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# HIDROBIOLÓGICA

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# Cultivo primario de células de manto de la madreperla *Pinctada mazatlanica* (Bivalvia: Pteriidae), con probable aplicación en el cultivo de perlas

# Primary culture of mantle cells of the pearl oyster *Pinctada mazatlanica* (Bivalvia: Pteriidae), with possible application to pearl farming

Pedro E. Saucedo*, Alex Olivera, Arturo Sierra-Beltrán, José M. Mazón-Suástegui y Héctor Acosta-Salmón

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## RESUMEN

**Antecedentes.** La técnica para inducir la producción de perlas en moluscos, que se basa en el injerto de un núcleo esférico y una pieza de manto de un donador en la gónada de un receptor, genera altas tasas de mortalidad y rechazo de injertos. **Objetivos.** Desarrollar bases metodológicas para el cultivo primario de células de manto de la madreperla *Pinctada mazatlanica*, con aplicación potencial en el cultivo de perlas. **Métodos.** Se evaluaron cinco formas de disgregación enzimática celular, tres medios de cultivo, dos sustratos celulares y cuatro osmolaridades del medio. Se estudió también la absorción *in vitro* de calcio por parte del manto mediante técnicas histoquímicas y de espectrofotometría de absorción atómica. **Resultados.** La adición de colagenasa I (414 U/mg), a 37 °C incrementó la viabilidad y desempeño de las células cultivadas en medio RPMI-1640 con poli-D-lisina. Bajo estas condiciones, las células cambiaron a la forma de fibroblasto desde el tercer día y se mantuvieron viables durante 25 días. El cultivo de explantes resultó mejor en medio RPMI-1640, a 37 °C, sin poli-D-lisina y a 0.6 M NaCl, donde la absorción de calcio por parte del manto fue evidente. **Conclusiones.** Estos resultados sientan las bases de las futuras investigaciones dirigidas a reformular nuevos medios de cultivo, evaluar factores de crecimiento e identificar las moléculas y genes más importantes por su implicación en la biomineralización y síntesis de $CaCO_3$, calcita y aragonita.

**Palabras clave:** Calcio, cultivo celular, cultivo de perlas, enzimas, explantes, osmolaridad

## ABSTRACT

**Background.** The technique for inducing pearl production in mollusks, which relies on the grafting of a round nucleus and a piece of mantle tissue from a donor within the gonad of a recipient, generates high mortality and rejection rates. **Goals.** To develop methodological basis for *in vitro* primary cultivation of mantle cells in the pearl oyster *Pinctada mazatlanica*, with potential application to pearl production. **Methods.** Five methods for enzymatic dissociation, three different culture media, two cell substrates, and four osmolarities of the culture medium were evaluated. *In vitro* intake of calcium by mantle tissue was also quantified through histochemistry and atomic absorption spectrophotometry. **Results.** The addition of collagenase I (414 U/mg), at 37°C increased viability and performance of disaggregated cells, which grew better in RPMI-1640 cell medium with poly-D-lysine. Under these conditions, the cells changed from the round-type cell to the fibroblast-type cell by day three and remained viable until day 25. Culture of explants resulted better with RPMI-1640 medium, at 37 °C, without poly-D-lysine, and at 0.6 M NaCl, where calcium absorption was evident. **Conclusions.** These results set the basis of future investigations reformulating new culturing media, evaluating growth factors, and identifying molecules and genes related to biomineralization and synthesis of $CaCO_3$, calcite and aragonite.

**Key words:** Calcium, cellular culture, pearl culture, enzymes, explants, osmolarity

## INTRODUCCIÓN

En biotecnología y medicina, el cultivo *in vitro* de células animales (vertebrados) se encuentra muy desarrollado y mayormente orientado al tratamiento y cura de padecimientos como el cáncer, enfermedades degenerativas y autoinmunes, etc. (Rinkevich, 1999, 2005). En invertebrados de fila como Porifera, Mollusca, Crustacea y Echinodermata, la tecnología de cultivo celular *in vitro* es más reciente y reporta resultados mucho más modestos (Odintsova *et al.*, 1994; Awaji & Machii, 2011). En moluscos, por ejemplo, los pocos estudios relativos a esta tecnología se han llevado a cabo en grupos productores de perlas, como ostras perleras (Zhang *et al.*, 2006; Gong *et al.*, 2008), almejas de agua dulce (Barik *et al.*, 2004; Van Phuc *et al.*, 2011), almejas marinas (Endoh & Hasegawa, 2006), y abulón (van der Merwe *et al.*, 2010; Pichon *et al.*, 2013; Kim *et al.*, 2014). Estos estudios surgen como una necesidad de reducir las altas tasas de mortalidad y rechazo de injertos (30–50%) derivados de la cirugía de inserción de un núcleo esférico y una pieza de manto de un molusco donador en la gónada de un molusco receptor, con el fin de provocar su irritación y la secreción de nácar para formar la perla (Taylor & Strack, 2008). La mayoría de estos estudios reportan la capacidad de algunas células somáticas, particularmente del manto, para regenerarse y proliferar *in vitro*, a expensas de moléculas y genes involucrados en el proceso de biomineralización y síntesis de cristales de aragonita y calcita. Sin embargo, la definición de una línea celular estable ha sido difícil de lograr en moluscos, básicamente por problemas de contaminación microbiana (Mirjalili *et al.*, 2005) y por el escaso entendimiento sobre la interacción de los principales factores que regulan la viabilidad e integridad del cultivo celular (Rinkevich, 2005).

A nivel mundial, el cultivo de perlas es una actividad acuícola consolidada y muy lucrativa en algunos países de Asia y el Pacífico Sur (Taylor & Strack, 2008). En esta actividad se utilizan comúnmente tres ostras perleras del género *Pinctada*: *P. fucata* (Gould)*, P. margaritifera* (Linnaeus) y *P. maxima* (Jameson). En América Latina, el cultivo de perlas fue una actividad muy rentable a finales del siglo XIX y principios del siglo XX, y aunque después fue un tanto olvidada, vive un gradual resurgimiento en países como México, Chile, Ecuador, Venezuela y Colombia (Saucedo *et al.*, 2017). En el noroeste de México en particular, existen dos especies que sustentan el cultivo de perlas, la madreperla *P. mazatlanica* (Hanley, 1856) y la concha nácar *Pteria sterna* (Gould, 1851) (Kiefert *et al.*, 2004). Dado que las estadísticas de mortalidad y rechazo post-injerto son altas en estas especies, la evaluación de opciones como el cultivo *in vitro* de manto, que representa una etapa previa al cultivo *in vitro* de perlas, resultan interesantes y novedosas para reducir estas cifras. El presente trabajo está dirigido a definir las condiciones básicas para el cultivo primario *in vitro* de células y explantes de manto de la madreperla *P. mazatlanica*, analizando la potencial aplicación de esta técnica en el cultivo de perlas.

## MATERIALES Y MÉTODOS

**Preparación del sustrato celular y medios de cultivo.** Se utilizaron adultos cultivados de *P. mazatlanica* (60 ± 7.8 mm de altura de la concha), los cuales fueron limpiados de epifauna con un cepillo y alcohol etílico al 70% y mantenidos en agua de mar filtrada e irradiada con luz UV para depurar los tejidos. Para el cultivo celular, una solución de Poli-D-lisina (Cat #81358, Sigma, St. Louis, MO) se diluyó en amortiguador estéril de boratos (0.15 M; pH 8.3; 0.1 mg/mL), se agregó en placas multipozos por triplicado (24 pozos, 6x4; Cat #3526, Corning, NY), y se incubó a 37 °C por 3 h. Para evitar contaminación, cada placa se lavó tres veces con solución estéril de fosfatos bajo condiciones de bioseguridad en una campana de flujo laminar (Thermo Fisher Scientific, Walthan, MA) (Odintsova et al., 1994; Mirjalili et al., 2005).

Se evaluaron tres diferentes medios de cultivo preparados también bajo la campana de flujo laminar: (1) Medio MegaCell® RPMI-1640 (Cat #3817, Sigma); (2) 50% de MegaCell® Minimun Essential Medium Eagle (Cat #M-4067, Sigma) y 50% de MegaCell® Dulbecco´s Modified Eagle's (Cat #M-3942, Sigma); y (3) un medio de cultivo control con solución Hanks (Cat #H-8264, Sigma). Todos los medios se adicionaron con L-Glutamina (4 mM), 0.1% de penicilina-estreptomicina y 10% de suero fetal de bovino (SFB) y se almacenaron a 4 °C hasta su uso.

**Aislamiento mecánico y disgregación enzimática del manto.** Se extrajo una pieza de manto de 40 mm de longitud de la región paleal de cada ostra depurada, la cual se colocó en una caja de Petri con solución Hanks, rojo Fenol y penicilina-estreptomicina (0.1%). Cada pieza se cortó a su vez en piezas más pequeñas (~1 mm) que se disgregaron con seis enzimas comerciales: (1) Tripsina-EDTA (E.C. 3.4.21.4; 1X); (2) Colagenasa I (5U/mg; 0.5%; E.C. 3.4.24.3); (3) Colagenasa I (414 U/mg; (4) Proteasa XIV (0.1%; 3.4.24.31); (5) Proteinasa K (2.5%; E.C. 3.4.21.64); y (6) 1% (p/v) de una enzima proteolítica de *Trichoderma herzianum* (Rifai).

La disgregación del manto se hizo también a tres temperaturas de incubación: 15, 37 y 46 °C. En cada caso se determinó el rendimiento (cel/mL) y viabilidad (%) de los cultivos mediante tinción con azul Tripano 0.4%. El conteo de células viables y no viables se hizo a intervalos de 20 min durante 120 min, utilizando un hemocitómetro (Zeiss, Oberkochen, Alemania).

**Siembra de células disgregadas y explantes de manto**. Las células disgregadas se centrifugaron (180 g, 15 min, 4°C), se pasaron a través de una columna de fibra de vidrio para su depuración y se sembraron en placas multipozo (24 pozos, 4x6) (Dharmaraj & Suja, 2002). Adicionalmente, dos explantes de manto de 3 mm de longitud se sembraron en cada pozo de nuevas placas de cultivo. Ambos modelos (células disgregadas y explantes) se manejaron por triplicado mediante un diseño experimental que incluyó los tres medios de cultivo (y el control), con sustrato y sin sustrato. Los cultivos se mantuvieron a 23 °C en una incubadora (Thermo Fisher Scientific) con 3% de flujo continuo de $CO_2$. La observación se hizo a diario bajo un microscopio invertido (Olympus The Americas, Central Valley, PA).

**Evaluación de la osmolaridad.** Se siguieron los mismos procedimientos arriba descritos, pero utilizando medio Megacell® (RPMI-1640) adicionado con 3% de SFB. Se evaluaron cuatro diferentes osmolaridades del medio de cultivo: 0.15, 0.30, 0.45 y 0.60 M de NaCl. El medio en cada caso se preparó con agua de mar estéril a 4 °C, 0.1% de penicilina-estreptomicina y L-glutamina (4 mM). Después de un periodo de incubación de 48 h, se evaluó el cambio de coloración de cada medio de cultivo por efecto de su acidificación (Perez-Camps & García-Ximénez, 2008).

**Evaluación de la absorción de calcio.** Para evaluar la absorción de calcio por parte del manto a cada osmolaridad, se siguió el mismo procedimiento anterior, sembrando dos explantes en placas de cultivo (24 pozos, 4x6), sin recubrimiento, con poli-D-lisina. Cada día se retiraron y se fijaron en formol al 10% dos explantes por tratamiento para evaluar la acumulación de calcio mediante la técnica histoquímica de rojo de Alizarina S (McGee-Russell, 1958). Este procedimiento se repitió en tres ocasiones tuvo una duración de siete días. El nivel de absorción de calcio por parte del manto se analizó también por medio de espectrofotometría de absorción atómica, según la norma NMX-AA-051-SCFI-2001.

## RESULTADOS

**Rendimiento y viabilidad celular**. No se presentó contaminación del sustrato ni los medios de cultivo durante la preparación y almacenamiento. El rendimiento de la colagenasa I (5 U/mg) y la enzima de *T. harzianum* fue muy pobre y no promovieron la liberación de células viables a ninguna de las tres temperaturas evaluadas (datos no mostrados). A 15 °C, un mayor número de células viables se liberaron con la colagenasa I a 414 U/mg (~100x$10^3$ cel/mL) y la proteasa XIV (~60x$10^3$ cel/mL) a los 60 min (Fig. 1a); la tripsina y proteinasa K liberaron muy pocas células (20 y 40x$10^3$ cel/mL). La mayor viabilidad celular se obtuvo durante los primeros 40 min con la proteasa XIV (70-100%) y la tripsina y proteinasa K (50-100%) y la menor viabilidad celular con la colagenasa I (5 y 414 U/mg) (20-70%) (Fig. 2a).

A 37°C, el número de células viables obtenidas con la colagenasa I fue del 100% (Fig. 1b) y el rendimiento de 120×$10^3$ cel/mL a los 60 min (Fig. 2b). La proteasa fue ineficiente bajo estas condiciones (<20×$10^3$ cel/mL), aunque mantuvo una elevada viabilidad celular (100%). El número de células liberadas con la tripsina y proteinasa K osciló entre 40 y 80×$10^3$ cel/mL, aunque con valores de viabilidad muy dispares, dependiendo del periodo de exposición a la enzima (0-100%).

A 46 °C, las cuatro enzimas promovieron una buena viabilidad celular durante los primeros minutos de exposición (Fig. 1c), pero con rendimientos mínimos (Fig. 2c). La colagenasa I promovió la liberación del mayor número de células a los 40 min (222×$10^3$ cel/mL), pero disminuyó su viabilidad (~40%).

**Adhesión y proliferación celular.** Los mejores resultados se obtuvieron con el medio RPMI-1640, con poli-D-lisina, a 37 °C. Bajo estas condiciones, las células disgregadas comenzaron a adherirse a la placa y a cambiar de la forma redonda a la típica de fibroblasto a partir de tres días (Fig. 3a). Aquí la viabilidad celular se mantuvo por 25 días sin contaminación y fue posible observar células en mitosis y proliferación celular continua. Por el contrario, los medios de cultivo restantes no permitieron obtener resultados satisfactorios en términos de adhesión y proliferación celular.

En los explantes se observó proliferación celular solo en el medio RPMI-1640, sin poli-D-lisina, a 37 °C. Bajo estas condiciones, la parte central del explante se regeneró, cubrió la totalidad del fondo y paredes del pozo y se mantuvo viable biológicamente hasta por 20 días. Incluso fue posible observar fibras musculares transversales y longitudinales en proceso de proliferación con abundante tejido conectivo (Fig. 3b).

**Osmolaridad del medio de cultivo.** Se trabajó con explantes de manto cultivados en el medio RPMI-1640, a 37 °C, sin sustrato, dado que estas variables arrojaron mejores resultados de los ensayos previos. El mayor crecimiento y migración de conglomerados de células hacia fuera del tejido ocurrió a partir del tercer día de siembra a 0.6 M, en comparación con las restantes osmolaridades. Estas células llegaron a cubrir casi la totalidad del pozo al cuarto día de cultivo (Fig. 3c), sin registro de crecimiento microbiano en ningún tratamiento.

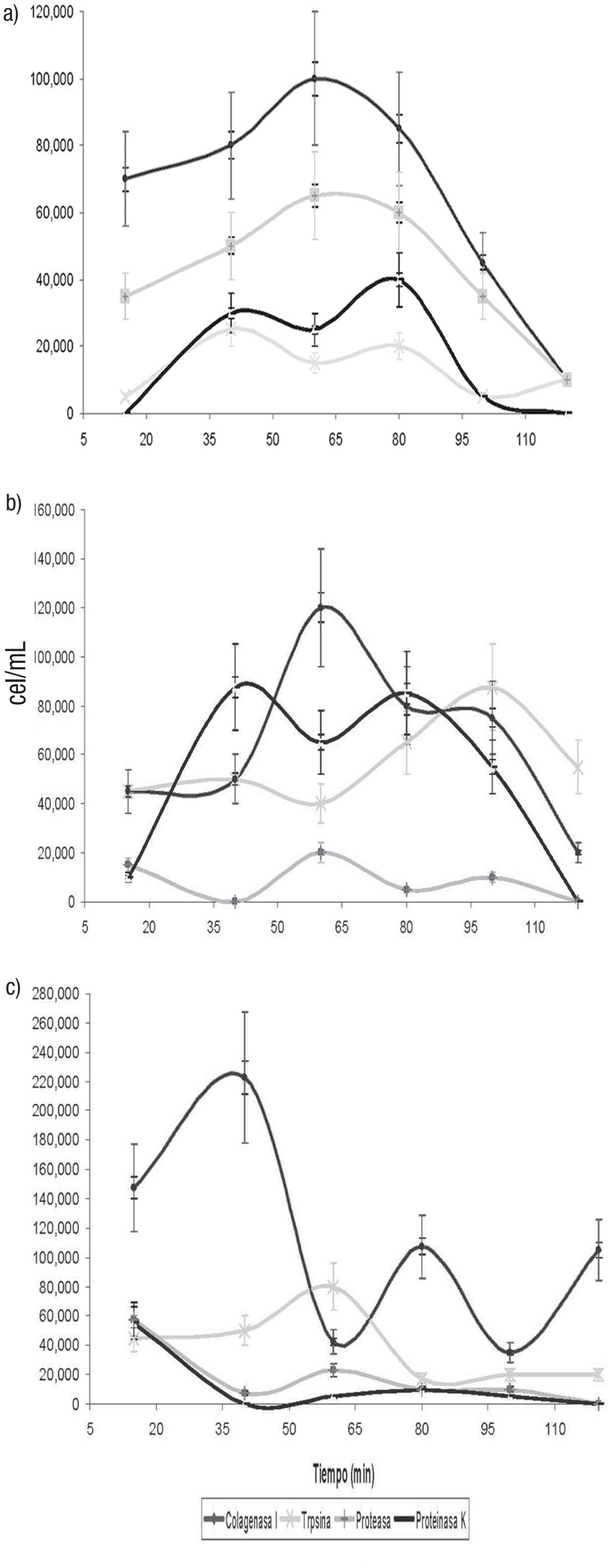
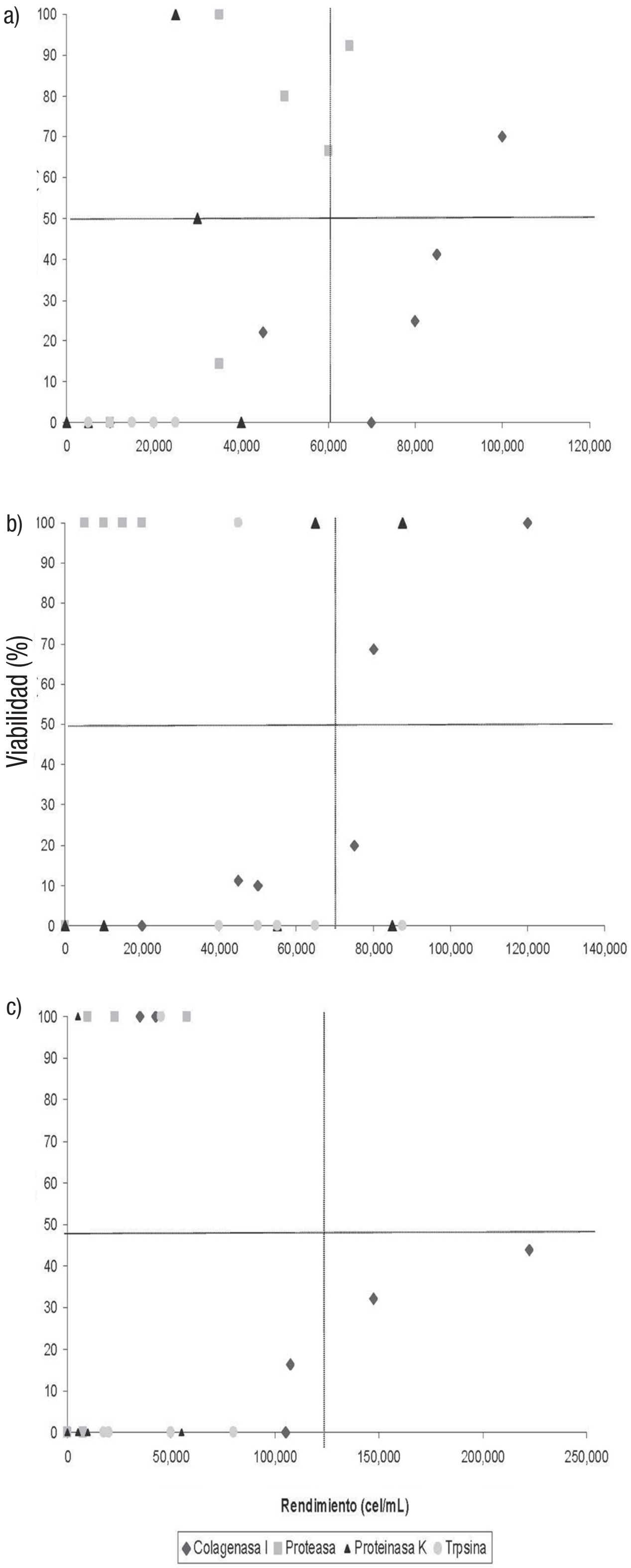


Figura 1a-c. Rendimiento *in vitro* (cel/mL) de células de manto de madreperla *Pinctada mazatlanica* disgregadas con cuatro enzimas a cuatro diferentes temperaturas de incubación: 15 °C (a), 37 °C (b), y 46 °C (c).



Figuras 2. Viabilidad *in vitro* (%) de células de manto de madreperla *Pinctada mazatlanica* incubadas a cuatro diferentes temperaturas: 15 °C (a), 37 °C (b), y 46 °C (c).

**Absorción de calcio.** La acumulación aparente de calcio no se detectó con la tinción de rojo de Alizarina en ninguna de las osmolaridades durante los siete días del ensayo. Por el contrario, la técnica de espectrofotometría de absorción atómica reveló un 55% de abatimiento en los niveles de calcio a 0.6 M (335 a 210 µg/mL) entre el inicio y final del cultivo de explantes, en contraste con lo ocurrido en las restantes osmolaridades (Fig. 4).

