and conservation issues since the 1980s; however, problems have continued and little progress has been achieved. Fleet size in all countries has been reduced as a result of resource reduction, not of management strategies. Currently, this fishery has overexploited its resources due to fleet overcapacity (FIINPESCA 2007).

Fishing closures, license restrictions and catch quotas established in Central America could contribute towards shark and ray management because they reduce fishing pressure. However, these measures have not even been sufficient to ensure the recovery of fast growing resources such as shrimp (Nanne 2007), and there are no specific management measures for sharks and rays in the shrimp fishery (Herrera-Ulloa *et al.* 2011). Costa Rica can learn from measures implemented in other Central American countries such as: (1) creating a permanent fishing closure along the first three miles from the coast, (2) carrying out stock assessments, (3) restricting the entry of new licenses into the fishery, and (4) prohibiting the entry of new vessels into the fishery

Social, political and economical impacts.

In Costa Rica, the shrimper sector directly benefits 235-282 fishermen (Álvarez and Ross-Salazar 2009). Are the economic benefits afforded to this small sector proportionate to the environmental impact it is creating? Though displacement of these fishermen would cause problems, the entry of new vessels and licenses to the fishery should be prohibited to slowly eliminate the fishery without causing great social conflicts (Arauz 2008, Patterson and Tudman 2009). This would improve conditions for mainly artisanal fishermen, which reach a total of 6000 along the central Pacific coast (Beltran 2001).

While the shrimp fishery is still operating, additional management measures need to be established considering ecological, economic and social aspects. All conservation measures should take into consideration the overall impact they will have in order to achieve social responsibility and support from the surrounding communities. The incorporation of results of scientific studies into fisheries management is a slow but necessary process that should involve all stakeholders (Fernández *et al.* 2011).

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TABLES

Table 1. Management strategies for the shrimp fisheries in Central America that reduce fishing effort, increase gear selectivity and make data management efficient.

	Guatemala	Honduras	El Salvador	Nicaragua	Costa Rica	Panama
Seasonal fishing closures	No	Yes	Yes	Yes	Yes	Yes
Permanent fishing closures	Yes	Yes	Yes	Yes	Yes	Yes
License restrictions	Yes	No	Yes	Yes	No	Yes
Shrimp catch quotas	No	No	No	Yes	No	No
Bycatch quotas	No	No	No	No	No	No
TED use	Required	Required	Required	Required	Required	Required
BRD use	No	No	No	No	No	No
Net specifications	Yes	Yes	Yes	Yes	Yes	Yes
Specific regulation for bycatch	No	No	No	No	No	No
Specific regulation for sharks and rays	No	No	No	No	No	No
Onboard observers	No	No	No	No	No	No
Fishery monitoring program	No	No	No	No	Yes	No
Handling practices	No	No	No	No	No	No
Stock assessments	No	No	Yes	No	No	No

Sources: Alvarado *et al.* 2012, Álvarez and Ross-Salazar 2010, Arauz 2008, Beltran 2001, Cajiao-Jiménez 2003, FAO 2004a, FAO 2004b, FAO 2004c, FAO 2004d, Fernández *et al.* 2011, FIINPESCA 2007, Fuentes 2007, García *et al.* 2008, Gutierrez 2001, Herrera-Ulloa 2001 Herrera-Ulloa *et al.* 2011, Lamilla *et al.* 2008, López-Mendoza 2003, Lopez-Mendoza 2009, Marchena-Sanabria *et al.* 2008, Marín 2001, Nanne 2007, OLDEPESCA 2011, Proambiente 1999, Rivera 2011, Rodríguez and Windevoxhel 1998, Wehrtmann and Nielsen-Muñoz 2009