## DISCUSIÓN

La evidencia de este estudio indica que los mejores resultados de disgregación, adhesión y regeneración celular, así como de estructura celular (cambio a la forma de fibroblasto) del manto de *P. mazatlanica* ocurrieron con el medio RPMI-1640, a 37 °C, con poli-D-lisina (células) y sin poli-D-lisina (explantes). Considerando que el manto en los moluscos es responsable de numerosas funciones especializadas, incluyendo la biomineralización y formación de la perla, y que ambos procesos están regulados por una compleja interacción entre componentes orgánicos e inorgánicos (García-Gasca *et al.*, 1994; Levi *et al.*, 1997; Zang *et al.*, 2006), la definición de condiciones óptimas para su cultivo *in vitro* es aún contradictoria dependiendo de la especie y el tejido cultivado. Por ejemplo, la evaluación de medios de cultivo reporta una mayor adhesión, viabilidad y regeneración de las células del manto en el medio DMEN/F12 para el caso de las almejas de agua dulce *Lamellidens marginalis* (Sippi) (Barik *et al.*, 2004) y *Sinohyriopsis cumingii* (Lea) (Van Phuc *et al.*, 2011); el 2'L15 de Leibovitz para el manto de la almeja japonesa *Patinopecten yessoensis* (Jay) (Endoh y Hasegawa, 2006); el L15 y M199 para las células del manto del abulón *Haliotis varia* (Linnaeus) (Suja *et al.*, 2007) y el Pf-CM2.5 (mezcla 1:1 de 2´ Leibovitz y M199) con la ostra perlera japonesa *P. fucata* (Gong *et al.*, 2008).

El uso de sustratos celulares y factores de crecimiento también se mantiene como un aspecto controversial en el desarrollo de tecnología para el cultivo *in vitro* de células somáticas en moluscos. Existen reportes de una mejora en la adhesión de diferentes células del mejillón *Mytilus* sp. con el uso de poli-L-lisina y fibronectina (Odintsova *et al.*, 1994), así como de un mejor anclaje de las células de larvas trocóforas del abulón rojo *H. rufescens* (Linnaeus) con poli-D-lisina y fibronectina (Naganuma *et al.*, 1994). Sin embargo, también se ha señalado la inexistencia de efectos claros de estas mismas moléculas en las propiedades de adhesión de las células de glándula digestiva del mejillón *M. galloprovincialis* (Lamarck) (Robledo & Cajaraville, 1997). Algunos autores han sugerido incluso que las diferencias en las propiedades de adhesión, regeneración y estructura celular se deben al efecto de otros factores reguladores, como la temperatura de incubación (Awaji y Machii, 2011), la salinidad (Kim *et al.*, 2014) y molaridad del medio de cultivo (Perez-Camps & García-Ximénez, 2008). Estos resultados hacen necesario investigar más sobre el efecto de estos factores reguladores en la estabilidad e integridad de los cultivos de manto en *P. mazatlanica* y otras especies de moluscos productores de perlas, tanto para confirmar como para mejorar los resultados obtenidos en este estudio.

Todas las células de manto obtenidas mediante disgregación enzimática se adhirieron con éxito al sustrato, y después de iniciar un proceso de proliferación en monocapa, cambiaron de la forma redonda a la típica forma de fibroblasto después del tercer día de cultivo. Sin embargo, la gran variabilidad en la concentración de células libres que se obtuvieron (0–100%) sugiere que las enzimas evaluadas fueron inespecíficas para cultivar células del manto y/o que actuaron sobre sustratos análogos. Bajo estas condiciones, la colagenasa I (ampliada de 5 a 414 U/mg) fue la enzima que claramente incrementó más la viabilidad y rendimiento celular a todas las temperaturas de cultivo, alcanzando una densidad máxima de 120 $\times 10^3$ cel/mL a 37 °C. Se sabe que la mayoría de las colagenasas degradan hebras helicoidales de colágeno que son abundantes en el tejido conectivo de muchos invertebrados (Engel, 1997; Rinkevich *et al.*, 2005) y García-Gasca *et al.* (1994) confirmaron su presencia en el manto de la madreperla *P. mazatlanica*. Si bien la proteinasa K, proteasa y tripsina hicieron posible la liberación de poblaciones de células viables a todas las temperaturas durante las primeras etapas de la digestión, fueron agresivas en etapas posteriores y las dañaron parcial o totalmente, por lo que su rendimiento final fue pobre. Igualmente, la enzima proteolítica de *T. herzianum* demostró ser ineficiente para liberar células del manto y mantener su viabilidad, probablemente por no existir en este tejido un sustrato específico para la enzima. Se sugiere evaluar con más precisión la temporalidad de la acción benéfica y el posible efecto nocivo de estas enzimas para avanzar en la optimización de una técnica para cultivo *in vitro* de células y explantes de manto de *P. mazatlanica*.

La técnica de rojo de Alizarina fue poco sensible a la detección de calcio tisular, no obstante su abatimiento en un 55% a 0.6 M (que es la molaridad más alta y similar a la del agua de mar a 35 g/L), fue confirmada por espectrofotometría de absorción atómica. Este resultado sugiere una posible bio-disponibilidad de $CaCO_3$ en el medio de cultivo para la proliferación de células y explantes, lo cual a su vez podría favorecer la síntesis de nácar como cimiento de la perla. Al respecto, algunos autores señalan que la síntesis de $CaCO_3$ y nácar por parte del manto durante la biomineralización y formación de una perla puede estar regulada por "moléculas relacionadas con la síntesis del péptido calcitonina" (CGRP)" y "proteínas de unión al calcio" en el abulón *H. tuberculata* (Linnaeus) (Auzoux-Bordenave *et al.*, 2007), así como por la proteína "nacarina" y el péptido "p10" en la ostra perlera *P. fucata* (Gong *et al.*, 2008; Zhang *et al.*, 2010). Estudios dirigidos a la identificación de algunas de estas moléculas se están realizando en *P. mazatlanica* y *P. sterna* en este momento, como una estrategia para implementar gradualmente una tecnología que permita la formación segura *in vitro* del saco perlero, que es la primera capa basal de células de nácar secretada por el manto en 15-21 días para cubrir el núcleo esférico que se coloca durante la cirugía de injerto. El desarrollo de una tecnología de este tipo tiene aplicación directa en las actividades comerciales de producción de perlas, ya que el saco perlero formado *in vitro* podría colocarse en ostras receptoras para ayudar a reducir las altas tasas de rechazo post-injerto que se registran en todo el mundo.

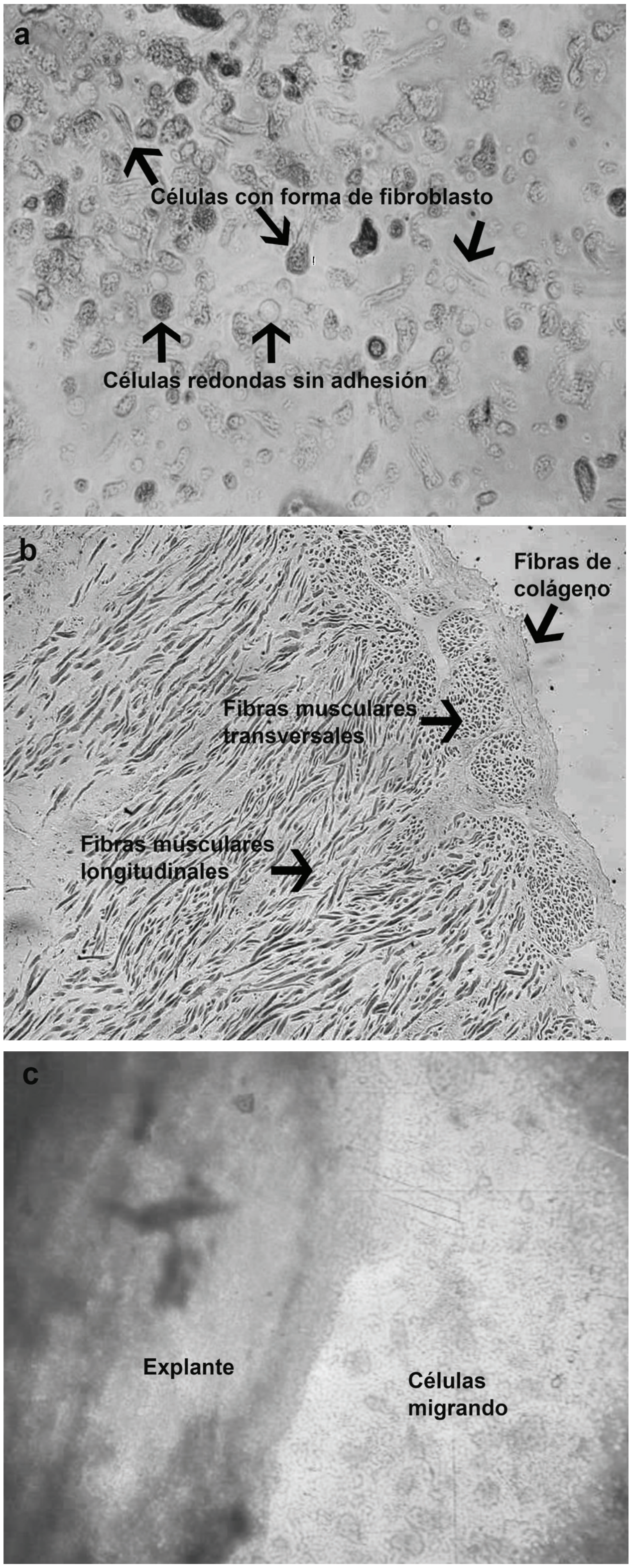


Figura 3. Microfotografías (40×) de manto de madreperla *Pinctada mazatlanica* cultivados en medio RPM-1640, mostrando células disgregadas cambiando de forma a fibroblastos (a), un explante con la típica estructura del tejido sano (b), y un explante con conglomerados de células migrando hacia fuera a la molaridad de 0.6 M (c).

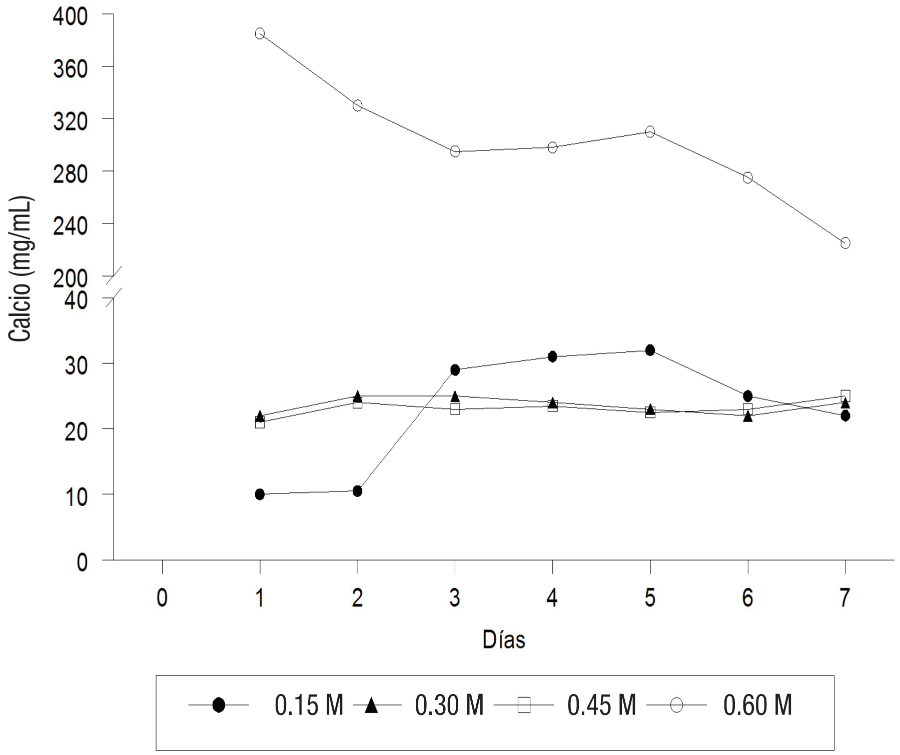


Figura 4. Variaciones en la concentración de calcio en medio de cultivo RPMI-1640 a diferentes molaridades, en explantes de manto de madreperla *Pinctada mazatlanica*.

En su conjunto, los resultados de este estudio cumplieron con el objetivo de definir las condiciones básicas para el cultivo primario de células del manto de *P. mazatlanica*; marcan también con claridad las futuras investigaciones por realizarse en torno a la reformulación de nuevos medios de cultivo, evaluación de factores de crecimiento y análisis del valor del cultivo celular 3D para maximizar la viabilidad y regeneración celular, así como la síntesis de $CaCO_3$ y cristales de aragonita y calcita. Finalmente, es recomendable cuantificar la expresión de enzimas y genes relacionados con todos estos procesos, lo que en un futuro cercano podría ayudar a definir una línea de cultivo celular de manto, con potencial aplicación en la producción *in vitro* del saco perlero (inicialmente) y de perlas (posteriormente).

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## REFERENCIAS

Auzoux-Bordenave, S., M. Fouchereau-Peron, M.N. Helleouet & D. Doumenc. 2007. CGRP regulates the activity of mantle cells and hemocytes in abalone primary cultures (*Haliotis tuberculata*). *Journal of Shellfish Research* 3: 887–894.

Awaji M. & A. Machii. 2011. Fundamental studies on *in vivo* and *in vitro* pearl formation: Contribution of outer epithelial cells of pearl oyster mantle and pearl sacs. *Aqua-BioScience Monographs* 4: 1-39.

Barik S. K., J. K. Jena & K. Janaki-Ram. 2004. $CaCO_3$ crystallization in primary culture of mantle epithelial cells of freshwater pearl mussel. *Current Science* 86 (March): 1-10.

Dharmaraj S. & C. P. Suja. 2002. Development of technology in *in-vitro* pearl production in India. *Bulletin of the Malacological Society of London* 39: 1-5.

Endoh, M. & Y. Hasegawa. 2006. Culture of mantle epithelial cells expressing shell matrix proteins from scallop *Patinopecten yessoensis*. *Fisheries Science* 72: 1277-1285. DOI: 10.1111/j.1444-2906.2006.01286.x.

Engel, J. 1997. Versatile collagens in invertebrates. *Science* 277: 1785–1786.

García-Gasca, A., R.I. Ochoa-Baez & M. Betancourt. 1994. Microscopic anatomy of the mantle of the pearl oyster *Pinctada mazatlanica* (Hanley, 1856). *Journal of Shellfish Research* 13: 297-303.

Gong, N., Z. Ma, Q. Li, Q. Li, Z. Yan, L. Xie & R. Zhang. 2008. Characterization of calcium deposition and shell matrix protein secretion in primary mantle tissue culture from the marine pearl oyster *Pinctada fucata*. *Marine Biotechnology* 10: 457-465. DOI: 10.1007/s10126-008-9081-1.

Kiefert, L., D. McLaurin, E. Arizmendi, H.A. Hänni & S. Elen. 2004. Cultured pearls from the Gulf of California, Mexico. *Gems* & *Gemology* 40: 26-38.

Kim, M.S., Y.K. Nam, D.S. Kim & S.P. Gong. 2014. Initial culture conditions for primary cell populations derived from radula tissue in abalone *Haliotis discus hannai*. *Fisheries and Aquatic Sciences* 17: 385-390. DOI: 10.5657/FAS.2014.0385.

Levi, Y., S. Albeck, A. Brack, S. Weiner & L. Addadi. 1998. Control over aragonite crystal nucleation and growth: an *in vitro* study of biomineralization. *Chemistry European Journal* 4: 389-396. DOI: 10.1002/(SICI)1521-3765(19980310)4:3<389::AID-CHEM389>3.0.CO;2-X.

McGee-Russell, S. M. 1958. Histochemical methods for calcium. *Journal of Histochemistry and Cytochemistry* 6: 22-42.

Mirjalili, A., E. Parmoor, B.S. Moradi & B. Sarkari. 2005. Microbial contamination of cell cultures: A 2 years study. *Biologicals* 33: 81-85.

Naganuma, T., B.M. Degnan, K. Horikoshi & D.E. Morse. 1994. Myogenesis in primary cell cultures from larvae of the abalone, *Haliotis rufescens*. *Molecular Marine Biology and Biotechnology* 3: 131-140.

Odintsova, N.A., A.V. Ermak & L.G. Tsal. 1994. Substrate selection for long-term cultivation of marine invertebrate cells. *Comparative Biochemistry and Physiology* 107A: 613-619.

Perez-Camps, M. & F. Garcia-Ximenez. 2008. Osmolarity and composition of cell culture media affect development and survival in zebrafish embryos. *Animal* 2: 595-599. DOI: 10.1017/S1751731108001572.

Pichon, D., B. Cudennec, S. Huchette, C. Djediat, T. Renault, C. Paillard & S. Auzoux-Bordenave. 2013. Characterization of abalone *Haliotis tuberculata-Vibrio harveyi* interactions in gill primary cultures. *Cytotechnology* 65: 759-772. DOI: 10.1007/s10616-013-9583-1.

Poncet, J. M., A. Serpentini, B. Thiébot, C. Villers, J. Bocquet, E. Boucaud-Camou & J. M. Lebel. 2000. *In vitro* synthesis of proteoglycans and collagen in primary cultures of mantle cells from the nacreous mollusk, *Haliotis tuberculata*: A new model for study of molluscan extracellular matrix. *Marine Biotechnology* 2: 387-398. DOI: 10.1007/PL00021685.

Rinkevich, B. 1999. Cell cultures from marine invertebrates: obstacles, new approaches and recent improvements. *Journal of Biotechnology* 70: 133-153.

Rinkevich, B. 2005. Marine invertebrate cell cultures: new millennium trends. *Marine Biotechnology* 7: 429-439.

Robledo, Y. & M. P. Cajaraville. 1997. Isolation and morphofunctional characterization of mussel digestive gland cells *in vitro*. *European Journal of Cell Biology* 72: 362-369.

Saucedo, P. E., A. Castillo-Domínguez & C. Melgar-Valdez. 2017. Aprovechamiento de almejas dulceacuícolas en Tabasco para formación de perlas y artesanías. Colección José N. Rovirosa, Universidad Juárez Autónoma de Tabasco, Villahermosa, México, 133 pp. ISBN: ISBN: 978-607-606-396-5.

Sud, D., D. Doumec, E. Lopez & C. Milet. 2001. Role of water-soluble matrix fraction, extracted from the nacre of *Pinctada maxima*, in the regulation of cell activity in abalone mantle cell culture (*Haliotis tuberculata*). *Tissue and Cell* 33: 154-160. DOI: 10.1054/tice.2000.0166.

Suja, C. P. & S. Dharmaraj. 2005. *In vitro* culture of mantle tissue of the abalone *Haliotis varia* Linnaeus. *Tissue and Cell* 37: 1-10.

Suja, C. P. N. Sukumaran & S. Dharmaraj. 2007. Effect of culture media and tissue extracts in the mantle explant culture of abalone, *Haliotis varia* (L). *Aquaculture* 271: 516-522. DOI: 10.1016/j.aquaculture.2007.04.086.

Taylor, J. & E. Strack. 2008. *Pearl production*. The Pearl Oyster. En: Southgate, P.C. J.S. Lucas (Eds.), Elsevier Science, Amsterdam, Holanda, pp. 273-302.

Van der Merwe, M., S. Auzoux-Bordenave, C. Niesler & R. Roodt-Wilding. 2010. Investigating the establishment of primary cell culture from different abalone (*Haliotis midas*) tissues. *Cytotechnology* 62: 265-277. DOI: 10.1007/s10616-010-9293-x.

Van Phuc, P., P. Quoc Viet, N. Minh Hoang, N. Thanh Tam & P. Kim Ngoc. 2011. Research on *in vitro* culture and inducing nacre crystal formation of freshwater pearl mussel mantle epithelial cell *Sinohyriopsis cumingii*. *International Journal of Fishery and Aquaculture* 3: 105-113.

Youbin, Z., S. Anjing & Z. Honyuan. 1994. The pharmacological functions of nacrum secreted by the cultured pallium cells of fresh water oyster. *Acta Hydrobiologica Sinica* 18: 327-333.

Zang, C., S. Li, Z. Ma, L. Xie & R. Zhang. 2006. A novel matrix protein p10 from the nacre of pearl oyster (*Pinctada fucata*) and its effect on both $CaCO_3$ crystal formation and mineralogenic cells. *Marine Biotechnology* 8: 624-633. DOI: 10.1371/journal.pone.0066564.

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# Relation between the sharpnose shark *Rhizoprinodon terranovae* in the southern Gulf of Mexico and the average number of sunspots

# Relación entre capturas del tiburón *Rhizoprionodon terraenovae* al sur del Golfo de México y el número de manchas solares

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## ABSTRACT

**Background**. The Antillean or sharpnose shark is one of the main exemplars of shark species in the commercial catch in the southern Gulf of Mexico. Oceanic dynamics on the planet Earth vary year to year due to the oscillation of solar radiation; fish abundance (and catches) likely respond to these oscillations. **Goals**. This study focuses on analyzing the variability of landings of the Antillean sharpnose shark (*Rhizoprionodon terraenovae*) on the Mexican coast of the Gulf of Mexico, from 1940 to 2006, and its possible connection with solar activity as assessed by the average sunspot number (Zürich Index). **Methods**. A polynomial curve by least-squares best fitting was used to eliminate the tendency from the sharpnose-shark-landing time series. Spectral techniques of Maximum Entropy (ME) and Fast Fourier Transform (FFT) were used to analyze the time series of sharpnose-shark landings and the Zürich Index. **Results**. The time series of sharpnose-shark landings showed a remarkable spectral peak with a period of about 12.8 years, while the Zürich Index showed a marked peak at a period of 11.6 years. Cross-correlation revealed a delay between the average number of solar spots and sharpnose-shark landings. **Conclusions**. This study is the first to report such low frequency variability for landings of the *R. terraenovae* fishery in the Gulf of Mexico, using a particular methodology that can provide information for the design of predictive models in the future. The analyzed landing volumes of the sharpnose shark *R. terraenovae* showed as a result a periodical behavior that coincided with Wolf's solar activity cycle of 10.6 years.

**Key words:** Antillean sharpnose-shark landings, Fast Fourier Transform and Maximum Entropy, Gulf of Mexico, solar activity, time series.