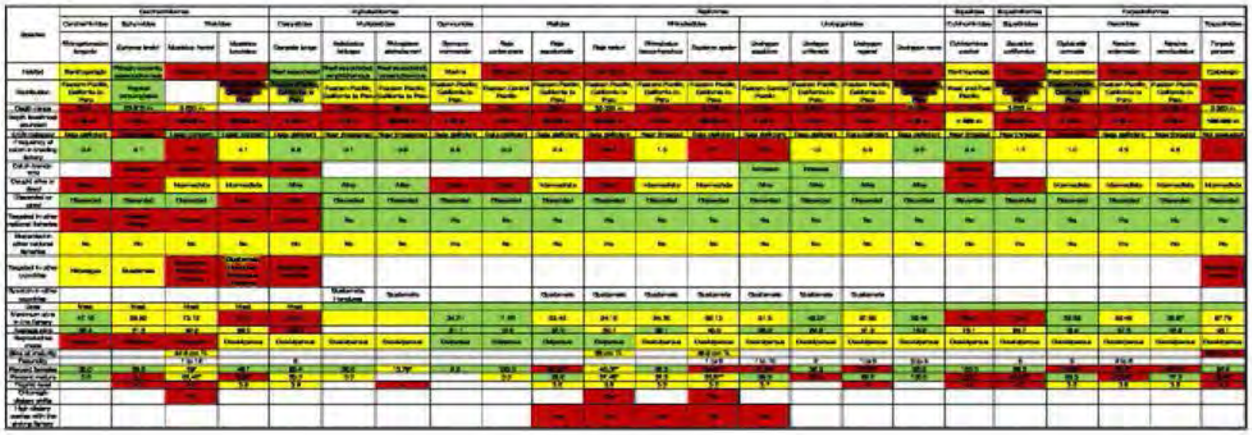
Table 2. Management recommendations for the Costa Rican shrimp fishery with the goal of reducing its environmental impact.