## RESUMEN

**Antecedentes**. El cazón antillano o tiburón picudo, es uno de los ejemplares principales de las especies de tiburón en la captura comercial en el sur del Golfo de México. La dinámica oceánica en el planeta tierra varía de forma interanual debido a la oscilación de la radiación solar; las abundancias (y capturas) de peces responden a estas oscilaciones. **Objetivos**. Analizar la variabilidad de las capturas del cazón antillano *Rhizoprionodon terraenovae* en el litoral mexicano del Golfo de México, de 1940 a 2006 y su posible relación con la actividad solar, evaluada mediante el número promedio de manchas solares (Índice de Zürich). **Métodos**. Se empleó el polinomio de mejor ajuste por mínimos cuadrados para eliminar la tendencia de la serie temporal de las capturas; y se utilizaron las técnicas espectrales de la Transformada Rápida de Fourier (FFT) y de Máxima Entropía (ME) para analizar las series temporales de las capturas de cazón y del índice de Zürich. **Resultados**. Se muestra un pico espectral distintivo en la serie de capturas con una frecuencia de alrededor de 12.8 años, en tanto que el índice de Zürich muestra un pico marcado a los 11.6 años. La correlación cruzada reveló un retraso entre el número promedio de manchas solares y las capturas de tiburón. **Conclusiones**. Este trabajo es el primero en reportar una frecuencia tan baja en la variabilidad de las capturas de la pesquería de *R. terraenovae* del Golfo de México, empleando una metodología particular que puede proporcionar información para el diseño de modelos predictivos en el futuro. Los volúmenes de captura analizados del cazón antillano *R. terraenovae* mostraron como resultado un comportamiento periódico en coincidencia con el ciclo de actividad solar de Wolf de 10.6 años.

**Palabras clave:** Actividad solar, captura del cazón antillano, Golfo de México, series de tiempo, Transformada Rápida de Fourier y Máxima Entropía.

## INTRODUCTION

In terms of catch volume, shark fishing in the southern Gulf of Mexico, both multi-specific and artisanal, is the 10th most important in Mexico. According to Rodríguez-De la Cruz *et al.* (1996) and Martínez-Cruz *et al.* (2016), the sharpnose shark *Rhizoprionodon terraenovae* (Richardson 1836), is one of the main exemplars of dominant shark species in the commercial catch (45.9%), in terms of weight (SEMARNAT, 2000).

The sharpnose shark is a particular coastal species that is adapted to tropical water and its adult length ranges from 29 cm to 110 cm. This shark has a viviparous development and a gestation length estimated at 11 or 12 months, bearing between five and twelve pups (Castillo-Géniz, 1992). As a result of these characteristics, this shark is considered a k-type strategist, implying that its capacity to respond to environmental variations –such as changes in human activities, especially overfishing– is quite limited (Hoenig & Gruber, 1990). For this reason, the review of oscillations in its capture may provide insight to the potential influence of different environmental variables on this shark's landing volumes behavior. Among the environmental variables that could affect the abundance of sharks, primary production fluctuations caused by solar radiation oscillations related to solar activity are among the main ones (Lluch-Cota, 2004). Therefore, the joint analysis of time series for landings of *R. terraenovae* and solar activity cycles may allow the identification of possible coincidences when subjected to an innovative approach that we discuss below. Similar exercises have been carried out for other fisheries in Mexico, such as the Gulf of California sardines –where evidence showed a dominant frequency of about 5 years (Huato-Soberanis & Lluch-Belda, 1987)– but have never been applied before to the *R. terraenovae* fishery in the southern Gulf of Mexico. This type of analysis may be an important contribution and baseline for the construction of future predictive models.

The effect of solar activity –as determined by the number of sunspots– on the biosphere, on fluctuations of the Earth's magnetism, temperature, radiance intensity, and energy fluxes, has already been tested. Several studies have related fish catch with solar cycles. Helland-Hanses and Nansen, quoted by Hjort (1914), conducted one similar pioneer analysis and provided evidence on an existing relationship between water temperature, currents, and their effects on fishing activities resulting from solar activity. Likewise, the study conducted by Bulatov (1995) in the Bering Sea is one of the most comprehensive studies on this subject, consisting of a historical review of fishing activity according to spawning, demographic structure, size, cohort composition, and particular conditions of the pollock *Theragra chalcogramma* (Pallas, 1814) stocks. In his research, Bulatov (1995) concluded that the largest classes were constituted during the ascendant phase of the Wolf's cycle curve. Harmonics of 11 years in catch volumes of salmon *Coregonus lavaretus (Linnaeus, 1758*), perch (*Perca fluviatilis Linnaeus, 1758*), and cyprinids *Rutilus rutilus (Linnaeus, 1758*) were detected in Lake Constance, Canada, and provided evidence about an existing relationship. This was determined by an indirect tie with cyclical conditions from environmental variables, which were accordingly related to solar activity and striking over such populations' biological stages (Hartmann, 1995). A cyclical variation of scallop recruitment was estimated in southern Australia, associated to corresponding harmonics of the west wind blowing in that region (Thresher, 1994). Oscillations in solar activity are responsible for climatic fluctuations in a scale ranging from 40 to 60 years and are related to variations on abundance of diverse commercial fisheries in Russia (Davydov, 1986). Similarly, Guisande *et al.* (2004) proved that abundance of sardine *Sardina pilchardus* (Walbaum, 1792) in the Iberian Atlantic is governed by solar activity. Vanselow and Ricklefs (2005) demonstrated the existence of a relationship between solar activity and stranded sperm whales *Physeter macrocephalus* Linnaeus, 1758, in the North Sea.

Time series analysis is a research technique that was developed many years ago. Its application to biological research has been limited, due to the inherent difficulty in gathering a data series of sufficient length. Thus, even though there is ample recognition of space and time oscillations of biological and ecological processes, and the fact that they respond to oscillatory forcing of high and low frequencies –such as diel variation, among the former and Earth translation, El Niño events, the North Atlantic Oscillation and sunspot cycles, for the latter– its application to the analysis of biological systems behavior has not really been fully exploited (Platt & Denman, 1975).

Consequently, this study aims to analyze the possible relation between solar activity and the landing behavior of the sharpnose *R. terraenovae* along the Mexican shoreline of the southern Gulf of Mexico between 1940 and 2006.

## MATERIALS AND METHODS

Registries of the annual volumes of catches of *Rhizoprionodon terraenovae* were reported as fresh weight landed on the different harbors of the southern Gulf of Mexico, as listed by the Governmental Statistical Yearbooks from 1940 to 2006 (SEMARNAP, 1940-2006; Fig. 1). Annual averages of sunspot numbers (Zürich Index) were obtained from Solar-Geophysical Data Comprehensive Reports of NOAA (2007) at the following web address: www.ngdc.noaa.gov/stp/Solar/ftpsunspotnumber, and plotted on Figure 2.

**Processing the shark landings.** The literature dealing with Catch per Unit Effort (CPUE) has approached the problem of splitting the original data into their different temporal components in several ways: linear methods, sine function, and spectral analysis. For the jumbo squid (*Dosidicus gigas* d'Orbigny [in 1834-1847], 1835), monthly catch data from 2002 to 2005 were grouped into three large zones, and the trend of the time series was removed by using a LOESS smoother. The residuals between the original and the LOESS trend curve were computed and analyzed using autocorrelation and cross-correlation at different lags, and a trigonometric model was fitted to detect seasonal oscillation (Zúñiga *et al.*, 2008). As for the sailfish fisheries in the Mexican Pacific, time series methods (the removal of two harmonics from their original CPUE data) were used to estimate CPUE trends as an abundance indicator (Macías-Zamora *et al.*, 1994).

If a survey is conducted in a time series looking for periods of around 11 years, high frequency events far from the target period must be eliminated (Emery & Thomson, 2004). In the special case of shark-landing time series, due to a growing trend in fishing activities through time (Fig. 1), a very low frequency wave (1/64 Yr) with high energy was generated. Thus, in order to detect 11-year periodicity, a method must be applied in a way that eliminates the fishing -activity trend.

To eliminate this low frequency trend, we implemented the following procedure: a) A centered smooth (moving) average was computed for the shark-landing time series $(L_{n-2} + L_{n-1} + L + L_{n+1} + L_{n+2})/5$,

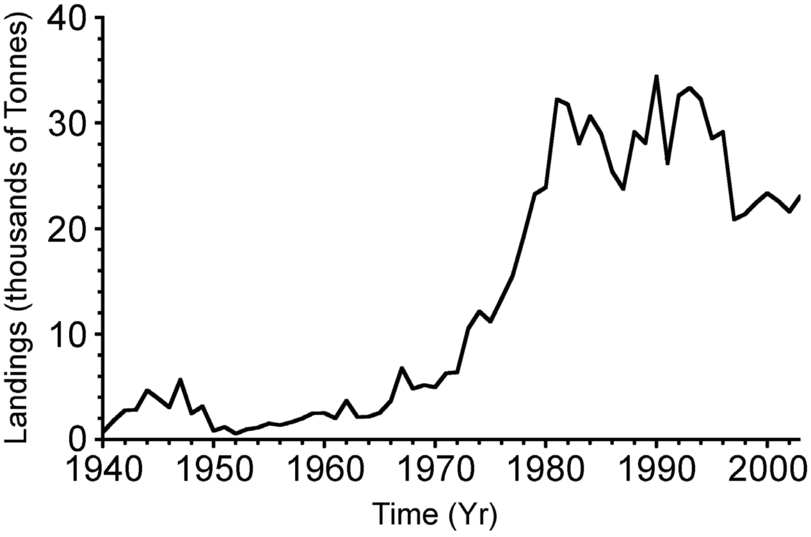

Figure 1. Time series (Yr) of sharpnose (*Rhizoprionodon terraenovae*) landings (thousands of tons) in the Gulf of Mexico between 1940 and 2003. There has been a strong increase in landings since the late 60s.

where L is the landing in the nth time. b) By the least-squares method, a best-fit polynomial was computed for the smoothed series with a FORTRAN program prepared according to Lawson and Hanson (1974). The resultant polynomial was:

$$\text{CompLand}(t) = 5\text{x}10^{-05}\, t^6 - 0.0085\, t^5 + 0.4981\, t^4 - 11.504\, t^3 + 91.268\, t^2 - 45.349\, t + 1759 \qquad \text{eq. 1}$$

where CompLand(t) is the computed landing at time t. c) The polynomial was used to compute the landings as a function of time, as seen in Figure 3. d) From CompLand(t) and ObsLand(t) a catch-difference (anomaly) time series was generated (Dif(t), (Fig. 4). The differences time series (Dif(t)) was standardized. The procedure was as follows.

The polynomial was computed from the smoothed landing time series, as stated above, while the differences were computed according the following equation:

$$\text{Dif}(t) = \text{ObsLand}(t) - \text{CompLand}(t) \qquad \text{eq. 2}$$

where ObsLand(t) is the observed landing at time t, and CompLand(t) is the shark landing at time t computed from the polynomial. As usual in time series, analysis data were standardized (Bendat & Piersol, 1986) by using z(t) values defined as follows:

$$z(t) = (\text{Dif}(t) - \text{Dif}\,') / \text{Stadev} \qquad \text{eq. 3}$$

where z(t) is the normalized value at time t, Dif(t) is the difference obtained from the landings and the polynomial computed from eq. 2, and Dif' and Stadev were the average and standard deviation of the Dif(t) time series. The z(t) time series was detrended as explained bellow.

The standardized difference time series of sharpnose landings (z(t)) and Zürich Index were studied through a spectral analysis, using two distinctive methods: Fast Fourier Transform (FFT, Bendat & Piersol, 1986) and Maximum Entropy (ME, Calmet *et al.*, 1984). FFT is a model coherent in the definition of energy density, but has the disadvantage that the number of data needed has to be cut down to a power of 2 ($\sim 2^{6,8}$). Through the ME method a good frequency resolution might be obtained, but energy densities and spurious frequencies may suffer from alterations when the number of used poles (m) is not properly computed (Calmet *et al.,* 1984).

Data used for the analysis of shark catches came from a series of 67 years, where the series trend was removed. The time series was competed to $2^8$. The time series obtained through this technique was analyzed afterwards in order to obtain specific spectral figures.

The trend was removed from the sunspot time series, although it was not necessary to append it up recursively as the data came from ~ 307 years. The most common technique for trend removal is to fit a straight-line equation using econometric tools such as least-squares procedures. The linear regression takes the form of a straight line with an intercept of $b_0$ and a slope $b_1$, which is subtracted from the original data values $\{x_n\}$ (Bendat & Piersol, 1986). That is, if $x_1$' is the new value without the trend, then

$\{x_1'\}=\{x_1\} - \{1\, b_1 + b_0\}$,

$\{x_2'\}=\{x_2\} - \{2\, b_1 + b_0\}, \ldots$

$\{x_n'\}=\{x_n\} - \{n\, b_1 + b_0\}$

The new time series so obtained were detrended and the requisite of stationarity for the FFT method accomplished (Brigham, 1974).

The processes of energy transference between the sun and the biosphere are not registered immediately by the latter. The reason is that, in general, there is a lag between a general stimulus and its response; thus, the potential correlation between both would not be statistically significant if an immediate response was supposed. If an appropriate delay is considered –that is to say, if the correlation is estimated for a response displayed 1, 2,.., n intervals later– linear correlations become statistically significant.

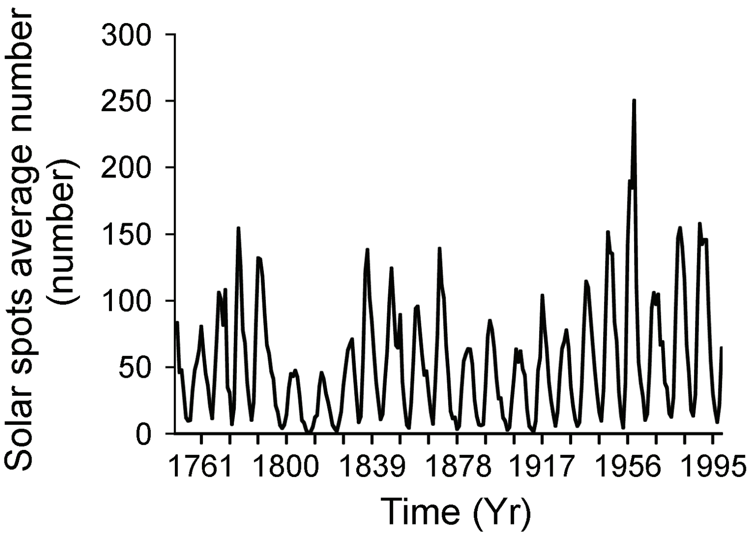

Figure 2. Time series (Yr) of the average number of sunspots per year (Zürich Index) between 1749 and 2003**.**

In order to determine the delay between *R. terraenovae* landings and solar activity, a cross-correlation analysis was computed, using the differences series (z(t)) and Sspot(t). Through this technique, the level of likeliness between both variables was not only visible –defining the independent variable as "fixed" and the dependent variable as "lagged"–, but the delay time between both processes could be observed as well (Legendre & Legendre, 1979).

Briefly, removal of a trend through a polynomial of shark landings was applied. Time series of shark landings and sunspots were detrended. Spectral analyses were applied with the FFT and ME techniques in an effort to add the advantages of the implementation of both methods. Different authors have performed a similar analysis to the same data set and obtained a frequency of 10.6 years for the Zürich Index (Vanselow & Ricklefs, 2005).

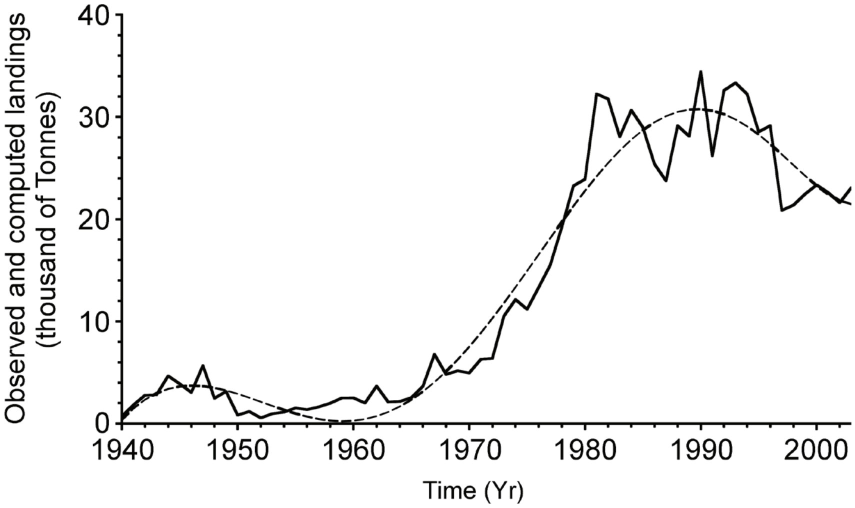

Figure 3. Time series (Yr) of sharpnose (*Rhizoprionodon terraenovae*) landings (thousands of tons) black line, and computed landings from the least-squares polynomial (dashed line). Differences between the two series were used for spectrum computations.

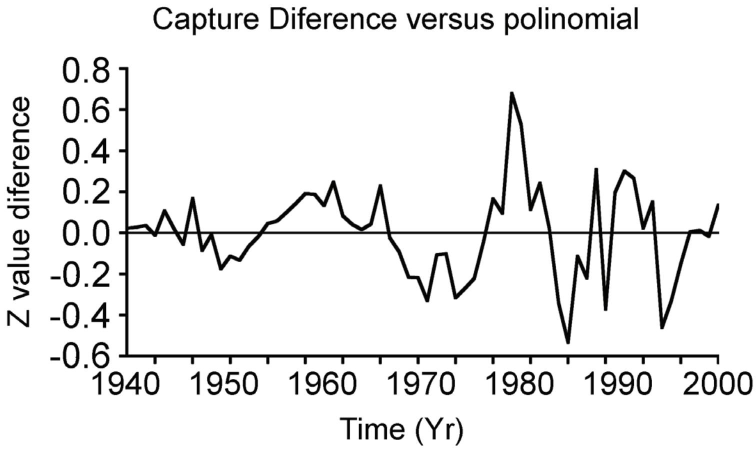

Figure 4. Z standardized values of the difference between the observed landings and the polynomial computed data (z-landings). Z is defined as (x' - $x_i$)/σ, where x' is the average, $x_i$ the i-th landing difference data, and σ the standard deviation).

## RESULTS

Original time series of data from *R. terraenovae* landings (Fig. 1) and solar activity ($R_z$) (Fig. 2) are presented. *R. terraenovae* landings show a clear trend to increase with time, which reflects an increase in fishing activities. Thus, in order to detect any cyclical behavior, for both series the trend was removed through the polynomial (Fig. 3).

Normalized values (z(t)) of the differences between the observed sharpnose shark (*R. terraenovae*) landings (ObsLand(t)) and the computed landings through the polynomial (ComLand(t)) are observed in Figure 4. The series, thus transformed and normalized, is referred to as *sharpnose shark time series* in the text that follows and should not be confused with the sharpnose-shark landings series.

The power spectra of the *sharpnose shark time series*, through the joint examination using both methods (ME and FFT), are shown on Figure 5. The resulting spectrum of shark landings showed other peaks of higher frequency. The most striking feature detected in the shark spectrum is that the major oscillation energy reached a frequency of 2.51 x $10^{-9}$ Hz (the peak of 12.8 years), (Fig. 5).

Different peaks of lower frequency can be identified as well (Fig. 5). It is likely that the peak around 22 years is, up to where we can analyze the series, the second one of major energy, although the sharpnose shark landings series is not large enough to provide absolute certainty.

Figure 6 shows the power spectrum of the average number of solar spots (Zürich Index) time series. The main harmonic detected for ME analysis is a sharp peak of 10.88 years. For FFT analysis two peaks are present: 11.1 years and 10.66 years. Note that the data of the yearly average of sunspot numbers resulted in a neat peak for both spectra, for that obtained by ME, as well as by FFT (Fig. 6).

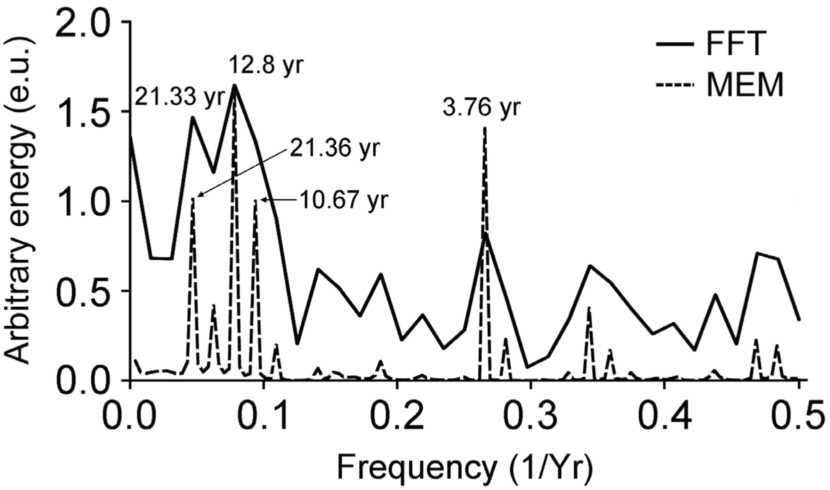

Figure 5. Power spectrum by the Maximum Entropy Method (MEM; m= 60 poles) of the z-landings time series (dashed line), and by the Fast Fourier Transform method (FFT), (solid line). Conspicuous frequencies are noted with their equivalent period in years.

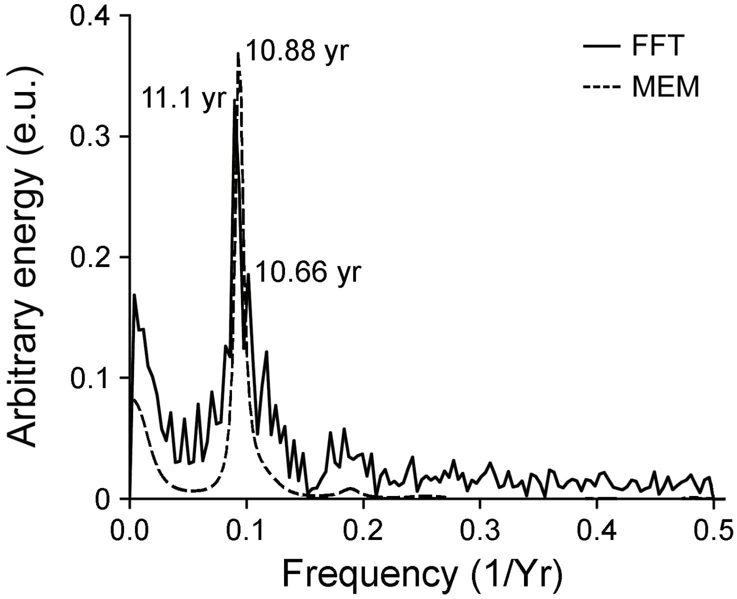

Figure 6. Power spectrum by the Maximum Entropy Method (MEM; m= 40 poles) of the average number of sunspots (Zürich Index) time series (dashed line), and by the Fast Fourier Transform method (FFT), (solid line). The well-defined sunspot frequency is noted with its equivalent period in years.

Cross-correlation reveals a delay between the average number of solar spots and sharpnose-shark landings (Fig. 7). A good correlation was obtained when sharpnose-shark landings were delayed one year (R= 0.65) and two years (R= 0.60); further delay times had lower R's.