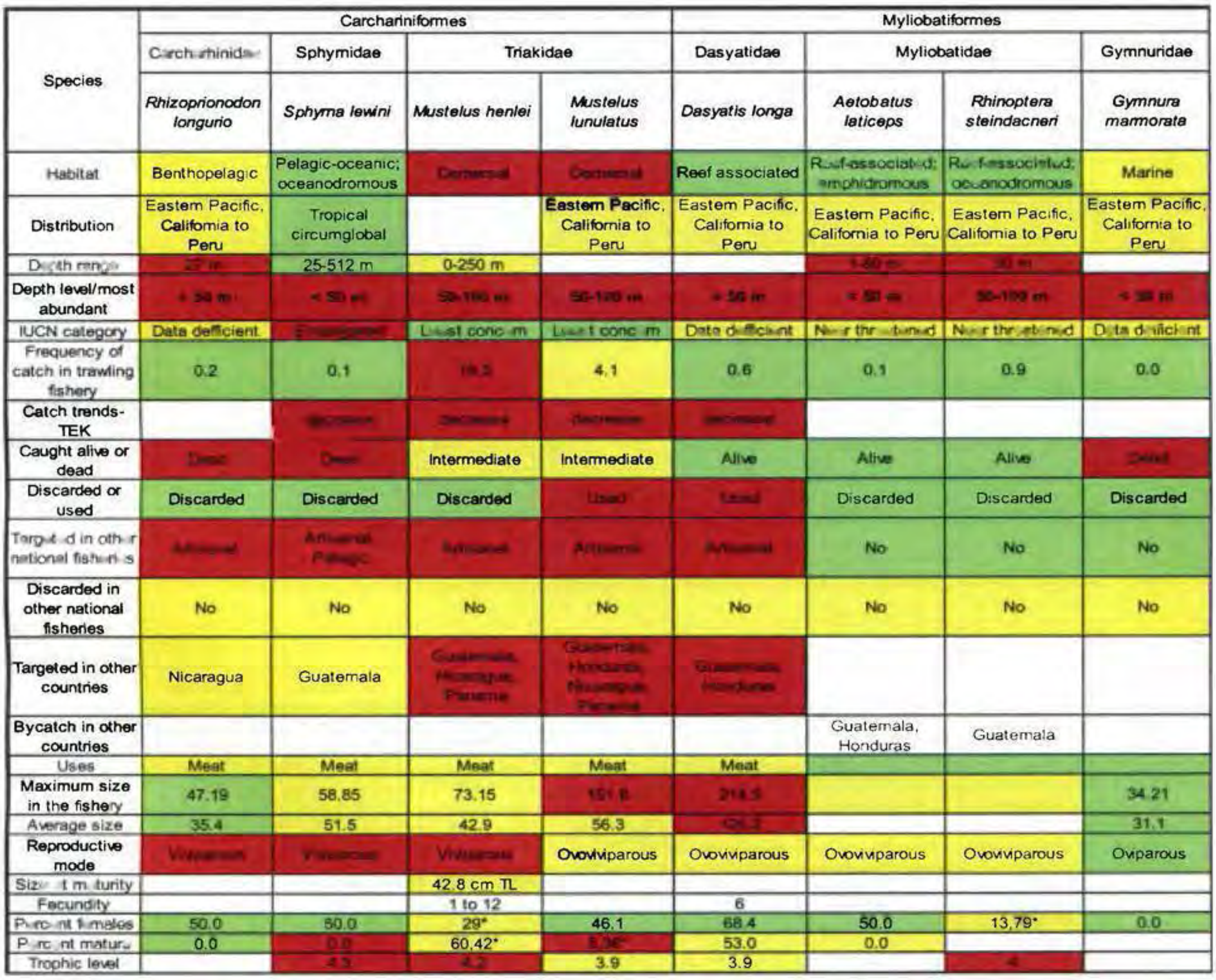
Goal # 1: Reduction of the trawling fishery`s environmental impact		
Recommended measures	**Justification**	**Sources**
Evaluate efficiency of bycatch reduction devices (BRD) that have yielded positive results in Australian tropical fisheries. The recommended BRDs are: "*square mesh window attachment*", "*radial escapement device*", "*fisheye bycatch reduction device*", "*Popeye fishbox bycatch reduction device*".	The average discard rate estimated from scientific survey data was of 92.7%. Discards include 67 fish species, 20 crustacean species and approximately 20 mollusk species.	Robins *et al* 1999, Hartil *et al.* 2006, Raudzens 2007, Petersen *et al.* 2008, Patterson & Tudman 2009, Clarke *et al.* 2011
The efficiency of the modified nets that successfully reduced bycatch in Chile`s *Heterocarpus reedi* fishery should be tested in the Costa Rican *Heterocarpus vicarious* fishery, as they operate at similar depths.		Queirolo *et al.* 2011a,b
Establish areas where shrimp trawling is prohibited in the Central Pacific, <50 m.	The highest shark and ray diversity was found <100 m deep, mainly in the Central Pacific (Table 1, Fig. 1, Fig. 2). Most gravid females were captured in shallow waters (<50 m) in areas surrounding coastal wetlands, such as Quepos-Manuel Antonio, and the Humedal Nacional Tèrraba-Sierpe (Fig. 3).	Clarke *et al.* 2011
Up to 25% of landings may be of byactch destined for human consumption.	As a result of the overexploitation of both deep water and shallow water shrimp, demersal trawlers began to target shallow water shrimp such as congrio, pargo, cabrilla, corvine, corvineta and lenguado. Between November 2010 and April 2011, as well as	Clarke et al. 2011
Establish a monitoring and surveillance program for the shrimp trawling fishery that includes both onboard observers and landing supervision.		

Table 3. Management recommendations for the Costa Rican shrimp fishery with the goal of ensuring the long-term conservation of shark and ray bycatch species.

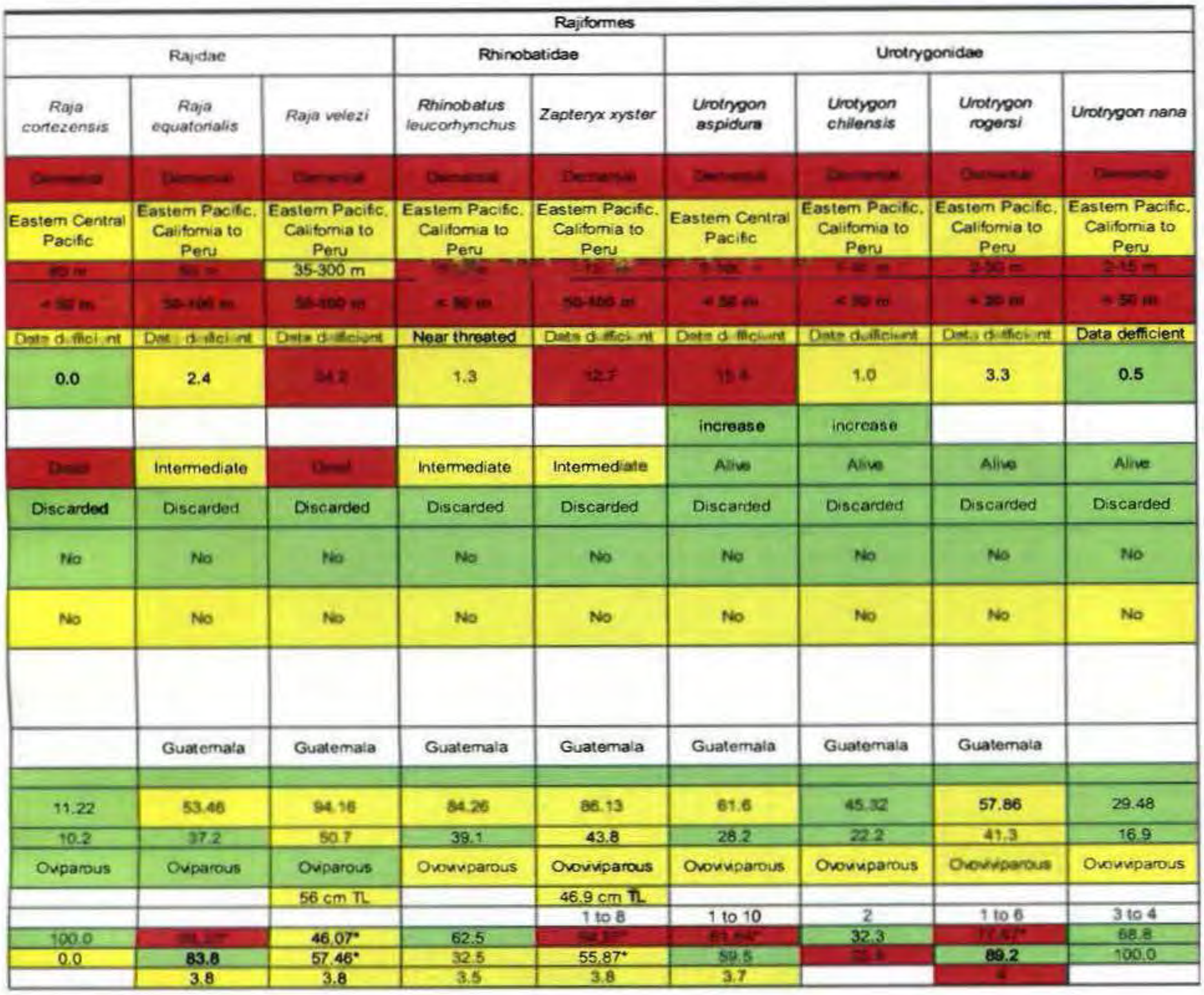
Goal #2: Shark and ray conservation		
Recommended measures	**Justification**	**Sou**
An improvement in handling practices may be beneficial for some species. Such improvements could include the use of hoppers.	The Costa Rican shrimp trawling fishery includes 24 species of sharks and rays (14 families and 5 orders) in its bycatch. This group`s life history strategies coupled with the lack of catch records may result in the unnoticed, yet drastic reduction of pop	Dulvy et Patterso 2009, Cla 20
Monitor shark and ray catch tendencies through onboard observer programs. The necessary information should be registered per fishing trip: vessel name, captain`s name, vessel traits, fishing trip dates, fishing areas used, trawling hours per depth categor		
The shark and ray Essential Fish Habitats identified in this study should be protected. The highest priority site is the area between the Tèrraba – Sierpe delta and the Isla del Caño. A biological corridor in which trawling is prohibited should be created	Several shark and ray reproduction areas were identified along the Pacific coast of Costa Rica. The areas, listed in order of importance are: ☐ Térraba - Sierpe delta ☐ Golfo de Nicoya ☐ Wetlands of Manuel Antonio and Quepos ☐ Golfo de Papagayo.	
The continuation of this project will allow us to generate detailed information on seasonal reproductive patterns of the most abundant shark and ray species in the shrimp fishery`s bycatch. This information will allow is to develop management strategies (	Several voids of information were detected: Although several gravid females were found during the 2010-2011 sampling period, a clear reproductive season has not been identified. Future studies should be aim to: ☐ Identify the habitats utilized by female smooth hound sharks (*M. henlei*), juvenile rays (*R. velezi*) and adult electric rays (*T. peruana*) along the Pacific continental platform of Costa Rica. ☐ Determine size at maternity and fecundity for the ray (*R. velezi),* the guitarfish (*Z. xyster*) and electric ray (*T. peruana*). ☐ Describe the reproductive cycle of the most abundant shark and ray species. ☐ Determine the size at maturity for less abundant species.	