## DISCUSSION

In time-series analysis, a common practice along the scientific community is the use of the complementary FFT and ME methods (Calmet *et al.*, 1984). Time series are useful to describe the potential environmental variations related to catch volumes of fish populations susceptible to exploitation (Ottersen *et al.,* 1994). The variation of catch volumes along different fishing stocks in distinctive parts of the world responds to periodical climatic variations of temperature, rainfall, cloud coverage, and evaporation, which interact with water temperature, salinity, density, and, consequently, water mass dynamics (Francis & Sibley, 1991; Mountain & Murawski, 1992; Ohtani & Azumaya, 1995; Studenetsky, 1995; Yang *et al.*, 1995).

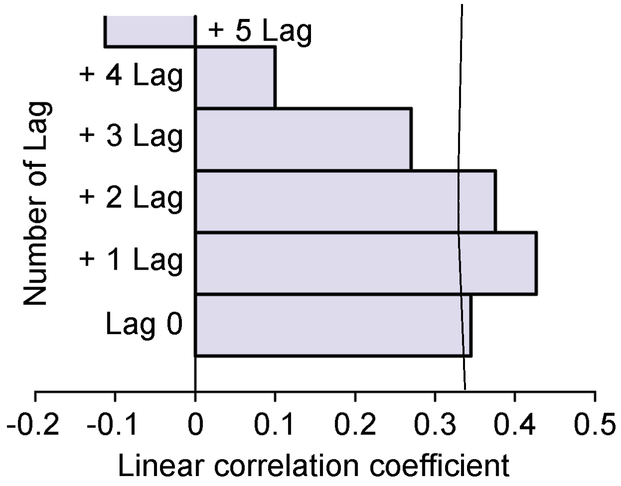

Figure 7. Linear cross-correlation coefficients of z-landing time series versus the average number of sunspots (Zürich Index) time series. Each bar corresponds to a forward lag of one year of the z-landings.

By building a polynomial, we were able to obtain a time series amenable for use in spectral analysis. Without this adjustment, the increase in catch per fishing activity would have complicated the analysis, due to the great wave or harmonic introduced by fishing activity, which started during the late 60s and finished until the late 90s.

In coastal regions inhabited by *R. terraenovae*, several variables exert a marked influence in environmental fluctuations. The first and main one is temperature: Its positive anomalies coincide with a wider access of solar irradiance unleashing changes in wind intensity throughout tropical latitudes that, overall, modify humidity and, thus, cloud coverage. While the ocean surface stores an important amount of heat, the sea surface temperature (SST) reacts directly to solar forcing, even though a lag occurs. Related to what was described before, Van Loon and Labitzque (1994) detected that the reaction scale under which the process of energy exchange operates –coming from irradiance inputs– with the consequential thermal increment of the SST in tropical latitudes- is year-to-year and responds to the same frequency of Wolf's solar cycle.

A complete understanding of the behavioral dynamics of one or more communities would involve their study for several decades, in order to determine the underlying mechanisms that jeopardize fluctuations in the populations resulting from the perennial search for system equilibrium, which is periodically broken and in different time scales as a result of the climate's influence.

Ocean-atmospheric variables, such as rainfall and water temperature –including their "modifiers"– are connected to solar activity cycles (Sánchez-Santillán, 1999). The relationship occurs in such a way that, if organisms have a narrow relationship with the respective environmental variables and the latter have a periodical nature (Haig, 2003; Haig *et al*., 2005), the same periodical pattern would be attained for the organisms' behavior.

In this study, the analysis of a short shark-landing time series –with data from 66 years– was possible with the combined aid of two spectral methods (the ME and FFT methods).

The analyzed landing volumes of the sharpnose shark *R.* appeared because of a periodical behavior that coincided with Wolf's solar activity cycle of 10.6 years.

## REFERENCES

Bendat, J. S. & A. G. Piersol. 1986. *Random Data: Analysis and measurement procedures*. 2nd Edition. John Wiley & Sons. New York, USA. 566 p.

Brigham, E. O. 1974. *The fast Fourier Transform*. Prentice Hall. Inc. Englewood Cliffs. New Jersey, USA. 252 p.

Bulatov, O. A. 1995. Biomass variations of walleye pollock of the Bering Sea in relation to oceanological conditions. *In*: Beamish, R. J. (Ed.). *Climate change and northern fish populations*. Canadian Special Publication of Fisheries and Aquatic Science. No. 121. National Research Council of Canada. Ottawa, Canada, pp. 631-640.

Calmet, D., S. Charmasson & F. Blanc. 1984. Application de l'analyse spectrale par maximisation de l'entropie dans la description des séries brèves en écologie marine. *Oceanologica Acta* 7 (1): 77-86.

Castillo-Géniz, J. L. 1992. *Diagnóstico de la pesquería de tiburón en México*. INE. Instituto Nacional de la Pesca. Secretaría de Pesca. México. 75 p.

Davydov, I. V. 1986. *On the nature of long-term fluctuations in fish abundance and possibilities of their prediction*. Dinamika Chislennosti Promyslovskh Zhivotnykh Dal Nevostochnykh Morej. TINRO. Vladivostok, pp. 5-17.

Emery, W. J. & R. E. Thomson. 2004. *Data analysis methods in physical oceanography.* 2da Edition. Elsevier Science. B. V. Inc. Amsterdam. 654 p.

Francis, R. C. & T. H. Sibley. 1991. Climate change and fisheries: What are the real issues? *Northwest Environmental Journal* 7 (2): 295-307.

Guisande, C., A. Ulla & P. Thejll. 2004. Solar activity governs abundance of Atlantic Iberian sardine *Sardina pilchardus*. *Marine Ecology Progress Series* 269: 297-301. DOI: 10.3354/meps269297

Haigh, J. D. 2003. The effects of solar variability on the Earth's climate. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 361 (1802): 95-111. DOI:10.1098/rsta.2002.1111

Haigh, J. D., M. Lockwood & M. S. Giampapa. 2005. *The sun, solar analogs and the climate*. Swiss Society for Astrophysics and Astronomy. Springer. New York, USA. 425 p. DOI: 10.1007/3-540-27510-X

Hartmann, J. 1995. The difficulty of tracing the effects of climate change on the fishes of Lake Constance. *In:* Beamish, R. J. (Ed.). *Climate change and northern fish populations.* Canadian Special Publication of Fisheries and Aquatic Science. No. 121. National Research Council of Canada. Ottawa, Canada, pp. 261-270.

Hjort, J. 1914. *Fluctuations in the great fisheries of Northern Europe: Viewed in the light of biological research*. Rapports et Proce`s-Verbaux des Re'unions du Conseil Permanent International Pour l'Exploration de la Mer 20. Copenhage, Denmark. 228 p.

Hoenig, J. M. & S. H. Gruber. 1990. Life-history patterns in the elasmobranchs: Implications for fisheries management. *In:* Pratt, H. L., S. H. Gruber, & T. Taniuchi (Eds.). *Elasmobranchs as living resources: Advances in the biology, ecology, systematics, and the status of the fisheries.* NOAA Technical Report NMFS 90. U.S. Department of Commerce. USA, pp. 1-16. also available at: http://spo.nwr.noaa.gov/tr90.pdf

Huato-Soberanis, L. & D. Lluch-Belda. 1987. Mesoscale cycles in the series of environmental indices related to the sardine fishery in the Gulf of California. *California Cooperative Oceanic Fisheries Investigation Reports* 28: 128-134.

Lawson, C. L. & R. J. Hanson. 1974. *Solving least squares problems.* Prentice Hall. Series in automatic computation. Englewood Cliffs. New Jersey, USA. 340 p.

Legendre, L. & P. Legendre. 1979. *Écologie numérique. Tome 2: La structure des données écologiques*. Collection d'Écologie No. 13. Masson, Paris et les Presses de l'Université du Québec. France, pp. 175-206.

Lluch-Cota, D. 2004. El sector pesquero. *In:* Martínez, J. & A. Fernández (Coords.). *Cambio climático: Una visión desde México*. Secretaria de Medio Ambiente y Recursos Naturales, Instituto Nacional de Ecología. México, pp. 327-335.

Macías-Zamora, R., A. L. Vidaurri-Sotelo & H. Santana-Hernández. 1994. Análisis de la tendencia de captura por unidad de esfuerzo en la pesquería del pez vela en el Pacífico Mexicano. *Ciencias Marinas* 20 (3): 393-408.

Martínez-Cruz, L.E., H. Zea-de la Cruz, J. L. Oviedo-Pérez, L. G. Morales-Parra* & L. I. Balan-Che. 2016. Aspectos biológico pesqueros del cazón tutzún R*hizoprionodon terraenovae*, en las costas de Campeche, México. *Ciencia Pesquera* n.e. 24: 23-35.

Mountain, D. G. & S. A. Murawski. 1992. Variation in the distribution of fish stocks on the northeast continental shelf in relation to their environment, 1980-1989. *In*: Dickson, R. R., P. Maelkki, G. Radach, R. Saetre & M. P. Sissenwine (Eds.). *Hydrobiological variability in the Ices Area, 1980-1989*. A symposium held in Mariehamn. No. 195. Copenhagen, Denmark, pp. 424-432.

NOAA. 2007. Annual averages of sunspot numbers (Zürich Index). Solar-Geophysical Data Comprehensive Reports. Available online at: www.ngdc.noaa.gov/stp/Solar/ftpsunspotnumber (downloaded February 03, 2016).

Ohtani, K. & T. Azumaya. 1995. Influence of interannual changes in ocean conditions on the abundance of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. *In*: Beamish, R. J. (Ed.). *Climate change and northern fish populations*. Canadian Special Publication of Fisheries and Aquatic Science. No. 121. National Research Council of Canada. Ottawa, Canada, pp. 87-95.

Ottersen, G., B. Ådlandsvik & H. Loeng. 1994. Statistical modelling of temperature variability in the Barents Sea. *In*: Counc. Meet. of the Int. Counc. for the Exploration of the Sea, St. John's. No. 5. Copenhagen, Denmark, pp. 1-16.

Platt, T. & K. L. Denman. 1975. Spectral analysis in ecology. *Annual Review of Ecology and Systematics* 6: 189-210.

Rodríguez-De la Cruz, Ma. C., J. L. Castillo-Géniz & J. F. Márquez-Farías. 1996. *Evaluación de la pesquería de tiburón del Golfo de México.* Informe Final de Proyecto de Investigación. Dirección General de Análisis de Pesquerías. Investigación, Evaluación y Manejo de Recursos Pesqueros del INP. SEMARNAP. CONACyT (Clave de Proyecto 116002-5-1314N-9206). México. 198 p.

Sánchez-Santillán, N. 1999. El cambio global del clima en el Golfo y Caribe Mexicano y su influencia en doce pesquerías de importancia comercial. PhD. Thesis, Universidad Nacional Autónoma de México. México. 593 p.

SEMARNAP. 1940-2006. *Anuarios estadísticos de pesca*. Secretaría de Medio Ambiente, Recursos Naturales y Pesca. México.

SEMARNAT. 2000. *Anuarios estadísticos de pesca*. Secretaría de Medio Ambiente. Recursos Naturales y Pesca. México.

Studenetsky, S. A. 1995. The extent of the effect of climate upon fisheries of Russia. *In:* Beamish, R. J. (Ed.). *Climate change and northern fish populations*. Canadian Special Publication of Fisheries and Aquatic Science. No. 121. National Research Council of Canada. Ottawa, Canada, pp. 529-530.

Thresher, R. E. 1994. Climatic cycles may help explain fish recruitment in South East Australia. *Australian Fisheries* 53: 20-22.

Van Loon, H. & K. Labitzke. 1994. The 10-12 year atmospheric oscillation. *Meteorologische Zeitschrift* 3: 259-266.

Vanselow, K. H. & K. Ricklefs. 2005. Are solar activity and sperm whale *Physeter macrocephalus* strandings around the North Sea related? *Journal of Sea Research* 53 (4): 319-327. DOI: 10.1016/j.seares.2004.07.006

Yang, J., L. Li & S. Xia. 1995. Influence of climate change of living resources in the Offshore Waters of China. *In:* Beamish, R. J. (Ed.). *Climate change and northern fish populations*. Canadian Special Publication of Fisheries and Aquatic Science. No. 121. National Research Council of Canada. Ottawa, Canada, pp. 531-535.

Zúñiga, M. J., L. A. Cubillos, & C. Ibáñez. 2008. Un patrón de periodicidad regular en las capturas mensuales de jibia (*Dosidicus gigas*) a lo largo de la costa de Chile (2002–2005). *Ciencias Marinas* 34 (1): 91-99.

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# Functional diversity in fish assemblages of the Tropical Eastern Pacific Ocean: A review of two decades of progress in the functional diversity approach

# Diversidad funcional en el ensamblaje de la ictiofauna del Océano Pacífico Oriental Tropical: Una revisión de dos décadas en su enfoque

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## ABSTRACT

**Background**. One of the most relevant topics in ecology and evolution is understanding the relationship between biological and functional diversity at the ecosystem level; both important in the evolutionary processes and the structuring of complex communities. **Goals.** In this essay, the explanatory hypotheses focused on global patterns of the distribution of species are described along with selected hypotheses relating species richness/biodiversity to ecosystem function, and the differentiation of the terms guild and functional group are discussed. **Methods.** Both biodiversity and functional diversity are key in the evolutionary processes and the structuring of complex communities and thus examples of functional equivalence of convergent evolution derivatives are presented in terms of the form and ecological habits of fishes of the Tropical Eastern Pacific Ocean. Finally, the importance of redundancy in ecosystem functioning is examined as well as the impact of environmental disturbances on ecosystem function. **Results**. In general, systems with low species richness and redundancy within functional groups are more vulnerable to disturbances. However, despite the extensive effort to understand the relationship between species richness/biodiversity and ecosystem functioning, there is no consensus on the effect of species loss on the functioning of the ecosystem. Some hypothesize that each species is unique and plays a unique role in the ecosystem whereas alternate hypotheses indicate that species overlap in function supporting sustainability at the ecosystem level, such that the removal of one species function may be replaced by another. **Conclusions**.The most widely accepted concept is that a greater number of species increases the efficiency in the use of resources and also provides resilience against environmental changes or impacts through functional redundancy.

**Keywords**: biological diversity, ecological redundancy, evolutionary convergence, functional equivalence

## RESUMEN

**Antecedentes.** Un tema relevante en ecología y evolución es la relación entre la diversidad biológica y la funcional a nivel del ecosistema; ambas importantes en los procesos evolutivos y la estructuración de comunidades complejas. **Objetivos.** Discutir hipótesis explicativas centradas en los patrones globales de la distribución de las especies junto con hipótesis seleccionadas que relacionen la riqueza y la biodiversidad de especies con la función del ecosistema. Diferenciar los términos de gremio y grupo funcional. **Metodología.** Presentar ejemplos de equivalencia funcional de los derivados de evolución convergente en términos de la forma y los hábitos ecológicos de los peces del océano Pacífico oriental tropical. Examinar la importancia de la redundancia en el funcionamiento de los ecosistemas, así como el impacto de las perturbaciones ambientales en la función del ecosistema. **Resultados.** En general, los sistemas con baja riqueza de especies y redundancia dentro de grupos funcionales son más vulnerables a las perturbaciones. Sin embargo, a pesar del extenso esfuerzo por comprender la relación entre la riqueza de especies/biodiversidad y el funcionamiento del ecosistema, se encontró que no existe consenso sobre el efecto de la pérdida de especies en el funcionamiento del ecosistema. Algunos suponen que cada especie es única y desempeña un papel particular en el ecosistema, mientras que las hipótesis alternativas indican que las especies se superponen en función de la sustentabilidad a nivel de ecosistema, de modo que la eliminación de la función de una especie puede ser reemplazada por la de otra especie. **Conclusiones**. El concepto más ampliamente aceptado es que un mayor número de especies aumenta la eficiencia en el uso de los recursos y también brinda resistencia contra los cambios o impactos ambientales a través de la redundancia funcional.

**Palabras clave:** convergencia evolutiva, diversidad biológica, equivalencia funcional, redundancia ecológica

## INTRODUCTION

Biological classification (taxonomy) aims to simplify and order the diversity of life into coherent units called taxa; however, there is currently no consensus among taxonomists concerning which classification scheme to use (Ruggiero *et al*., 2015). Simply, taxonomy integrates diverse, character-based data in a phylogenetic framework, which allows the use of this knowledge of shared biological properties of taxa but there is still strong debate over their accounting for evolutionary divergence or information content other than the branching pattern (Stuessy & Hoerandl, 2014). In contrast to taxonomy and phylogeny approaches to Earths biodiversity, a central issue in population and community ecology is species' geographical distribution and range size, which are important components needed for a better understanding of biodiversity. Generally, studies have focused on two different aspects: (1) patterns in species' range size distributions (Gaston, 1996; MacPherson, 2003); and (2) the effect of latitude on species' range sizes, *e.g.* Rapoport's rule (Stevens, 1989; 1996).

However, in contrast to earlier research on mechanisms driving known biodiversity patterns (Winemiller *et al*., 2015; Pianka *et al*., 2017), recent work highlights that evolution works on ecological similarities (redundancy) and differences (complementarity) of individuals and not on the number of species (Cadotte *et al*., 2013). A number of early studies that simultaneously examined aspects of species biodiversity and functional diversity (reviewed in Tilman *et al*., 1997) have shown that species biodiversity is an important indicator of ecosystem functioning but functional diversity and species composition together are most important in grassland ecosystems. Functional diversity (trait-based) is generally defined as "morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction, and survival, the three components of individual performance" (Violle *et al*., 2007). There is also evidence that functional traits strongly link to species composition and shifts in ecosystem processes (Villéger *et al*., 2010) and that the choice of functional traits is key to quantifying functional diversity and its use to examine anthropogenic modifications of ecosystems. This relationship is strong when many species have unique functional traits that are important in ecosystem functioning, whereas if many species have similar characteristics (redundancy), the relationship between species biodiversity and functional diversity is weak.

Natural or human-induced environmental modifications (*e.g*., fishing, climate change, habitat fragmentation) have had drastic impacts on habitats and species and thus biodiversity and ecosystem function worldwide (Costanza *et al*., 1997; Vitousek *et al*., 1997; Lotze *et al*., 2006; Halpern *et al*., 2008). These impacts are generally focused on habitat modification or loss as it relates to species loss and biodiversity reduction since it has long been postulated that habitat is the 'template for ecosystem strategies' (Southwood, 1977; Ferraro & Cole, 2010; Ferraro, 2013) and that habitat provides the organizing structure for ecosystem functionality. However, there are generally two approaches to assessing local and regional community assembly relative to diversity and ecosystem function: 1) taxonomic (phylogenetic); and 2) functional (trait-based) (Cadotte *et al*., 2013; Winemiller *et al*., 2015; Pianka *et al*., 2017).

The traditional approach is to examine changes by using species richness/biodiversity metrics but more recently a growing literature on functional diversity and its importance in better understanding ecosystem function (Violle *et al*., 2007; Villéger *et al*., 2010; Parravicini *et al*., 2014) is emerging, and, in particular, relative to species invasions and habitat degradation, and fishing pressure (Pecuchet *et al*., 2017; Silva-Junior *et al*., 2017; Villéger *et al*., 2017). For example, it has been shown in coral reef fish communities that functional diversity is lower than taxonomic diversity because of redundancy (Villéger *et al*., 2012, 2013; Mouillot *et al*., 2014) which suggests that one cannot use taxonomic diversity to predict changes in functional diversity nor one cannot use taxonomic diversity alone to assess habitat degradation and subsequent ecosystem functional capacity relative to stable and sustainable ecosystems (Villéger *et al*., 2014; Loiseau & Gaertner, 2015; Pecuchet *et al*., 2017; Silva-Junior *et al*., 2017).

The study of functional traits important to the community ecology and, by extension, ecosystem function has been most noticeable in plant communities worldwide with fewer examples in other taxa, including fishes and avifauna (Villéger *et al*., 2017). As a result of our empirical perception, we tend to assign a key role to a relatively small number of generally abundant and larger species, considering that their conservation is enough to maintain ecosystem processes and thus services. However, it was found that rare or unique species with the highest risk of extinction have, in some cases, a quantifiably important impact toward maintaining the functioning of the ecosystem, acting as key species (Lyons *et al*., 2005; Mouillot *et al*., 2013; Friedman *et al*., 2016; Escobar-Toledo *et al*., 2017).

Recent examination of freshwater, estuarine and marine fishes has illustrated the value of examining these communities based on functional traits in order to address pressing ecological issues associated with climate change, overfishing, invasive species, and habitat loss or alterations (Mouillot *et al*., 2014; Parravicini *et al*., 2014; Villéger *et al*., 2014; Chuang & Peterson, 2016; Pecuchet *et al*., 2016, 2017; Rodrigues-Filho *et al*., 2017; Silva-Júnior *et al*., 2017).

With this essay, we aim to (1) summarize patterns of fish species richness/biodiversity and distribution in the Tropical Eastern Pacific Ocean (TEP), (2) provide a selective review of hypotheses relating fish species richness/ biodiversity/functional diversity to ecosystem function, and (3) review the importance of redundancy in ecosystem function and the impact of environmental disturbances. This essay will focus on marine fishes of the TEP but may provide examples from freshwater and estuarine fishes, and other vertebrate groups to illustrate a point.

## MARINE FAUNAS TROPICAL EASTERN PACIFIC

The shallow, warm-water marine faunas of the world are traditionally divided into the Indo-West Pacific, Eastern Pacific, and western and eastern Atlantic regions (Ekman, 1953; Briggs, 1974). The Isthmus of Panama was established as one of the greatest natural events of the Cenozoic, driving profound biotic transformations on land and in the oceans, so faunas on the east and west sides are closely related and sister species are common (O'Dea *et al.*, 2016). Furthermore, the TEP is divided from the rest of the Pacific by a wide expanse of deep ocean, with very few islands, coupled with cold water masses flowing along west coasts of both North and South America towards the equator. This is not a complete barrier to shallow-water invertebrate dispersal, but rather is a filter, allowing only those larvae with an exceptionally long life to be transported from the central tropical Pacific (Scheltema, 1988).

There is a substantial variation in species composition from north to south through the TEP region, but boundaries among biogregraphical provinces are not always well defined. For example, mainly on ichthyological evidence, Briggs (1974) define four main provinces (Fig. 1), and places a boundary in the Gulf of Tehuantepec to separate the Mexicana province (Sinaloa to Oaxaca, on the coast of Mexico) and the Panamic province (Nicaragua to Ecuador, including Cocos and Malpelo). The Revillagigedo Islands was considered as part of the offshore Ocean Island province. However, the northern boundary of the Panamic province is debatable, the southern boundary is clearly defined by the cold Peruvian Current diverting offshore around Punta Aguja, Peru. Briggs (1974) set the northern boundary of the Mexican province in the Gulf of California and on Baja California at about 23°N. The Galapagos Islands are treated as a separate faunistic region and included in the offshore Ocean Island province along with the Revillagigedo and Clipperton Islands. The province of Cortez (southern Baja and the central Gulf of California) is isolated from its counterpart in the Mexican province by the Gap of Sinaloa, a band of 370 km of sandy and muddy shoreline extending between Topolobampo and Mazatlan, Mexico, whereas the Mexican province is separated from its counterpart in the Panamic province by the gap of Central America, a large 1,000 km section of coastline sand between the Gulf of Tehuantepec (south of Mexico) and El Salvador (Hastings, 2000).

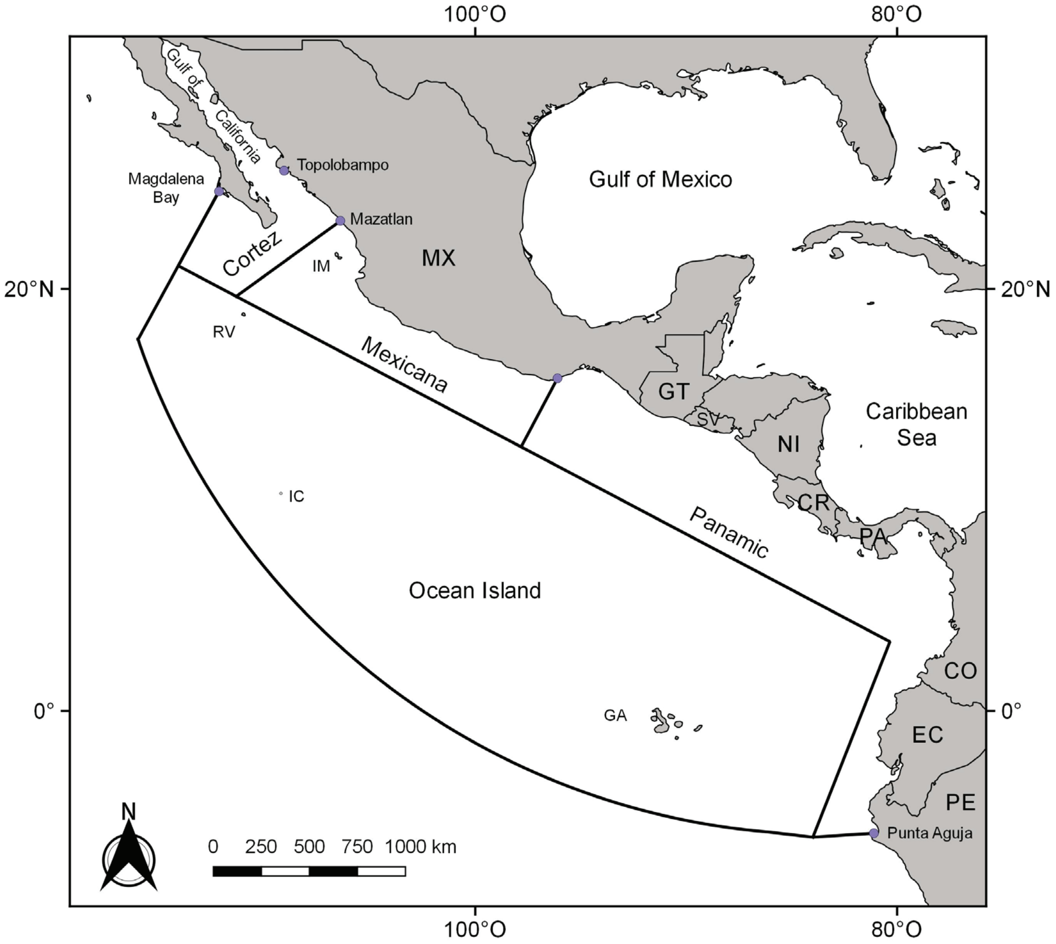

Figura 1. Biogregraphical provinces in Tropical Eastern Pacific (Briggs 1974)

Biogeographically, the TEP is fascinating in several respects. Its marine shore biota is most similar to that of the tropical western Atlantic, but, as a result of the independent evolution of their faunas in very different environments over the past 3.5 million years, the two regions share relatively few fish species (Rosenblatt, 1967; Castellanos-Galindo *et al.*, 2013). The TEP includes five oceanic islands or archipelagos whose fish faunas are relatively well known (McCosker & Rosenblatt, 1975; Robertson & Allen, 1996; Grove & Lavenberg, 1997; Garrison, 2000; Galland *et al.*, 2017). These islands harbor subsets of the mainland fauna, a significant number of insular endemics, and numerous species that also occur on the western side of the east Pacific barrier (Leis, 1984). The geographic isolation of the TEP has resulted in its having the highest level of regional endemism among shore fishes of any comparably sized region in the world. About 85 percent of its fishes are found nowhere else, although many of them regularly or periodically cross the thermal barrier to the north and are found in California (*e.g.*, during El Niño events; Lea & Rosenblatt, 2000). Although less well documented, a similar periodic transgression of the southern terminal barrier presumably also occurs.

Many TEP fish species have wide distributions within the region. Others have more limited distributions, with the Panamic province and the Cortez province serving as centers of regional endemism (Fig. 1). Precise distributions of many species of fishes between these provinces, along with the coast of southern Mexico southward to Honduras, are not well documented. Some species, particularly small, benthic reef fishes, support the recognition of a third, Mexicana province located between the Cortez and Panamic province (Hastings, 2000), as suggested by several studies on the systematics of coastal fishes (*e.g.*, Hubbs, 1952; Briggs, 1955; Springer 1959; Stephens, 1963).

## SPECIES RICHNESS / BIODIVERSITY AND DISTRIBUTION PATTERNS OF THE TEP FISHES

Species richness/biodiversity is distributed irregularly among ecosystems across biospheres. For example, there are 34 phyla alive in the marine environment, 17 in freshwater, and only 15 on land (Briggs, 1994; Mora *et al.*, 2011). The contrast is higher when considering only animals, as there are 32 marine phyla and only 12 terrestrial fauna (Benton, 2001). However, although the ocean has the greatest wealth of phyla and it is about 300 times larger than the Earth's terrestrial environment, species richness/biodiversity of the terrestrial realm is 25 times greater than the one found in the marine environment (Briggs, 1994; Mora *et al.*, 2011). This difference in species richness/ biodiversity is probably caused by three key conditions (Benton, 2001). First, land offers more endemism opportunities because of the effect of geographic isolation and independent evolution; marine environment barriers are not as efficient at reducing the possibility of endemism and diversification (*e.g.*, soft barriers; Cowman & Bellwood, 2013). Second, terrestrial habitats are more diverse and heterogeneous, with large fluctuations in temperature and humidity throughout the day both seasonally and latitudinally; the physical marine environment is more stable compared to land. Third, the size of primary producer's plays an important role as marine primary producers are mostly unicellular organisms that serve as food source for benthic and pelagic animals, but are unable to provide important habitat for other species of animals and plants like in terrestrial systems (Briggs, 1994; Mora *et al.*, 2011).

Fishes worldwide consist of about 33,395 known species (Eschmeyer & Fong, 2013). They have very diverse latitudinal, longitudinal, and bathymetric distributions and very complex morphological, biological and behavioral characteristics such that it is possible that both allopatric and non-allopatric speciation processes are involved in the formation of this biodiversity. How disjunct distributions (*e.g.*, distributions composed of multiple geographically discrete and widely spaced populations) arise is an interesting question in biogeography and has long been subject of the dispersalist–vicariance debate (Cowman & Bellwood, 2013; Cowman, 2014). Dispersalist theories emphasize the importance of species traits and dispersal in explaining the occurrence of highly isolated populations, whereas vicariant theories invoke landscape evolution and fragmentation of a species' ancestral range as the principal drivers of these biotic patterns. Species with geographically disjunct ranges are important for understanding the factors controlling species' distributions, population connectivity, and the process of allopatric speciation (Ronquist, 1997; Cowen & Spongaugle, 2009; Cowman, 2014). In both cases, allopatric speciation can take place if the gap in a species' range sufficiently limits gene flow (Crisp *et al.*, 2010).

In the Mexican Pacific Ocean, two geological events have played a key role in the formation of the current fish fauna - the formation of the Gulf of California and the rise of the Isthmus of Panama (Jacobs *et al.*, 2004). The formation of the Gulf of California dates about 5-8 mya during the Pliocene-late Miocene (De la Cruz-Agüero, 2000). The geological formation of Baja California divided a group of fish species that are disjunct populations on the Pacific coast and in the northern Gulf of California (Table 1); these eleven species represent an interesting case for studies of incipient speciation (Bernardi *et al.*, 2003). The origin of these species from Magdalena-Almejas Bay and San Ignacio Lagoon is explained by the existence of interpeninsular Pleistocene-Holocene channels (0.115 - 2.6 mya) on sandy plains that connected the Pacific with the Gulf of California.

The geological development and endemism of species of tropical lineage support this hypothesis (Castro-Aguirre *et al.*, 1995, 2005; De la Cruz-Agüero, 2000). In fact, most of the disjunct species of the Pacific and Gulf of California (Table 2) show few morphological and color differences, but in some cases divergence has been detected, as in members of the genus *Leuresthes, Gillichthys*, *Girella,* and *Hypsoblennius* (Crabtree, 1983; Orton & Buth, 1984; Huang & Bernardi, 2001; Bernardi, 2014). Bernardi *et al.* (2003) analyzed 12 species with disjunct populations and found that eight species had strong genetic differences between populations of the Gulf of California and the Pacific and four of them are in the process of incipient speciation, indicating that the physic separation of populations (considered as the first step towards speciation) is very commonly responsible for the creation of new geminate species.

In the TEP, families that experienced wide speciation patterns are Gobiidae (111 species), Sciaenidae (82 species), Serranidae (56 species), Labrisomidae (48 species), Gobiesocidae (43 species), Ophichthidae (41 species), Haemulidae (37 species), Labridae (36 species), Carangidae (35 species), Chaenopsidae (34 species), and Muraenidae (33 species). A number of these species groups can be partitioned into habitat-based subcategories like soft-bottom environments, coastal pelagic environments, estuarine, coastal lagoons, coastal pelagic zones, coral reef and rocky intertidal habitats where redundancy is higher, and subtidal habitats (Table 3). Another remarkable example of adaptive radiation in the TEP is the moray eels of the genus *Gymnothorax*, with 11 indigenous species; some species inhabit subtidal reefs (*G. angusticeps* (Hildebrand & Barton, 1949), *G. castaneus* (Jordan & Gilbert, 1883), *G. dovii* (Günther, 1870), *G. mordax* (Ayres, 1859), *G. panamensis* (Steindachner, 1876), *G. porphyreus* (Guichenot, 1848), and *G. serratidens* (Hildebrand & Barton, 1949)), and other soft bottoms (*G. equatorialis* (Hildebrand, 1946), *G. eurygnathos* Böhlke, 2001, *G. phalarus* Bussing, 1998, and *G. verrilli* (Jordan & Gilbert, 1883)). This genus has been enriched with the addition of species of Indo-Pacific or trans-Pacific affinity (*G. buroensis* (Bleeker, 1857), *G. flavimarginatus* (Rüppell, 1830), *G. javanicus* (Bleeker, 1859), *G. meleagris* (Shaw & Nodder, 1795), *G. pictus* (Ahl, 1789) and *G. undulates* (Lacepède, 1803)), currently consisting of 17 species in total for TEP (Table 3).

Speciation events and the great topographic and bathymetric biodiversity have turned the Gulf of California into one of the most diverse regions of the TEP with about 875 species of fish, 92 of which are endemic (Thomson *et al.*, 2000); it is regarded as a center of origin along with the Central America landscape (Mora & Robertson, 2005).

According whith O'Dea *et al.* (2016), the formation of the Isthmus of Panama resulted in the absence of further gene flow between shallow marine animal populations after 3.2 millon years (mid-Pliocene) by the interrupted the communication between the Pacific and Atlantic and particularmente causing the effective isolatiion of fish populations, resulting in the formation of new species as well as the disappearance of others (Castro-Aguirre *et al.*, 1995).

It is hypothesized that the presence of a marine Pleistocene gap in the area of Panama (1.8-2 mya), initiated the divergence of some transisthmian species of the genus *Anisotremus* (Tavera-Vargas, 2006). While 85% of the coastal fish fauna of the TEP is derived from taxa present before the rising of the Isthmus of Panama, the low percentage of common species in the two regions of the American continent (> 100 sister species, pairs or transisthmian; see Table 4) is the result of independent evolution of their faunas in very different environments (Rosenblatt, 1967; Robertson *et al.*, 2004; Aguilar-Medrano, 2018). In some genera, the sister species have been separated taxonomically by minor morphological differences or genetic differences, such as the Pacific machete and Atlantic ladyfish (*Elops affinis* Regan 1909 - *E. saurus* Linnaeus, 1766), Pacific sleeper and bigmouth sleeper (*Gobiomorus maculatus* (Gunther,1859) - *G. dormitor* Lacepede, 1800), the Pacific fat sleeper and fat sleeper (*Dormitator latifrons* (Richardson, 1844) - *D. maculatus* (Bloch, 1792)), Atlantic and Pacific spadefish (*Chaetodipterus faber* (Brousonnet, 1782) - *C. zonatus* (Girard, 1858)), the Panamic banged blenny and the red-lip blenny (*Ophioblennius steindachneri* Jordan & Evermann, 1898 - *O. macclurei* (Silvester, 1915)). For the latter, a new species (*O. clippertonensis* Springer, 1962) has been recognized for Clipperton Atoll, a small isolated island at the western edge of the TEP (Allen & Robertson, 1997). In contrast, for some, the separation into two species is not possible or even questionable including the nurse shark *Ginglymostoma cirratum* (Bonnaterre, 1788), the lemon shark *Negaprion brevirostris*, the leatherjacket *Oligoplites saurus* (Poey,1868) the yellowfin mojarra *Gerres cinereus* (Walbaum, 1792) and the fringed flounder *Etropus crossotus* Jordan & Gilbert 1882; these are remarkably similar in external morphology, but also in their behavior and ecology (Castro-Aguirre *et al.*, 1995; Thomson *et al.*, 2000).

Table 1. Fish incipient speciation examples in the Mexican Pacific Ocean. Numbers= information from references below.

| Family | Species | Common name | Habitat | Reference |
|---|---|---|---|---|
| Atherinidae | *Atherinops affinis* (Ayres, 1860) | Topsmelt silverside | [1]Nearshore generalist | Bernardi *et al.* (2003) |
| Scorpaenidae | *Sebastes macdonaldi* (Eigenmann & Beeson, 1893) | Mexican rockfish | [1]Shallow generalist | Bernardi *et al.* (2003) |
| Haemulidae | *Anisotremus davidsonii* (Steindachner, 1876) | Xantic sargo | Rocky-sand bottom | Bernardi *et al.* (2003)<br>Bernardi & Lape 2005 |
| Sciaenidae | *Cheilotrema saturnum* (Girard, 1858) | Black croaker | Near sand bottom | Bernardi *et al.* (2003) |
| Embiotocidae | *Zalembius rosaceus* (Jordan & Gilbert, 1880) | Pink seaperch | Offshore deeper water | Bernardi *et al.* (2003) |
| Labridae | *Halichoeres semicinctus* (Ayres, 1859) | Rock wrasse | [2]Shallow nearshore, algal-covered substrata | Bernardi *et al.* (2003) |
| Blennidae | *Hypsoblennius jenkinsi* (Jordan & Evermann, 1896) | Mussel blenny | [3]Holes and crevices in rocky areas, in burrows of boring clams or tubes of marine worms, and in mussel beds | Bernardi *et al.* (2003) |
| Gobiidae | *Gillichthys mirabilis* Cooper, 1864 | Longjaw mudsucker | Bays and coastal sloughs, burrowing in shallow mud substrate in tidal flats and bays including coastal lagoons | Bernardi *et al.* (2003) |
| Paralichthyidae | *Paralichthys californicus (Ayres, 1859)* | California flounder | [1]Shallow generalist | Bernardi *et al.* (2003) |
| Pleuronectidae. | *Pleuronichthys ocellatus* (Starks & Thompson, 1910) | Ocellated turbot | Offshore over sand and sandy mud soft substrates | Bernardi *et al.* (2003) |
| Pleuronectidae. | *Pleuronichthys verticalis* Jordan & Gilbert, 1880 | Hornyhead turbot | [1]Nearshore soft bottom | Bernardi *et al.* (2003) |

[1] Allen, L.G. & D.J. Pondella. 2006. Ecological classification. *In:* Allen, L.G. D.J. Pondella & M.H. Horn (eds). The ecology of marine fishes: California and Adjacent Waters. University of California Press, Berkeley, California. pp 81-113.

[2] Eschmeyer, W.N., E. S. Herald & H. Hammann.1983. A field guide to Pacific coast fishes of North America. Houghton Mifflin Company, Boston, Massachuetts

[3] De La Cruz-Agüero, J. M. Arellano-Martínez, V. M. Cota-Gómez & G. De La Cruz-Agüero. 1997. Catálogo de los peces marinos de Baja California Sur. IPN-CONABIO. México, D.F.

Table 2. Examples of some fishes that exhibit disjunct or geographically discontinuous ranges between the Gulf of California and outer Pacific Coast.

| Family | Species | Common name | Geographical distribution | Source |
|---|---|---|---|---|
| Atherinidae | *Leuresthes tenuis* (Jenkins & Evermann, 1889) | Gulf grunion | The California grunion, is a common inhabitant of the inshore waters of the northeastern Pacific. This pelagic, schooling fish is usually found from just behind the surf line to a depth of about 18 m. It ranges from San Francisco to Magdalena Bay, Baja California, but is rarely found north of Point Conception in southern California. | (Miller & Lea 1972; Eschmeyer *et al.*, 1983; Love, 1996). |
| Atherinidae | *Leuresthes sardina* (Ayres, 1860) | California grunion | The California grunion ranges from Monterey Bay, California, to Magdalena Bay, Baja California Sur. | (Walker, 1952; Moffatt &Thomson. 1975). |
| Kyphosidae | *Girella nigricans* (Ayres, 1860) | Rudderfish, Opaleye | This species is endemic to the Eastern Pacific, and is found from California to southern Baja, and an isolated population in the central and northern Gulf of California. | Allen & Robertson (2010a) |
| Kyphosidae | *Girella simplicidens* Osburn & Nichols, 1916 | Gulf opaleye | Gulf of California; abundant in the northern Gulf, but scarce in the southern portion. | Robertson & Allen (2015) |
| Blennidae | *Hypsoblennius gentilis* Girard, 1854 | Bay blenny | This species is endemic to the Eastern Pacific, and is found from Monterey, California, USA to the northern and central Gulf of California. | Bessudo *et al.* (2010) |
| Chaenopsidae | *Chaenopsis alepidota* (Gilbert, 1890) | Orangethroat pikeblenny | This species is endemic to the Eastern Pacific, and has a disjunct distribution. It is found in southern California, USA and northern Baja California, Mexico and in the western and north-eastern Gulf of California. | Bessudo *et al.* (2010b) |
| Serranidae | *Paralabrax maculatofasciatus* Steindachner, 1868 | Spotted sand bass | The spotted sand bass has a historic range from Mazatlan, Baja California, to Monterey in Central California. Dense populations also occur in the northern portions of the Gulf of California. | (Allen *et al.*,1995; Stepien *et al.*, 2001) |
| Gobiidae | *Gillichthys mirabilis* Cooper, 1864 | Longjaw mudsucker | Inhabits sloughs and estuaries from Tamales Bay just north of San Francisco Bay to sites throughout Baja California. | Gracey (2008) |
| Haemulidae | *Anisotremus davidsonii* Steindachner, 1876 | Xantic sargo | This species is endemic to the Eastern Pacific, and is found from central California to central Baja, and the northwestern and eastern Gulf of California. | Allen *et al.* (2010b) |
| Gobiidae | *Lythrypnus dalli* (Gilbert, 1890) | Blue-banded goby | This species is endemic to the Eastern Pacific, ranging from Monterey Bay to the tip of Baja, and the Gulf of California to northern Peru, including the Malpelo, Galapagos, and Guadalupe Islands, at depths ranging from intertidal to 64 m, is most abundant in rocky subtidal habitats along the coast and offshore islands of southern California and northern Baja California, Mexico. | (Miller & Lea, 1972, 1976; Wiley, 1976; Van Tassell *et al.* 2010c) |
| Kyphosidae | *Hermosilla azurea* (Jenkins & Evermann, 1889) | Zebra-perch sea chub | This species is endemic to the Eastern Pacific, and is found from Monterey, California to Baja California, and in the Gulf of California. | Allen *et al.* (2010c) |
| Labridae | *Halichoeres semicinctus* (Ayres, 1859) | Rock wrasse | This species can be located from the Gulf of California, Mexico to Point Conception, California. | Miller & Lea (1972) |
| Labridae | *Semicossyphus pulcher* (Ayres, 1854) | California sheephead | The California sheephead is found from Monterey Bay, California, to the northern Sea of Cortez, Mexico, including the California Channel islands and the isolated Guadalupe Island, Mexico. | (Miller & Lea, 1972; Present, 1987; Poortvliet *et al.*, 2013) |
| Scorpaenidae | *Sebastes macdonaldi* (Eigenmann & Beeson, 1893) | Mexican rockfish | Mexican rock fish is the Northeast Pacific rockfish with the southernmost distribution, ranging from Point Sur, Central California, to offshore banks off Bahía Magdalena, Baja California. The species distribution is discontinuous since it has not been reported further south at the entrance to the Gulf of California. Within the gulf, Mexican rockfish is found near Guaymas and in Bahía de Los Angeles. | (Moser, 1971; Chen, 1975; Thomson *et al.*, 2000) |

Tabla 2. Continúa.

| Family | Species | Common name | Geographical distribution | Source |
|---|---|---|---|---|
| Pleuronectidae | *Pleuronichthys verticalis* (Jordan & Gilbert, 1880) | Hornyhead turbot | The hornyhead turbot is a common resident flatfish on the mainland shelf from Magdalena Bay, Baja California, Mexico to Point Reyes, California at depths from 9 to 201 m. | (Miller & Lea 1972; Eschmeyer *et al.*, 1983) |
| Embiotocidae | *Zalembius rosaceus* (Jordan & Gilbert, 1880) | Pink seaperch | Northern California to central Baja California, plus an isolated population in the upper and central Gulf of California. | Eschmeyer *et al.* (1983). |
| Scorpaenidae | *Scorpaena guttata* Girard, 1854 | Scorpionfish | California to lower Baja, with an isolated population in the upper half of the Gulf of California. | (Eschmeyer *et al.*, 1983; Love *et al.*, 1987; Eschmeyer & Alvarado, 2010) |
| Percichthydae | *Stereolepis gigas* Ayres, 1859 | Giant seabass | Their historical range is from Humboldt Bay, CA to Baja Mexico (Point Abreojos) and into the northern Gulf of California. However, they are primarily found south of Point Conception in shallow rocky reefs. | (Domeier, 2001; Cornish, 2004; Hawk & Allen, 2014) |
| Agonidae | *Xeneretmus ritteri* Gilbert, 1915 | Stripefin poacher | Eastern Central Pacific: Malibu in southern California, USA to central Baja California, Mexico; isolated population in northern Gulf of California. | Eschmeyer *et al.* (1983) |
| Pleuronectidae | *Hypsopsetta guttulata* (Girard, 1856) | Diamond turbot | Is an estuarine flatfish ranging from Cape Mendocino to Bahía Magdalena on the Pacific coast of North America, and from Bahía Concepción to Guaymas in the Gulf of California. | (Miller & Lea, 1972; Lane, 1975; Present, 1987). |

The *Stathmonotus* blennies provide a clear example of allopatric speciation. This genus is represented by three species in the TEP, the Gulf worm blenny *S. sinuscalifornici* (Chabanaud, 1942) from the province of Cortez, the Mexican worm blenny *S. lugubris* (Bohlke, 1953) from the Mexicana province and the Panamanian worm blenny *S. culebrai* Seale, 1940 from the Panamic province. Hastings (2000) proposed two hypotheses to explain the speciation of the genus. First, the final rise of the Isthmus of Panama isolated a population into the Caribbean, which was widely distributed in the region or initially restricted to the Panamic province, later dispersing throughout the Tropical Pacific Ocean (TPO). Subsequently, the gap of Sinaloa isolated *S. sinuscalifornici* from the other members of the genus of the TEP, then the gap in Central America isolated *S. lugubris*, and *S. culebrai*. The alternative hypothesis proposes that speciation of the Caribbean species (*S. gymnodermis* Springer, 1955, *S. hemphillii* Bean, 1855 and *S. stahli* (Evermann & Marsh, 1899)) occurred before the final rise of the Isthmus of Panama, in which case the divergence within the TEP could start before the final rise of the Isthmus. This hypothesis is reinforced because in all other paired species of blenny, sister species are phenotypically very similar which is consistent with a short time period since its divergence (Lin & Hastings, 2013).