Table 4. Vulnerability assessment of the 24 species that compose the elasmobranch bycatch of the Costa Rican shrimp fishery.

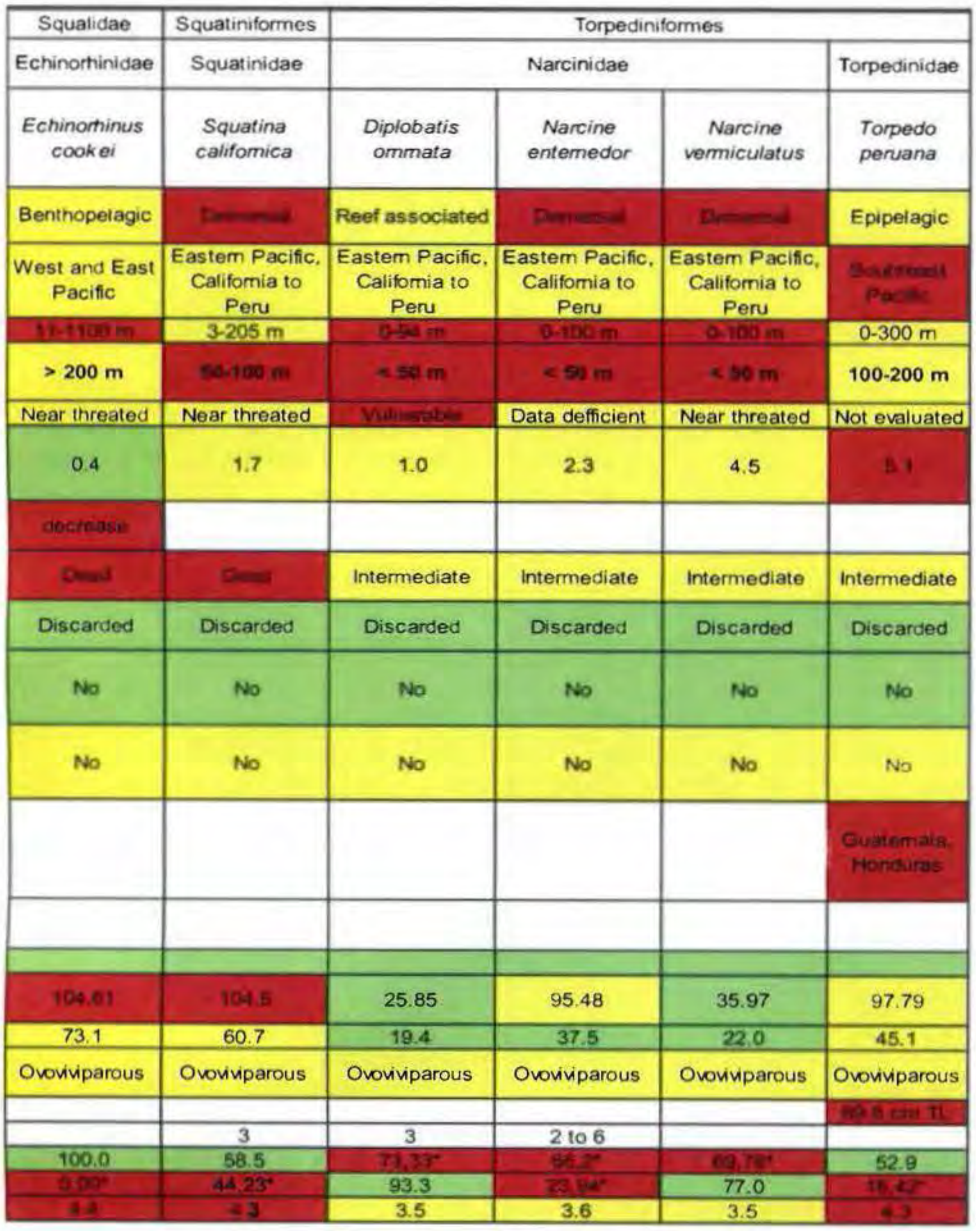




Species	Carcharhiniformes				Myliobatiformes			
	Carcharhinidae	Sphymidae	Triakidae		Dasyatidae	Myliobatidae		Gymnuridae
	Rhizoprionodon longurio	*Sphyrna lewini*	*Mustelus henlei*	*Mustelus lunulatus*	*Dasyatis longa*	*Aetobatus laticeps*	*Rhinoptera steindacneri*	*Gymnura marmorata*
Habitat	Benthopelagic	Pelagic-oceanic; oceanodromous	Demersal	Demersal	Reef associated	Reef-associated; amphidromous	Reef-associated; oceanodromous	Marine
Distribution	Eastern Pacific, California to Peru	Tropical circumglobal		Eastern Pacific, California to Peru	Eastern Pacific, California to Peru	Eastern Pacific, California to Peru	Eastern Pacific, California to Peru	Eastern Pacific, California to Peru
Depth range	27 m	25-512 m	0-250 m			1-60 m	30 m	
Depth level/most abundant	< 50 m	< 50 m	50-100 m	50-100 m	< 50 m	< 50 m	50-100 m	< 30 m
IUCN category	Data defficient	Endangered	Least concern	Least concern	Data deficient	Near threatened	Near threatened	Data deficient