Furthermore, there are 190 trans-Pacific species, 126 coastal species, and 64 oceanic pelagic species representing about 12% of the fish fauna of the TPO in the TEP (Robertson & Allen 1996; Robertson *et al.*, 2004). The conditions that favor the establishment and residence of these species are not clear, although the horizontal ocean temperature gradients tend to restrict the latitudinal ranges of species, whereas extending their ranges longitudinally has fewer restrictions. According to Briggs (1961) and Margalef (1972), the strong interspecific competition that is generated in a very integrated ecosystem like the western Pacific (an ecosystem of high biodiversity) can cause outward emigrations and colonization, which are directed towards the central and eastern Pacific (areas of low biodiversity). A similar case is observed in the fish fauna of coral and rocky reefs of the TPO where richness is high and therefore the degree of competition as well. In this way, several species inhabit these systems (*e.g.*, *Chaetodon humeralis* Gunther, 1860, *Diodon holocanthus* Linnaeus, 1758, and *Hippocampus ingens* Girard, 1858) or emigrate to soft bottom systems for feeding (*e.g.*, *Haemulon flaviguttatum* Gill,1862, and *H. maculidauda* (Gill,1862). However, movement of species from reef systems to soft bottoms is rare, since they can hardly compete for resources with resident species.

In the offshore Ocean Island province of the TEP, an interesting case occurs. Briggs (1961) remarks that for the Indo-Pacific migrant fishes it is easier to recruit to oceanic islands populations because these areas represent less competition than the mainland. A migrant group of fishes is well represented in the Revillagigedo Islands (18°49' N 112°46' W; some 390 km southwest of Cabo San Lucas, Baja California del Sur, Mexico; Fig. 1) with 21% of the fauna (Castro-Aguirre & Balart, 2002) and in the Clipperton Atoll (10°17' N, 109°13' W) with about 75% of species (Robertson & Allen, 1996). This atoll has been regarded as a bridge that connects the coastal biota of the TEP and western Pacific (Robertson & Allen, 1996). Only 99 species of shore fish are endemic to oceanic islands and – 30% of the remaining has self-sustaining insular populations (Robertson & Allen, 1996, 2002) which may favor the colonization of trans-Pacific species.

Table 3. Examples of some families of marine fish with wide speciation patterns in the Tropical Eastern Pacific Ocean.

| Habitat type | Family | Genus | Common name | Species |
|---|---|---|---|---|
| Soft-bottom | Cynoglossidae | *Symphurus* | Tonguefish | *S. atramentatus* Jordan & Bollman, 1890,*S. atricaudus* (Jordan & Gilbert, 1880),*S. callopterus* Munroe & Mahadeva, 1989, *S. chabanaudi* Mahadeva & Munroe, 1990, *S. diabolicus* Mahadeva & Munroe, 1990; *S. elongatus* (Günther, 1868), *S. fasciolaris* Gilbert, 1892, *S. gorgonae* Chabanaud, 1948, *S. leei Jordan &* Bollman, 1890, *S. melanurus* Clark, 1936, *S. melasmatotheca* Munroe & Nizinski, 1990, *S. microlepis* Garman, 1899, *S. ocellaris* Munroe & Robertson, 2005, *S. oligomerus* Mahadeva & Munroe, 1990, *S. prolatinaris* Munroe, Nizinski & Mahadeva, 1991, *S. undecimplerus* Munroe & Nizinski, 1990, *S. varius* Garman, 1899, *S. williamsi* Jordan & Culver, 1895. |
|  | Sciaenidae | *Stellifer* | Drums | *S. chrysoleuca* (Günther, 1867), *S. ephelis Chirichigno F., 1974, S. ericymba* (Jordan & Gilbert, 1882), *S. fuerthii* (Steindachner, 1876), *S. mancorensis Chirichigno F., 1962, S. melanocheir* Eigenmann, 1918, *S. minor* (Tschudi, 1846), *S. oscitans* (Jordan & Gilbert, 1882), *S. pizarroensis* Hildebrand, 1946, *S. walkeri* Chao, 2001, *S. wintersteenorum* Chao, 2001, *S. zestocarus* Gilbert, 1898. |
| Coastal Pelagic | Engraulidae | *Anchoa* | Anchovy | *A. analis* (Miller, 1945), *A. argentivittata* (Regan, 1904), *A. chamensis* Hildebrand, 1943, *A. compressa* (Girard, 1858), *A. curta* (Jordan & Gilbert, 1882), *A. delicatissima* (Girard, 1854), *A. eigenmannia* (Meek & Hildebrand, 1923), *A. exigua* (Jordan & Gilbert, 1882), *A. helleri* (Hubbs, 1921), *A. ischana* (Jordan & Gilbert, 1882), *A. lucida* (Jordan & Gilbert, 1882), *A. mundeola* (Gilbert & Pierson, 1898), *A. mundeoloides* (Breder, 1928), *A. nasus* (Kner & Steindachner, 1867), *A. panamensis* (Steindachner, 1876), *A. scofieldi* (Jordan & Culver, 1895), *A. spinifer* (Valenciennes, 1848), *A. starksi* (Gilbert & Pierson, 1898), *A. walkeri* Baldwin & Chang, 1970. |
| Intertidal zone | Gobiesocidae | Gobiesox | Skilletfish | *G. adustus* Jordan & Gilbert, 1882, *G. aethus* (Briggs, 1951), *G. canidens* (Briggs, 1951), *G. crassicorpus* (Briggs, 1951), *G. daedaleus* Briggs, 1951, *G. eugrammus* Briggs, 1955, *G. fluviatilis* Briggs & Miller, 1960, *G. fulvus* Meek, 1907, *G. juradoensis* Fowler, 1944, *G. maeandricus* (Girard, 1858), *G. marijeanae* Briggs, 1960, *G. mexicanus* Briggs & Miller, 1960, *G. milleri* Briggs, 1955, *G. multitentaculus* (Briggs, 1951), *G. papillifer* Gilbert, 1890, *G. pinniger* Gilbert, 1890, *G. potamius* Briggs, 1955, *G. rhessodon Smith, 1881, G. schultzi* Briggs, 1951, *G. stenocephalus* Briggs, 1955, *G. woodsi* (Schultz, 1944). |
|  |  | *Tomicodon* | Clingfishes | *T. absitus* Briggs, 1955, *T. abuelorum* Szelistowski, 1990, *T. bidens* Briggs, 1969, *T. boehlkei* Briggs, 1955, *T. chilensis* Brisout de Barneville, 1846*, T. eos* (Jordan & Gilbert, 1882), *T. humeralis* (Gilbert, 1890), *T. myersi* Briggs, 1955, *T. petersii* (Garman, 1875), *T. prodomus* Briggs, 1969, *T. vermiculatus* Briggs, 1955, *T. zebra* (Jordan & Gilbert, 1882). |
|  | Labridae | *Halichoeres* | Wrasse | *H. adustus* (Gilbert, 1890), *H. aestuaricola* Bussing, 1972, *H. chierchiae* Di Caporiacco, 1948, *H. discolor* Bussing, 1983, *H. dispilus* (Günther, 1864), *H. insularis* Allen & Robertson, 1992, *H. malpelo* Allen & Robertson, 1992, *H. melanotis* (Gilbert, 1890), *H. nicholsi* (Jordan & Gilbert, 1882), *H. notospilus* (Günther, 1864), *H. salmofasciatus* Allen & Robertson, 2002, *H. semicinctus* (Ayres, 1859). |
| Subtidal reef | Muraenidae | *Gymnothorax* | Morays | *G. angusticeps* (Hildebrand & Barton, 1949), *G. castaneus* (Jordan & Gilbert, 1883), *G. dovii* (Günther, 1870), *G. mordax* (Ayres, 1859), *G. panamensis* (Steindachner, 1876), *G. porphyreus* (Guichenot, 1848), *G. serratidens* (Hildebrand & Barton, 1949), *G. equatorialis* (Hildebrand, 1946), *G. eurygnathos* Böhlke, 2001, *G. phalarus* Bussing, 1998, *G. verrilli* (Jordan & Gilbert, 1883), *G. buroensis* (Bleeker, 1857), *G. flavimarginatus* (Rüppell, 1830), *G. javanicus* (Bleeker, 1859), *G. meleagris* (Shaw, 1795), *G. pictus* (Ahl, 1789), *G. undulates* (Lacepède, 1803). |

Finally, tropical trans-Pacific fishes occur on both sides of the world's largest deep-water barrier to the migration of marine shore organisms, the 4,000km to 7,000km-wide Eastern Pacific Barrier. They include 64 epipelagic oceanic species and 126 species of shore fishes known from both the TEP and the central and West Pacific. However, although trans-Pacific species are characterized by long larval stages, surprisingly, species with appropriate characteristics have not yet managed to colonize the TEP. While the region has a poor fauna, indigenous species are adapted to a very dynamic ocean environment with wide temperature fluctuations and salinity, heavy sediment discharges, reduced tidal ranges, many areas of upwelling, diverse estuarine-lagoon systems, a very narrow continental shelf, few islands and coral reef formations, extensive oxygen minimum layer, and especially the El Niño Southern Oscillation (Boschi, 2000; Glynn & Ault, 2000; Hastings, 2000; Lea & Rosenblatt, 2000; Robertson & Cramer, 2009; Aguilar-Medrano, *et al.*, 2015).

The latter two phenomena are probably intolerant conditions for alien species. Fish migrations of the TEP to the western Pacific (Hawaii and the Marquesas islands) are also known but in a smaller proportion (1:3; Robertson *et al.*, 2004) and are characteristic of a high number of pelagic species or species associated with floating objects (Table 5). While trans-Pacific species contribute to an increase in species richness/biodiversity of the TEP, these species have different ecological characteristics compared to the local fauna, except in a few cases such as the genera *Acanthurus* and *Ctenochaetus*, and the two species of the genus *Arothron*. Despite these, there is no evidence of the invaders having biological or ecological characteristics that offer adaptive capabilities that may provide an advantage over members of the native fauna (Robertson *et al.*, 2004).

## SELECTED REVIEW OF RICHNESS / BIODIVERSITY HYPOTHESES AND ECOSYSTEM FUNCTION

Species richness depends solely on the number of species and thus the speciation processes whereas biodiversity depends on the abundance of each species in the ecosystem (Willig & Presley, 2017). Overall, there are about 50 hypotheses relating biodiversity to ecosystem function through simple hypothetical relationships that generally do not exemplify the true complexity of relationships in ecosystems (Naeem, 1998; Naeem *et al.*, 2002; Thibaut & Connolly, 2012). All of these studies use sets of traits (morphological, physiological, phenological, ethological and biochemistry convergence, or similar trophic characteristics; Violle *et al.*, 2007; Cadotte *et al.*, 2013; Laureto *et al.*, 2015; Villéger *et al.*, 2017) to separate and enumerate species phylogenetically or functionally; these traits may link phylogenetic lineages and ecological processes in ecological and evolutionary time (Willig & Presley, 2017; Floeter *et al.*, 2018).

Collectively, a functional trait is defined as one that can be measured in an organism and which is related to an effect on one or more ecological processes or a response to one or more environmental variables (Naeem & Li, 1997; Tilman, 2001; Diaz *et al.*, 2007; Martín-López *et al.*, 2007; Cadotte *et al.*, 2013; Winemiller *et al.*, 2015). This strategy used to represent the relationship between biodiversity and ecosystem function is a useful approach to simplify complex ecosystems based on a set of traits into units that facilitate comparative study among communities and are a low-resolution proxy to predict changes in the ecosystem. These traits can be compared directly or through calculation of functional diversity (*e.g.*, Winemiller *et al.*, 2015; Villéger *et al.*, 2017) that can further our understanding of the mechanisms and processes shaping patterns of biodiversity. Regardless of definitions, the functioning of ecosystems is carried out by the joint action of physical processes and natural attributes (solar radiation, evaporation, rainfall, currents, tides, etc.), the activities of the species (nitrogen fixation, feeding, breeding, growth, competition, migration, waste excretion, etc.), and the effects their activities have on the physical and chemical conditions of their environment. Thus, the function of an ecosystem is not singularly determined by the phylogenetic biodiversity of biota (Floeter *et al.*, 2018), but the functional traits of individuals, the distribution and abundance of these individual, and their biological activity (Naeem & Wright, 2003; Violle *et al.*, 2007; Cadotte *et al.*, 2013; Díaz *et al.*, 2013; Laureto *et al.*, 2015; Villéger *et al.*, 2017).

In recent years, the concept of functional groups has gained considerable popularity, particularly in plant ecology. Unlike the phylogenetic classifications, the approach is based on groups of functional traits that are ecologically significant and provide flexible classifications (Diaz *et al.*, 2002; Villéger *et al.*, 2017; Violle *et al.*, 2007). Many of these ideas stem from Southwood (1977) who presented a view that habitat features provide the template for recurring properties of biotic communities and that habitats could be viewed as ecological periodic tables organizing communities. In fact, Lopez de Casenave (2001) indicates that the functional groups could represent the basic building blocks of communities and become the standard currency of the ecologists in their efforts to understand community relations. The forerunner that considered organismal traits in the classification of plants of ancient Greece into trees, shrubs and herbs was Theophrastus (300 BC; Diaz *et al.*, 2002). In animals, Root (1967) was the first to employ classifications based on bird feeding strategies; these were called "guilds" and defined as a group of species that exploit a basic common resource in a similar way. Guilds or functional groups are comprised by generalist and opportunistic species with ambiguous boundaries that may in some cases be arbitrary (Root, 2001).

Pianka (1980) characterized guilds as arenas of intense interspecific competition with strong interactions, but weak interactions with the rest of their community. In contrast, Silvestre *et al.* (2003) indicates species belonging to a functional group would be those that exploited the resources within the n-dimensional niche in different ways, with a preference for certain portions of the food supply, differences in spatial occupation, or are active during different periods of the day. Furthermore, in tropical environments the effects of competition within functional groups appear minimized by the provision of non-limiting resources and the plasticity of behavioral strategies adopted by each species, avoiding agonistic encounters.

Some authors mistakenly use guild as a synonym of functional group. However, while functional groups simultaneously employ many traits related to the role of the species in the ecosystem, guilds are only based on the classification of a particular attribute (*e.g.*, feeding, reproduction, etc.). Elton (1927) was one of the first to use the term niche in the sense of the "functional state of the organism within its community" and defined the niche as "the basic function of an organism in the community because of relationships with food and their enemies." Subsequently, Root (2001) proposed to replace the Eltonian niche with "guild". This change produced contradictions that occur when several similar species are said to occupy the same niche; niche as a category is supposed to be a property of individual species (Blonder *et al.*, 2014). Therefore, species exploit niches while guilds exploit niche corners (Root, 2001). In contrast, the more ecological traits of species (Winemiller *et al.*, 2015) are employed to form functional groups, the closer we come to the definition of the niche; the fewer variables we have in the grouping of species, the closer we will approach the definition of guild (Root, 1967). Thus, Hutchinson (1957) suggested that niche could be viewed as the n-dimensional hypervolume within which the environment allows the individual or the species to survive indefinitely. Hutchinson also differentiated the maximum fundamental niche: "the hypervolume inhabited abstractly "when the species is not restricted by competition or other limiting biotic interactions, and the realized (true) niche: the smallest hypervolume occupied" under specific biotic constraints (Odum & Barrett, 2006; Blonder *et al.*, 2014; Pianka *et al.*, 2017).

Finally, the guild approach has been developed emphazing different life-history traits such that there is now a need to review the use of guild. The wide use of the guild approach has involved increasing overlap and/or confusion between different studies, which therefore increases the need for standardization while at the same time providing the opportunity to reconsider the types of guilds and their use worldwide. In fact, this term has lost its accuracy since its introduction, and has acquired a variety of meanings, ranging from functional analogs, ecological species, community guild, structural guild, functional guild, ecological species group, functional group, functional type, and many more (see Lopez de Casenave, 2001 for a review).

Until 2010, more than 90% of the studies using functional classifications were focused on terrestrial ecosystems. Of these, about 45% were plants, over 40% derived from experimental studies, and more than 30% were focused on the lifestyle of the species (Naeem & Wright 2003; Blaum *et al.*, 2011). In plants, two main approaches are used to form functional groups on the basis of environmentally significant traits (Diaz *et al.*, 2002), which can be generalized for animal studies (Barnett *et al.*, 2007). The *a priori* strategy based on a single character or a very small number of traits to define different groups. The definition of groups is required prior to the study in question (subjective classification, Jaksic, 1981; Terborgh & Robinson, 1986; Blondel, 2003; Naeem & Wright, 2003) and *a posteriori* method, which is based on the collection of information on a number of traits and the subsequent identification of functional groups from the simultaneous consideration of all these traits through multivariate statistics (Winemiller *et al.*, 2015; Pianka *et al.*, 2017). Typically, the functional groups and the most relevant traits are not defined before starting the study, but arise as a result of the study (objective classification; Hawkins & MacMahon, 1989; Simberloff & Dayan, 1991; Naeem & Wright, 2003; Winemiller *et al.*, 2015; Pianka *et al.*, 2017) regarding the environment or particular influence on ecosystem processes responses (Hooper *et al.*, 2002).

The type and number of traits used in functional classifications vary according to the scale of analysis and research objectives. Clearly, identifying key ecological traits involved in the processes of ecosystems is a major challenge to understand how species biodiversity affects ecosystem function. In general, most species within a specific ecosystem have similar environmental tolerances and occupy similar niches (Elliott *et al.*, 2007). Naeem & Wright (2003) indicated that the relationship between taxonomic biodiversity and functional diversity is sensitive to the character response and effect employed, function being assessed, the degree of redundancy and uniqueness of species, biotic interactions and trophic structure, and the biogeographic factors controlling species composition, distribution and abundance. Thus, if rare species are redundant, then ecosystem function may be insensitive to the loss of some of them, while the opposite happens if the rare species is unique. Redundancy and uniqueness may vary depending on the trait measured and effect response employed (Tilman *et al.*, 1997; Petchey & Gaston, 2006; Villéger *et al.*, 2010, 2014). In fish, morphology plays an important role in determining the type of prey consumed and morphological variation can lead to changes in foraging ability and a subsequently differential exploitation of food resources (Karpouzi & Stergiou, 2003; Cruz-Escalona *et al.*, 2005).

For example, the caudal fin generates propulsion and is important in maintaining swimming speed over long sustainable periods and also provides speed and acceleration (Fulton, 2007). However, the existence of species with different requirements and different evolutionary histories hinders determining a standard functional classification scheme to define functional groups. Some traits may be expressed by one or a few species in an association, whereas, others may have many unique traits, but it should be noted that some functional traits differently ontogenetically within a species (Vilà, 1998; Naeem & Wright, 2003; Winemiller *et al.*, 2015).

This variation challenges the classifications in functional *a priori* groups. For example, the classic fish example is the pinfish *Lagodon rhomboides* (Linnaeus, 1766) that presents an orderly progression of changes in trophic preferences (Livingston, 2002). One-year-old young recruits (< 20 mm standard length, SL) are primarily planktivorous, but as they grow (21-33 mm SL) they have a gradual transition to benthic carnivores, feeding on amphipods, mysids, and harpacticoid copepods, and at ~60 mm SL, they prefer amphipods, shrimp, algae and detritus. Fish between 61-120 mm SL eat crabs, shrimps and bivalve molluscs and once they exceed 120 mm SL they generally feed on seagrass, being practically herbivorous. The transition from one feeding stage to the next is gradual, but, in general, related to stages of growth associated with ontogenetic changes in morphology (dimension of the mouth, teeth, and size of the stomach) and body shape (Livingston, 2002).

Some authors suggest that there is a degree of predictability in the process of convergence. If there are similar resources in two geographically isolated locations, it is possible that a group of similar species may eventually converge despite phylogenetic differences (Schluter & Ricklefs, 1993; Winemiller *et al.*, 2015; Pianka *et al.*, 2017). However, despite ecosystems having quite similar structure, the organization of the species niches may be different; that is, a function performed by a species in an ecosystem can be equivalent within a second similar ecosystem, but in a third ecosystem, its function can be divided among several species, or included as part of the functions of another species (Smith & Smith, 2001). Furthermore, as a result of convergent evolution, some groups of plants and animals worldwide with independent evolutionary histories but under similar environmental conditions, adapt to similar ecological niches, and thus represent ecological equivalents (Whittaker & Levin, 1975; Pianka, 2000).

Table 4. Examples of sister species of marine fish with wide speciation in the Tropical Eastern Pacific Ocean.

| Family | Sister species | Common name | Distribution |
|---|---|---|---|
| Elopidae | *Elops affinis*, Regan, 1909 | Pacific ladyfish, machete | This species is present in the eastern Pacific stretching from southern California to Peru, including Isla del Coco (Adams *et al.,* 2012; Eschmeyer & Fong, 2013). |
| | *Elops saurus*, Linnaeus, 1766 | Atlantic ladyfish, northern ladyfish, tenpounder | The species is only distributed in the Western Atlantic from southern New England (but uncommon north of Cape Hatteras, NC) south to Florida, and throughout the Gulf of Mexico to the Yucatan Peninsula (McBride & Horodysky 2004; McBride *et al.*, 2010; Adams *et al.,* 2012). *Elops saurus* was recently split into two species, *E. saurus* and *E. smithi* (McBride *et al.*, 2010). |
| Eleotridae | *Gobiomorus maculatus* (Günther, 1859) | Pacific sleeper | This species is endemic to the Eastern Pacific, and is found from the tip of Baja California and the mouth of the Gulf of California, Mexico to northern Peru, including the Galapagos and Cocos Islands (Van Tassell, 2010a). |
| | *Gobiomorus dormitor*, Lacepède, 1800 | Bigmouth sleeper | This species is distributed in the western Atlantic from Bermuda, southern Florida, in the Bahamas from Andros Island, in the Gulf of Mexico from Louisiana (USA) down along Mexico to Cuba, throughout the Caribbean except the Cayman Islands and the northern Lesser Antilles, and along the Central and South American coast from Quintana Roo, Mexico to Touros, Brazil (Gilmore, 1992; McEachran & Fechhelm, 2005, Page &Burr, 2011). It can be found a considerable distance upstream at altitudes up to 300 m (Hildebrand, 1935). This species is most abundant in the Caribbean region, but is also common in tributaries to the southern Gulf of Mexico (Gilmore, 1992; Pezold *et al.*, 2015). |
| | *Dormitator latifrons* (Richardson, 1844) | Pacific fat sleeper | This species is endemic to the Eastern Pacific, and is found from southern California, USA and the Gulf of California, Mexico to Ecuador, including the Galapagos Islands (Van Tassell, 2010b). |
| | *Dormitator maculatus* (Bloch, 1792) | Fat sleeper | This species is distributed in the western Atlantic from North Carolina (USA) south along the U.S. and in the Bahamas, throughout the Gulf of Mexico and Caribbean Sea to southeastern Brazil. It has been recorded as far north as Massachusetts, however, rarely occurs past North Carolina. It can be found up to nine meters depth (Robins & Ray, 1986; Rezendes-Medina, 1973; Felder *et al.*, 2009; Nordlie, 2012). It is not known from the Cayman Islands. In the southern Gulf of Mexico is has been recorded from Pantanos de Centla, Mexico in Arroyo Punteada, the dredged canal San Román, the drains Narváez Norte and Narváez Sur, the lagoons Cantemoc, Concepción, El Coco, El Guanal, El Viento, Landeros, Larga, Los Ídolos, Punteada, El Sauzo, San Isidro, San Isidro El Jobo, San Pedrito, the Grijalva Centro River and the first section of the Ribera, Alta River (Usumacinta River) in 28.4°C and PSS 0.6, on average (Macossay-Cortez *et al.*, 2011; Aiken *et al.*, 2015). |
| Ephippidae | *Chaetodipterus zonatus* (Girard, 1858) | Pacific spadefish | This eastern Pacific species is found from southern California to the Gulf of California to northern Peru, and Malpelo (Smith-Vaniz *et al.*, 2010). |
| | *Chaetodipterus faber* (Broussonet, 1782) | Atlantic spadefish | Atlantic spadefish species is distributed in the western Atlantic from Massachusetts south along the U.S. coast, Bermuda, the Bahamas, throughout the Gulf of Mexico and Caribbean Sea, and along the South American coast to southern Brazil. Its depth range is 0-30 m (Dooley *et al.*, 2015). |
| Blenniidae | *Ophioblennius steindachneri*, Jordan & Evermann, 1898 | Panamic banged blenny | This species is endemic to the Eastern Pacific, and is found from central Baja California and the northern Gulf of California, Mexico to Peru, and including the Revillagigedo, Cocos, Malpelo and Galápagos Islands (Bessudo *et al.*, 2014). |
| | *Ophioblennius macclurei*, (Silvester, 1915) | Redlip blenny | Redlip Blenny is distributed in the western Atlantic from the Gulf of Mexico in Vermillion Bay, Louisiana south to the Yucatan, Cuba, and Florida Keys, the Bahamas, and throughout the Caribbean Sea. It is also found on offshore reefs and banks in the eastern and northwestern Gulf of Mexico from Florida in the Dry Tortugas, off Texas, Veracruz, Mexico, and on Alacranes Reef off Yucatan (McEachran & Fechhelm, 2005; Williams, 2014). |

Table 5. Examples of tropical trans-Pacific fishes. Asterisks = information from reference below.

| Family | Specie | Common name | Distribution | Habitat |
|---|---|---|---|---|
| *Sphyrnidae | *Sphyrna zygaena*, (Linnaeus, 1758) | Smooth hammerhead | Cirncumglobal in tropical and temperate seas; California to Mexico, Colombia to Chile. | A coastal-pelagic and semi-oceanic hammerhead often sighted near Surface. |
| **Carangidae | *Decapterus muroadsi* (Temminck & Schlegel, 1844) | Amber-striped scad, Mexican scad | An Indo-Pacific species; southern California to the tip of Baja, Ecuador to Chile, the Revillagigedos and Galapagos. | The Amberstriped scads are a coastal pelagic species found at depths up to 1,050 feet. Adults are pelagic, in oceanic and inshore waters forming schools. |
| *Echinorhinidae | *Echinorhinus cookei*, Pietschmann, 1928 | Prickly shark | A subtropical to temperate Pacific species; Oregon to Chile. | Demersal, 10-1100 m depth. Reef associated (reef + edges-water column and soft bottom). Soft bottom (mud/sand/gravel/beach) |
| Mugilidae | *Mugil cephalus*, Linnaeus, 1758 | Striped mullet | This species is widespread throughout the tropics and sub-tropical seas to warm temperate regions. | This species is pelagic near shores, it sometimes forages in lagoons, estuaries and lower courses of rivers and can tolerate freshwater. It is known to breed in its third year of life: adults school in estuaries then move out to sea to spawn in coastal surface water, before returning to estuaries and freshwater (Harrison and Senou 1999). Juveniles feed on zooplankton, larger individuals filter algae, detritus, sediment and small invertebrates. |
| Lobotidae | *Lobotes pacificus*, Gilbert, 1898 | Pacific tripletail | Southern California to the Gulf of California to Perú, Coccos islands. | Occurs in bays and brackish estuaries or sometimes well out to sea around floating objects; juveniles sometimes in flotsam, they may lay on their side at the Surface and mimic a drifting dark leaf. |
| **Carangidae | *Caranx caballus*, Günther, 1868 | Green jack | Green jack are widely distributed along the Pacific coast of the Americas, from southern California, USA, to Peru (Mair *et al.* 2012; Robertson and Allen 2008). | Often caught in open water between the islands on spoons or feather lures trolled by fishermen. |
| **Carangidae | *Seriola rivoliana*, Valenciennes, 1833 | Almaco jack | Througout tropical and subtropical waters, in the eastern Pacific from Oceanside, California to Perú, and Galápagos. | Open water or near escarpments, occasionally moving into more shallow waters to feed. Species associated with floating objects. |
| **Carangidae | *Uraspis helvola* (Forster, 1801) | Whitemouth jack | This species is widely distributed in the Indo-West Pacific but rarely collected. Verified records from the Western Central Pacific area are pending and if *U. secunda* is a junior synonym, this species is also widely distributed throughout the Atlantic. In the Eastern Central Atlantic, *Uraspis helvola* occurs off St. Helena and Ascension Islands, and there is also a record from off Cape Verde. In the Indo-West Pacific, this species occurs from off South Africa, Mozambique, Somalia, the Red Sea, off Oman and Bahrain, Sri Lanka, the Andaman Sea, the northern South China Sea, the Hawaiian Islands and offshore islands of the tropical eastern Pacific. Records from the Philippines south to Australia need verification. | A pelagic schooling species that prefers waters over the continental shelf, and around islands (Smith-Vaniz & Williams, 2015). The depth range for this species is 50 to 300 m (Jiménez Prado & Béarez, 2004). |
| *Khiphosidae | *Kyphosus ocyurus*, (Jordan & Gilbert, 1882) | Bluestriped sea-chub | From southern California to Perú (excluding the bulk of the Gulf of California) and all the oceanic islands. Occasional specimens have also reached Tahiti and Hawai, and there is a resident population in the Marquesas Islands of Polynesia. | Most common around offshore islands, also frequently seen near floating logs far out to sea. |

Tabla 5. Continúa.

| Family | Specie | Common name | Distribution | Habitat |
|---|---|---|---|---|
| Scombridae | *Euthynnus lineatus*, Kishinouye, 1920 | Black skipjack | The occurrence of black skipjack is sometimes reported in the logbooks of commercial tuna fishing vessels, although this species is not taken by these vessels. A search of the tuna boat log- book records of the Inter-American Tropical Tuna Commission revealed that this species has been encountered, at various times, nearly everywhere along the coast from the middle of Baja California to Guayaquil Bank, off northern Peru. They have frequently been reported from the Gulf of California, the Revillagigedo Islands, all along the coast of Mexico and Central America, and the Galapagos Islands. In addition, black skipjack have occasionally been reported from Clipperton and Cocos Islands and there is a single report from Shimada Bank (l6°52’N by 17°30’W), 1.80 miles southwest of Clarion Island. | This species is associated with floating objects. |
| Ballistidae | *Balistes polylepis, Steindachner, 1876* | Finescale triggerfish | In the eastern Pacific, this species ranges from northern California to the Gulf of California to central Chile and all the offshore islands. It also occurs in Hawaii (may be a vagrant), where it may be establishing a population, and seen in the Marquesas islands in 1999. | This reef-associated species occurs in rocky reefs, boulder strewn slopes, and adjacent areas of sand. Adults are demersal; and young are pelagic. It feeds on sea urchins, small crustaceans, and mollusks. This species is known to occur to 50m but may occasionally be found deeper. This species is associated with floating objects (Nielsen *et al.*, 2010). |

**Grove, J.S. & R.J. Lavenberg. 1997. The fishes of the Galápagos Islands. Stanford University Press, Stanford, California

*Robertson, D.R. & G.R., Allen. 2008. Shore fishes of the Tropical Eastern Pacific. Panamá: Smithsonian Tropical Research Institute. Retrieved from: http://www.neotropicalfishes.org/sftep; www.stri.org/sftep.

For example, members of the Labridae are one of the most structurally and functionally diversified fish families on coral and rocky reefs around the world, having evolved a diverse array of skull forms for feeding on diverse prey ranging from molluscs, crustaceans, plankton, detritus, algae, coral, and other fishes (Westneat *et al.*, 2005). Despite the importance of labrids to coastal reef ecology, Westneat *et al.* (2005), determined a repeated phylogenetic pattern of functional divergence in local regions of the labrid phylogenetic tree that produces an emergent family-wide pattern of global convergence in jaw function. The divergence of close relatives, convergence among higher clades, and several unusual ‘breakthroughs’ in skull function characterize the evolution of functional complexity in these diverse groups of reef fishes. Finally, closely related species are not necessarily similar morphologically and functionally as Steneck (2001) illustrated that taxonomically unrelated species, which are similar in anatomy, ethology, physiology and function within natural communities, have evolved similar functional traits under similar environmental conditions from disjunct geographic locations. For example, feeding behavior and diet associations between Brazilian offshore rocky reef and freshwater lake communities showed a great similarity despite the taxonomic differences between preys (Sazima, 1986). The feeding behavior of about a third of the fish in each community was ecologically equivalent, even though the author excluded species with close phylogenetic relationships (*e.g.*, Belonidae). Despite having very different floristic and faunal communities, there were a number of similar structural and functional characteristics; the similarity in the feeding strategy in some species was very strong, including behavior, appearance, and structure of the alimentary tract.

The territorial behavior exerted by species of the Pomacentridae and Serranidae families in reef systems is similar to species of Characidae and Cichlidae families in lakes (Sazima, 1986). However, each system has species with specific tactics, such as cleaning characteristic of reef systems, and piranha attacks on large predators and scavengers in lakes. In both communities, species richness was similar (rocky reefs: 64 species, 35 families, and 10 orders vs Lakes: 61 species, 16 families and 5 orders), but the marine reefs were taxonomically more diverse (3.9 vs 1.9 genera per family). These observations support the idea that associations of unrelated species have the ability to evolve into a suite of behavioral, structural, and functional organization patterns, based, in part, on similarity in environmental selective pressures on functional traits (Whittaker & Levin, 1975; Pianka, 2000).

Several generalities have been recognized in regard to biodiversity and species’ distribution patterns. One of the most important is the “latitudinal gradient in species richness” which suggests the existence of high species richness at low latitudes (the tropics) that gradually decreases towards higher latitudes (Willig & Bloch, 2006; Willig & Presley, 2017). This gradient is maintained in terrestrial, marine and freshwater ecosystems and is more pronounced in taxa with higher species richness. Over 30 scenarios have been proposed to explain this trend (*e.g.*, average domain-climatic stability, spatial heterogeneity, species-energy, historical disturbance, among others), but none has gained general acceptance and the issue is still debated (Willig *et al.*, 2003; Willig & Presley, 2017).

Briggs (2006) proposed an explanation of the latitudinal pattern of biodiversity in the marine environment based on historical events and the types of speciation involved. According, tectonic events during the Jurassic period (~ 200 mya) caused the separation of Pangea and the combination of four significant factors stimulated the increase in marine biodiversity. These are (1) an increase in sea level, (2) the formation of biogeographic barriers, (3) an increase in the areas of continental shelves, and (4) an increase in global temperature. Then, between the Cretaceous (~ 145 mya) and the Tertiary periods, sea level and the temperature dropped, and a mass extinction occurred which extinguished about half of the species of the planet; the recovery took two million years. During the Cenozoic (~ 66 mya to present), the present temperature gradient from the tropics to the poles was established as well as the consequent global gradient of organic biodiversity.

The first key process that contributed to the increase of biodiversity of the Cenozoic was the formation of biogeographic regions and provinces due to the temperature gradients, promoted by tectonic movements and changing ocean currents. Subsequently, four centers of evolutionary origin (Antarctica, the North Pacific, eastern Indonesia, and the southern Caribbean) are suggested to be the main sources of diversification in the marine environment, increasing biodiversity in other parts of the world (Briggs, 2007). The centers of origin hypothesis (Briggs, 2000; 2006; 2007) assumes that interspecific interactions (competition, predation, etc.) are the main determinants of the number of coexisting species in a habitat, that all available energy is used by the resident species, and that only through finer subdivision of habitat may increase the richness of a community (Pianka, 2000; Ruggiero, 2001; Ruggiero *et al.*, 2015). However, adjustment of the centers of origin hypothesis indicates that species richness at the local scale is increased by processes that occur at the regional scale (Ruggiero, 2001). Thus, typical processes of speciation and migration occurring within biogeographic provinces can add species to these communities without speciation and niche differentiation at the local scale.

The species occupying centers of origin appear to be highly competitive, well adapted, and have the necessary genetic resources to adjust to environmental changes. When species extend their distribution ranges, they can displace less competitive species, and in turn, are exposed to a variety of barriers that can disrupt their genetic integrity (Briggs, 2007). Eventually, the barrier can result in allopatric speciation and ultimately, the generation of new species. Populations of geographical provinces isolated by physical barriers contribute to the overall richness/biodiversity of populations of endemic species produced by allopatric speciation.

The characteristic sympatric speciation within centers of origin and the allopatric speciation of peripheral provinces seem to be the main sources of marine biodiversity. However, Krebs (2003) notes that environmental factors control natural selection in temperate and polar areas, whereas in the tropics, biological competition is more important for evolution. This concept reflects that the core processes for the functioning of ecosystems can be maintained by very few species and questions if there is really a relationship between biodiversity and ecosystem function (Tilman *et al.*, 2014). Finally, although the centers of origin hypothesis (Briggs, 2007) is often supported by certain patterns of species distribution (Mora *et al.*, 2003), it is often not considered valid on multiple grounds by some experts (Morrone, 2002); thus, it is necessary to be taken with caution. In contrast, the species-energy hypothesis (Hillebrand, 2004a) based on a great number of indirect variables such as air temperature, sea temperature, radiation, biomass, productivity, and potential and actual evapotranspiration, which reflect the availability of energy, has been widely accepted in marine environments. However, the major disadvantage of this hypothesis, is that it presents no mechanism that links the energy transfer to biodiversity (Hillebrand, 2004a).

Because increased species richness is a well-established pattern across many taxa and is pervasive in time and space (Willig & Presley, 2017), it is likely that a number of mechanisms are required to generate latitudinal gradients and may be species and habitat dependent; gradients appear not to be based solely on variation in species richness. For example, the evolutionary time hypothesis (Rohde, 1992) that assumes that tropical areas favor high rates of speciation and low rates of extinction because they have a larger geographic area, greater productivity (energy), increased spatial heterogeneity, and a greater geological stability. Furthermore, the area hypothesis predicts that species richness and biodiversity is generally associated with a high susceptibility to allopatric speciation through geographical barrier formation, high probability of covering more niches, and higher total population size (Rosenzweig, 1992; Ruggiero, 2001; Ruggiero *et al.*, 2015).

This hypothesis agrees well with observations of fossil record indicating that tropical areas are centers of evolution, with greater evolutionary speed than mild climate areas (Hillebrand, 2004b). However, the latitudinal gradient in species richness has a few exceptions to the observed spatial pattern. An interesting example (Bolton, 1994) is the green (Chlorophyta), brown (Phaeophyta) and red (Rhodophyta) macrophytic algae that has a tendency to increase towards the poles, attributed to competition for suitable habitats with tropical coral reef species. Another latitudinal gradient related to the distribution range of the species is the "Rapoport's rule." This suggests a progressive increase in the size of the geographic ranges of species with latitude, a pattern that is explained as an effect of selection for greater species climate tolerance inhabiting higher latitudes (Stevens, 1989). As species inhabiting temperate-cold regions are adapted to greater climatic variability than tropical species, this allows them to extend their geographical distribution. A similar pattern occurs in marine fish where fishes that live near the ocean surface are distributed in narrow depth ranges, while fishes in deeper areas are distributed over wide ranges (Stevens, 1989; Hughes *et al.*, 2002; Macpherson, 2003; Tittensor *et al.*, 2010; Willig & Presley, 2017).

In parallel, it has been identified that biodiversity also decreases with altitude, aridity, depth, and environmental homogeneity, among other factors. A model based on planktonic foraminifera (Allen *et al.*, 2006) indicated that environmental temperature affects the metabolic speed of individuals and influences in the divergence rate and therefore the tempo of speciation. This indicates that the environmental temperature may be an important controlling factor in speciation rates and, in turn, helps explain the overall decline in species richness with increases in latitude (Briggs, 2007). However, although the temperature is a good indicator of speciation rates, this does not explain why the distribution range can differ in the longitudinal plane. Finally, Allen & Gillooly (2006) reported positive correlations between species richness and speciation rates for some groups of plankton, indicating that the speciation rate varies with species abundance; overall, new species, genera and families evolve under conditions of high biodiversity.

Based on these models and the idea that "biodiversity generates biodiversity," Briggs (2007) argues that a high rate of speciation developed a high concentration of species in the Indo-Pacific and the southern Caribbean Sea, and that outward migration to warm-temperate latitudes occurred and from there the migration reaches the poles. One trophic strategy driving such a pattern in tropical centers of origin, is herbivory which is a widespread feeding strategy but is rare in temperate waters. Cold waters are a complicated physiological barrier relative to the increase in energy demand; thus, Briggs (2006) suggests some groups have shifted into a type of omnivorous feeding or perform seasonal changes between herbivorous and carnivorous habits. In some locations, between 57 and 79% of the species depends on their diet of algae and sea grasses (Kieckbusch *et al.*, 2004).

This suggests that a considerable portion of the tropical marine biodiversity can be attributed to the presence of species that tend to evolve by means of ecological specializations, using low energy food sources. This shift towards an alternative food supply under high competition suggests that sympatric speciation may partially drive evolution in the tropics. The processes of sympatric speciation (or parapatric) are suggested to be faster than allopatric processes (Bush & Butlin, 2004), indicating that the exponential increase in biodiversity during the Cenozoic might be mainly due to the production of centers of origin (Busch & Butilin, 2004; Mittelbach *et al.*, 2007).

## IMPORTANCE OF FUNCTIONAL REDUNDANCY IN ECOSYSTEM FUNCTION AND THE IMPACT OF ENVIRONMENTAL DISTURBANCES

Naeem *et al.* (2002) grouped the biodiversity and ecosystem functioning hypotheses that emerged as mechanisms into three classes according to how the relationship is modified by removing or adding species that can include temporally or trait-based trait redundancy. First, species are mostly redundant. This premise assumes that systems are sensitive to variation in biodiversity and implies that the loss of species is compensated by other species or by the incorporation of alien species that do not add new functions to the system. The basis of this premise is a classification of species into functional groups formed by redundant species (Walker, 1992). Functional redundancy is based on the premise that some species perform the same function in communities and ecosystems, and can, therefore, be replaced with little impact on ecosystem processes (Walker, 1992; Rosenfeld, 2002).

For the maintenance of ecosystem functions, a minimum number of species is required in each functional group or ecosystem stability may become reduced or lost to the extent that the functional groups disappear (Lawton & Brown 1993); thus, to ensure stable ecosystem functions, redundancy is required. Second, species are mostly unique which implies that each species contributes to ecosystem functioning in a unique way, therefore, species loss or addition causes a noticeable change in ecosystem function and stability (Naeem *et al.*, 1994; Naeem & Li, 1997; Pratchett *et al.*, 2011).