Frequency of catch in trawling fishery	0.2	0.1	[illegible]	4.1	0.6	0.1	0.9	0.0
Catch trends-TEK		Decrease	Decrease	Decrease	Decrease			
Caught alive or dead	Dead	Dead	Intermediate	Intermediate	Alive	Alive	Alive	Dead
Discarded or used	Discarded	Discarded	Discarded	Used	Used	Discarded	Discarded	Discarded
Targeted in other national fisheries	Artisanal	Artisanal Pelagic	Artisanal	Artisanal	Artisanal	No	No	No
Discarded in other national fisheries	No	No	No	No	No	No	No	No
Targeted in other countries	Nicaragua	Guatemala	Guatemala, Nicaragua, Panama	Guatemala, Honduras, Nicaragua, Panama	Guatemala, Honduras			
Bycatch in other countries						Guatemala, Honduras	Guatemala	
Uses	Meat	Meat	Meat	Meat	Meat			
Maximum size in the fishery	47.19	58.85	73.15	151.8	214.5			34.21
Average size	35.4	51.5	42.9	56.3	[illegible]			31.1
Reproductive mode	Viviparous	Viviparous	Viviparous	Ovoviviparous	Ovoviviparous	Ovoviviparous	Ovoviviparous	Oviparous
Size at maturity			42.8 cm TL					
Fecundity			1 to 12		6			
Percent females	50.0	60.0	29*	46.1	68.4	50.0	13,79*	0.0
Percent mature	0.0	0.0	60,42*	[illegible]	53.0	0.0		
Trophic level		4.3	4.2	3.9	3.9		4	



Rajiformes								
Rajidae			Rhinobatidae		Urotrygonidae			
Raja cortezensis	*Raja equatorialis*	*Raja velezi*	*Rhinobatus leucorhynchus*	*Zapteryx xyster*	*Urotrygon aspidura*	*Urotygon chilensis*	*Urotrygon rogersi*	*Urotrygon nana*
Demersal	Demersal	Demersal	Demersal	Demersal	Demersal	Demersal	Demersal	Demersal
Eastern Central Pacific	Eastern Pacific, California to Peru	Eastern Pacific, California to Peru	Eastern Pacific, California to Peru	Eastern Pacific, California to Peru	Eastern Central Pacific	Eastern Pacific, California to Peru	Eastern Pacific, California to Peru	Eastern Pacific, California to Peru
60 m	50 m	35-300 m	[illegible]	[illegible]	1-100 m	1-60 m	2-30 m	2-15 m
< 50 m	50-100 m	50-100 m	< 50 m	50-100 m	< 50 m	< 50 m	< 20 m	< 50 m
Data deficient	Data deficient	Data deficient	Near threated	Data deficient	Data deficient	Data deficient	Data deficient	Data defficient
0.0	2.4	34.2	1.3	12.7	15.4	1.0	3.3	0.5
					increase	increase		
Dead	Intermediate	Dead	Intermediate	Intermediate	Alive	Alive	Alive	Alive
Discarded	Discarded	Discarded	Discarded	Discarded	Discarded	Discarded	Discarded	Discarded
No	No	No	No	No	No	No	No	No
No	No	No	No	No	No	No	No	No
	Guatemala	Guatemala	Guatemala	Guatemala	Guatemala	Guatemala	Guatemala	
11.22	53.46	94.16	84.26	86.13	61.6	45.32	57.86	29.48
10.2	37.2	50.7	39.1	43.8	28.2	22.2	41.3	16.9
Oviparous	Oviparous	Oviparous	Ovoviviparous	Ovoviviparous	Ovoviviparous	Ovoviviparous	Ovoviviparous	Ovoviviparous
		56 cm TL		46.9 cm TL				
				1 to 8	1 to 10	2	1 to 6	3 to 4
100.0	[illegible]	46.07*	62.5	[illegible]	61.54*	32.3	77.67*	68.8
0.0	83.8	57.46*	32.5	55.87*	59.5	[illegible]	89.2	100.0
	3.8	3.8	3.5	3.8	3.7		4	



Squalidae	Squatiniformes	Torpediniformes			
Echinorhinidae	Squatinidae	Narcinidae			Torpedinidae
Echinorhinus cookei	*Squatina californica*	*Diplobatis ommata*	*Narcine entemedor*	*Narcine vermiculatus*	*Torpedo peruana*
Benthopelagic	Demersal	Reef associated	Demersal	Demersal	Epipelagic
West and East Pacific	Eastern Pacific, California to Peru	Eastern Pacific, California to Peru	Eastern Pacific, California to Peru	Eastern Pacific, California to Peru	Southeast Pacific
11-1100 m	3-205 m	0-54 m	0-100 m	0-100 m	0-300 m
> 200 m	**50-100 m**	**< 50 m**	**< 50 m**	**< 50 m**	**100-200 m**
Near threatened	Near threatened	Vulnerable	Data defficient	Near threatened	Not evaluated
0.4	1.7	1.0	2.3	4.5	5.1
decrease					
Dead	Dead	Intermediate	Intermediate	Intermediate	Intermediate
Discarded	Discarded	Discarded	Discarded	Discarded	Discarded
No	No	No	No	No	No
No	No	No	No	No	No
					Guatemala, Honduras
104.61	104.5	25.85	95.48	35.97	97.79
73.1	60.7	19.4	37.5	22.0	45.1
Ovoviviparous	Ovoviviparous	Ovoviviparous	Ovoviviparous	Ovoviviparous	Ovoviviparous
					89.5 cm TL
	3	3	2 to 6		
100.0	58.5	73.33*	86.2*	69.78*	52.9
5.00*	44.23*	93.3	23.94*	77.0	18.42*
4.4	4.3	3.5	3.6	3.5	4.3