Keystone species or ecosystem engineering species are often cited as examples of unique species. Engineer species modify the available resources for the other members of the community through the modification of the habitat (*e.g.*, oysters or beaver dam builders; Lawton, 1994). These species have a disproportionate functional impact (positive or negative depending on the processes under study) on community or ecosystem abundance and biodiversity (Scherer-Lorenzen, 2005). Third, the impacts of species are context-dependent and therefore idiosyncratic or unpredictable (Fariña *et al.*, 2003). The idiosyncratic response hypothesis (Lawton, 1994) argues that the impact based on the loss or addition of a species in an ecosystem can be insignificant or highly significant, depending on environmental conditions (*e.g.*, fertility, food availability, disturbance regime, etc.), the nature of the added or loss species, and the nature of the species with which it interacts.

To illustrate how the functional redundancy of species in a community depends on the environmental context (premise three above), Wellnitz & Poff (2001) developed a theoretical scenario based on a hypothetical feeding guild formed by three lotic species (A, B and C). These three species belong to a guild of grazers and current velocity is vital to their permanence. These species are potentially redundant at low velocities since they feed on algae and associated organisms and detritus, with overlap in their fundamental niche. On average, all three species have the same effect on the rate at which algae are removed from the substrate. However, the relative importance of each species in this process changes dramatically as velocity increases with their functions being similar under low speed conditions, but not redundant at intermediate and high current velocities. Thus, if we conclude that the three species are redundant based on their functional contributions in the low velocity or the average value of the three gradients, and then we remove species C, the community would lose an important functional component in the system. Unfortunately, there are a limited number of studies that address this type of issue that provides an unlimited overview of the functions of the species, and thus may give a false diagnosis of redundancy.

Studies that do address such changes or impacts indicate variable results depending on duration/frequency of disturbances and these are scale-dependent (local, regional). For example, Bellwood *et al.* (2006) conducted an experimental study in the Great Barrier Reef, simulating changes from a macroalgae-dominated to a coral- and epilithic-dominated state, inducing the reversal of the dominance of macroalgae through functional herbivorous fishes. Surprisingly, the reversal through direct removal of macroalgae was not the result of grazing parrotfish (Scaridae) and surgeonfish (Acanthuridae), the most common herbivorous reef fish, or any of the other 43 herbivores species in the area, but primarily from a single species, the batfish *Platax pinnatus* (Linnaeus, 1758) (Ephippidae, that was previously listed as zoobentivore). The species was observed consistently ingesting large pieces of *Sargassum* (the dominant macroalgae) and algae. The batfish is relatively rare in the Great Barrier Reef (1.6 individual/ha), but it has the ability to remove 12,750 kg/yr; however, the importance of removing macroalgae by this species was unknown.

This species, according to Bellwood *et al.* (2006), represents a ‘sleeping’ functional group-species or group of species able to perform a particular function role but only under certain exceptional circumstances. This case highlights the importance of identifying and protecting these species or species groups that support resilience and regeneration of complex ecosystems. Similarly, the green humphead parrotfish, *Bolbometopon muricatum* (Valenciennes, 1840), from the Indo-Pacific, was primarily responsible for bioturbation of coral reefs, each fish consumes about five tons of carbonate coral reef per year, corresponding to about half of the live coral (Bellwood *et al.*, 2003, Bellwood & Choat, 2011). Overfishing of this species has changed the dynamics of accretion of reefs (Bellwood *et al.*, 2003; Bellwood & Choat, 2011).

Coral reef ecosystems are increasingly subject to severe, large-scale disturbances caused by climate change (*e.g.*, coral bleaching) and other more direct anthropogenic impacts causing coral loss; these cause changes in habitat structure, which has additional effects on abundance and biodiversity of coral reef fishes (Wilson *et al*., 2006). Declines in the biodiversity and abundance of coral reef fishes are of considerable concern, given the subsequent loss of ecosystem function (reviewed in Pratchett *et al*., 2008). Pratchett *et al*. (2011) reviewed the effects of coral loss throughout the world on the biodiversity of fishes and also on individual functional responses of fishes. Extensive (> 60%) coral loss led to declines in fish biodiversity; most fishes declined in abundance following disturbances that caused > 10% declines in local coral cover. Response biodiversity, which is considered critical in maintaining ecosystem function and promoting resilience, was very low for corallivores, but was much higher for herbivores, omnivores and carnivores. They indicated that sustained climate change poses a significant threat to coral reef ecosystems and biodiversity hotspots are no less susceptible to projected changes in biodiversity and function (Pratchett *et al*., 2011). Although there is no global agreement on the effects of species loss on ecosystem functioning, it has been noted that deforestation, introduction of exotic species, habitat destruction, isolation or fragmentation of habitats and pollution can contribute to local, regional and global extinction of species causing an inevitable ecosystem degradation and loss of services to society (Sodhi *et al*., 2009).

However, Cheal *et al*. (2008) suggested that coral reef fish biodiversity may not be a reliable indicator of reef resilience but predicted declines in coral cover due to global warming are likely to cause changes in the observed structure of reef fish communities; the nature of these changes and associated functional capacity to assist ecosystem recovery will vary among reefs because of differences in functional diversity. Finally, Denis *et al*. (2017) based on the 1983 severe coral reef bleaching data off Tikus Island Indonesia, found clear signs of coral assemblage complexity recovery approaching pre-El Niño conditions five years after the event. They also noted that, independent of the changes in species richness, this return in structural complexity was accompanied by a global decrease in species number associated with functional redundancy (each morphological entity) and an increase in the functional vulnerability (number of unique single-species/functional groups). They suggested an overall functional erosion of the coral assemblage and indicated that the role of the coral reef habitat could be strongly imperiled under repeated or synergistic disturbances.

Currently, there has been a surge of studies examining the relationship between phylogenetic (species) biodiversity, functional diversity, and ecosystem sustainability (*e.g.*, Cowman, 2014; Floeter *et al*., 2018) using different approaches and relative to a better understanding of anthropogenic-induced impacts on sustainability. Although there are multiple definitions (Naeem & Li, 1997; Tilman, 2001; Diaz *et al*., 2007; Martín-López *et al*., 2007; Cadotte *et al*., 2013; Winemiller *et al*., 2015), all agree on the importance of evaluating the functional role of species within an ecosystem. The approaches vary but most are through multidisciplinary and multivariate studies (Schulze & Mooney, 1994; Winemiller *et al*., 2015; Pianka *et al*., 2017; Floeter *et al*., 2018) where functional groups are defined according to the concept that species with high overlap of information on ecological and morphological traits are placed together and thus play similar ecological roles (Alvarez-Filip & Reyes-Bonilla, 2006; Cadotte *et al*., 2013; Winemiller *et al*., 2015; Pianka *et al*., 2017).

Each group is characterized by its own unique combination of functional features and outcomes provide a manageable number of groups that maximize the biological coherence of its members (Field *et al*., 1982; Simberloff & Dayan, 1991; Petchey & Gaston, 2002; Winemiller *et al*., 2015). Recently, Floeter *et al*. (2018) documented that functional traits and the environment influence phylogenetic lineages, such that acquiring a functional trait may drive evolution of other traits or behaviors and that an improvement of our understanding of mechanisms of species assemblages are enhanced using both metrics in coral reef fish communities.

In theory, the presence of multiple dominant or subordinate species increases the functional redundancy within each functional group and provides ecosystem resilience to respond or adapt to disturbances (Giller & O'Donovan, 2002). Further, functional redundancy also reduces the likelihood of invasion of exotic species (Naeem *et al*., 1994; Walker *et al*., 1999; Steneck, 2001; Rosenfeld, 2002; Hooper *et al*., 2005). The greater the number of functionally similar species, each with different responses to environmental constraints, the greater the likelihood that at least one species survives against possible disturbances (Walker, 1992, 1995; Naeem, 1998; Diaz *et al*., 2013).

For example, let us assume that an ecosystem is facing a drought, then a fire, and then is on flood. According to the functional diversity hypothesis, the ecosystem will have species that can tolerate drought, some that are fire-tolerant, and some that are resistant to flooding. If true, then two scenarios are likely: 1) the ecosystem may show resistance, remaining unchanged because species richness moderates the damage; or 2) the ecosystem may show resilience, quickly returning to its original state because tolerant species contribute to recovery and compensate for the functional loss of other species who showed less resistance (Naeem, 2002).

After removing a species within a fully formed group, reduced redundancy makes the remaining species increase their density to offset the functional contribution of the lost species. For example, in algae when a compensating effect between species of the same functional group is observed; biomass remains relatively constant despite fluctuations in species abundance (Steneck, 2001). Functional redundancy is good because it increases ecosystem resilience (Walker, 1992; Cheal *et al*., 2008) and important functional groups comprised of a few or a single species deserve attention regarding conservation priority because their functions may be rapidly lost (Walker, 1992).

## CONCLUSIONS

The analysis of functional diversity is a powerful and complementary tool to the classic indices of biological biodiversity (richness, dominance, equity, etc.) and taxonomic biodiversity indices (taxonomic biodiversity, taxonomic differentiation, average taxonomic differentiation, variation in taxonomic distinction). Biodiversity indicates richness and proportions, taxonomic biodiversity reflects the structure and phylogenetic variability, and functional diversity suggests the role of species in the ecosystem. Moreover, functional diversity studies can be used as a tool to predict the functional consequences of invasions or invasion front speciation events (Chuang & Peterson, 2016) and biotic changes caused by humans like overfishing, habitat loss, and climate change (Heenan & Williams, 2013; Villéger *et al*., 2017). The functional diversity approach offers an opportunity for a better understanding of coral reef ecosystem responses, and the associated fish communities, to natural and anthropogenic disturbances.

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## REFERENCES

Adams, A., K. Guindon, A. Horodysky, T. MacDonald, R. McBride, J. Shenker & R. Ward. 2012. *Elops affinis*. The IUCN Red List of Threatened Species 2012: e.T184047A1745464. DOI:10.2305/IUCN.UK.2012.RLTS.

Adams, A., K. Guindon, A. Horodysky, T. MacDonald, R. McBride, J. Shenker & R. Ward. 2012. *Elops saurus*. The IUCN Red List of Threatened Species 2012: e.T191822A2006513. DOI:10.2305/IUCN.UK.2012.RLTS.

Aguilar-Medrano, R., P. D. Polly & H. Reyes-Bonilla. 2015. Adaptive radiation of damselfishes (Perciformes, Pomacentridae) in the Eastern Pacific. *Marine Ecology* 162: 2291-2303. DOI:10.1007/s00227-015-2759-9.

Aguilar-Medrano, R. 2018. Ecomorphological trajectories of reef fish sister species (Pomacentridae) from both sides of the Isthmus of Panama. *Zoomorpholog*y 137:315-327. DO:10.1007/s00435-017-0391-6.

Aiken, K. A., J. van Tassell, F. Pezold, L. Tornabene & J. L. Bouchereau. 2015. *Dormitator maculatus*. The IUCN Red List of Threatened Species 2015: e.T185972A1796964. DOI:10.2305/IUCN.UK.2015-2.RLTS.

Allen, G. R. & D. R. Robertson. 1997. An annotated checklist of the fishes of Clipperton Atoll, Tropical Eastern Pacific. *Revista de Biologìa Tropical* 45 (2): 813-843.

Allen, L.G., T.E. Hovey, M.S. Love & J. T. Smith. 1995. The life history of the spotted sand bass (*Paralabrax maculatofasciatus*) within the Southern California Bight. *California Cooperative Oceanic Fisheries Investigations Report* 36:193-203.

Allen, A. P., J. F. Gillooly, V. M. Savage & J. H. Brown. 2006. Kinetic effects of temperature on rates of genetic divergence and speciation. *Proceedings of the National Academy of* Sciences *of* the United States *of America* 103:9130-9135. DOI:10.1073/pnas.0603587103.

Allen, G. & R. Robertson. 2010a. *Girella nigricans*. The IUCN Red List of Threatened Species 2010: e.T184016A8219255. DOI:10.2305/IUCN. UK.2010-3.RLTS. T184016 A8219255.

Allen, G., R. Robertson & B. Lea. 2010b. *Anisotremus davidsonii*. The IUCN Red List of Threatened Species 2010: e.T183736A8167224. DOI:10.2305/IUCN.UK.2010-3.RLTS. T183736A8167224.en Downloaded on 6 October 2017.

Allen, G., R. Robertson, B. Lea & L. Findley. 2010c. *Hermosilla azurea*. The IUCN Red List of Threatened Species 2010: e.T183465A8117976. DOI:10.2305/IUCN.UK.2010-3.RLTS.T183465A8117976

Allen, A.P. & J.F. Gillooly. 2006. Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. *Ecology Letters* 9 (8): 947-954. DOI:10.1111/j.1461-0248.2006.00946.x.

Álvarez-Filip, L. & H. Reyes-Bonilla. 2006. Comparison of community structure and functional diversity of fishes at Cabo Pulmo coral reef, B.C.S. Mexico between 1987 and 2003. *In:* Proceedings of 10th International Coral Reef Symposium. Okinawa, Japan, pp. 216-225.

Barnett, A. J., K. Finlay & B. E. Beisner. 2007. Functional diversity of crustacean zooplankton communities: towards a trait-based classification. *Freshwater Biology* 52: 796-813. DOI:10.1111/j.1365-2427.2007.01733.x.

Bellwood, D. R, & J. H. Choat. 2011. Dangerous demographics: the lack of juvenile humphead parrotfishes *Bolbometopon muricatum* on the Great Barrier Reef. *Coral Reefs* 30:549-554. DOI: 10.1007/s00338-011-0738-2

Bellwood, D.R., A.S. Hoey & J.H. Choat. 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters* 6: 281-285. DOI:10.1046/j.1461-0248.2003.00432.x.

Bellwood, D. R., T. P. Hughes & A. S. Hoey. 2006. Sleeping functional group drives coral reef recovery. *Current Biology* 16: 2434-2439. DOI:10.1016/j.cub.2006. 10.030.

Benton, M. J. 2001. Biodiversity on land and in the sea. *Geological Journal* 36: 211-230. DOI:10.1002/gj.877.

Bernardi, G. 2014. Baja California disjunctions and phylogeographic patterns in sympatric California blennies. *Frontiers in Ecology and Evolution* 2 (53): 1-9**.** DOI:10.3389/fevo.2014.00053.

Bernardi, G., L. Findley & A. Rocha-Olivares. 2003. Vicariance and dispersal across Baja California in disjunct marine fish populations. *Evolution* 57: 1599-1609. DOI:10.1111/j.0014-3820.2003.tb00367.x.

Bessudo, S., A. Dominici-Arosemena, H. Espinosa & P. Hastings. 2010a. *Hypsoblennius gentilis*. The IUCN Red List of Threatened Species 2010: e.T183611A8144381. DOI:10.2305/IUCN.UK.2010-3.RLTS. T183611A 81 44381.en.

Bessudo, S., A. Dominici-Arosemena, H. Espinosa & P. Hastings. 2010b. *Chaenopsis alepidota*. The IUCN Red List of Threatened Species 2010: e.T183941A8203769. DOI:10.2305/IUCN.UK.2010-3.RLTS. T183941A8 203769.en.

Bessudo, S., A. Dominici-Arosemena, H. Espinosa & P. Hastings. 2014. *Ophioblennius steindachneri*. The IUCN Red List of Threatened Species 2014: e.T183308A46224332. DOI:10.2305/IUCN.UK.2014-3.RLTS. T183308 A46224332.en.

Blaum, N., E. Mosner, M. Schwager & F. Jeltsch. 2011. How functional is functional? Ecological groupings in terrestrial animal ecology: towards and animal functional type approach. *Biodiversity and Conservation* 20: 2333-2345. DOI: 10.1007/s10531-011-9995-1.

Blondel, B., C. Lamanna, C. Violle & B.J. Enquist. 2014. The n-dimensional hypervolume. *Global Ecology and Biogeography* 23: 595-609. DOI:10.1111/geb.12146.

Blondel, J. 2003. Guilds or functional groups: does it matter? *Oikos* 100:223-231. DOI:10.1034/j.1600-0706.2003.12152.x

Bolton, J. J. 1994. Global seaweed diversity: patterns and anomalies. *Botanica Marina* 37: 241-245. DOI:10.1515/botm.1994.37.3.241.

Boschi, E. 2000. Species of decapod crustaceans and their distribution in the American marine zoogeographic provinces. *Revista de Investigaciòn y Desarrollo Pesquero* 13: 7-136. http://hdl.handle.net/1834/2606.

Briggs, J. C. 1955. A monograph of the clingfishes (order Xenopterygii). *Stanford Ichthyological Bulletin* 6: 1-224.

Briggs, J. C. 1961. The East Pacific Barrier and the distribution of marine shore fishes. *Evolution* 15:545-554. DOI:10.1111/j.1558-5646.1961.tb03184.x.

Briggs, J. C. 1974. Marine Zoogeography. McGraw-Hill, New York. 475 p.

Briggs, J.C. 1994. Species diversity: land and sea compared. *Systematic Biology* 43 (1): 130-135. DOI:10.2307/2413586.

Briggs, J. C. 2000. Centrifugal speciation and centres of origin. *Journal of Biogeography* 27:1183-1188. DOI:10.1046/j.1365-2699.2000.00459.x.

Briggs, J. C. 2006. Proximate sources of marine biodiversity. *Journal of Biogeography* 33: 1-10. DOI:10.1111/j.1365-2699.2005.01374.x.

Briggs, J. C. 2007. Marine longitudinal biodiversity: causes and conservation. *Diversity Distribution* 13: 544-555. DOI:10.1111/j.1472-4642.2007.00362.x.

Bush, G. L. & R. K. Butlin. 2004. Sympatric Speciation in Insects. *In*: Dieckmann, U., M. Doebeli, J. A. J. Metz & D. Tautz (eds). *Adaptive Speciation*. Cambridge University Press. pp. 229-248.

Cadotte, M., C. H. Albert & S. C. Walker. 2013. The ecology of differences: Assessing community assembly with trait and evolutionary distances. *Ecology Letters* 16: 1234-1244. DOI:10.1111/ele.12161.

Castellanos-Galindo, G. A., U. Krumme, E. A. Rubio & U. Saint-Paul. 2013. Spatial variability of mangrove fish assemblage composition in the tropical eastern Pacific Ocean. *Reviews in Fish Biology and Fisheries* 23: 69-86. DOI:10.1007/s11160-012-9276-4.

Castro-Aguirre, J. L. & E. F. Balart. 2002. La ictiofauna de las Islas Revillagigedo y sus relaciones zoogeográficas, con comentarios acerca de su origen y evolución. *In*: Lozano-Vilano, M. L. (ed). *Libro jubilar en honor al Dr. Salvador Contreras Balderas*. Universidad Autónoma de Nuevo León, México, pp. 153-170.

Castro-Aguirre, J. L., E. F. Balart & J. Arvizu-Martínez. 1995. Contribución al conocimiento del origen y distribución de la ictiofauna del Golfo de California, México. *Hidrobiológica* 5:57-78.

Castro-Aguirre, J. L., A.F. González-Acosta, J. de la Cruz-Agüero. 2005. Lista anotada de las especies ícticas anfipacíficas, de afinidad boreal, endémicas y anfipeninsulares del golfo de California, México. *Universidad y Ciencia* 21 (42): 85-106.

Cheal, A. J., S. K. Wilson, M. J. Emslie, A. M Dolman & H. Sweatman. 2008. Responses of reef fish communities to coral declines on the Great Barrier Reef. *Marine Ecology Progress Series* 372: 211-223. DOI:10.3354/meps07708.

Chen, L. C. 1975. The rockfishes, genus *Sebastes* (Scorpaenidae), of the Gulf of California, including three new species with a discussion of their origin. *Proceedings of the California Academy of Sciences* 40: 109-141.

Chuang, A. & C. R. Peterson. 2016. Expanding population edges: theories, traits, and trade-offs. *Global Change Biology* 22: 494-512. DOI: 10.1111/gcb.13107.

Cornish, A. 2004. *Stereolepis gigas*. The IUCN Red List of Threatened Species 2004:e.T20795A9230697. DOI:10.2305/IUCN.UK.2004.RLTS.T20795A 9230697.en.

Costanza, R., R. d'Arge, R. de Groot, S. Farberk, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. O'Neill,J. Paruelo, R. G. Raskin, P. Suttonkk & M.van den Belt. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387:253-260. DOI:10.1038/387253a0.

Cowen, R. K. & S. Sponaugle. 2009. Larval dispersal and marine population connectivity. *Annual Review of Marine Science* 1: 443-66. DOI:10.1146/annurev.marine010908.163757.

Cowman, P. F. 2014. Historical factors that have shaped the evolution of tropical reef fishes: a review of phylogenies, biogeography, and remaining questions. *Frontiers in Genetics* 5: 394. DOI:10.3389/fgene.2014.00394.

Cowman, P. F. & D. R. Bellwood. 2013. Vicariance across major marine biogeographic barriers: temporal concordance and the relative intensity of hard versus soft barriers. *Proceedings of the Royal Society B: Biological Science* 280: 20131541. DOI:10.1098/rspb.2013.1541.

Crabtree, C. B. 1983. Assessment of genetic differentiation within the atherinid genus *Leuresthes*. *Isozyme Bulletin* 16:77.

Crisp, M. D., Y. Isagi, Y. Kato, L. G. Cook, D. M. J. S. Bowman. 2010. *Livistona* palms in Australia: Ancient relics or opportunistic immigrants? *Molecular Phylogenetics and Evolution* 54 (2):512-23. DOI:10.1016/j.ympev.2009.09.020.

Cruz-Escalona, V. H., M. S. Peterson, L. Campos-Dávila & M. Zetina-Rejon. 2005. Feeding habits and trophic morphology of inshore Lizardfish (*Synodus foetens*) on the Central Continental Shelf off Veracruz, Gulf of Mexico. *Journal of Applied Ichthyology* 21 (6): 525-530. DOI:10.1111/j.1439-0426.2005.00651.x.

De La Cruz-Agüero, J. 2000. Origen y distribución de la ictiofauna de Laguna de San Ignacio, Baja California Sur, México. *Ciencia Ergo Sum* 7 (2): 157-165.

De La Cruz-Agüero, J., M. Arellano-Martínez; V.M. Cota-Gómez & G. De La Cruz-Agüero.1997. *Catálogo de los peces marinos de Baja California Sur*. IPN-CONABIO. México, D.F. 346 p.

Denis, V., L. Ribas-Deulofeu, N. Sturaro, C.Y Kuo & C.A. Chen. 2017. A functional approach to the structural complexity of coral assemblages based on colony morphological features. *Scientific Reports* 7: 9849. DOI:10.1038/s41598-017-10334-w.

Díaz, S., D. E. Gurvich, N. Pérez-Harguindeguy & M. Cabido. 2002. ¿Quién necesita tipos funcionales de plantas? *Boletín de la Sociedad Argentina de Botánica* 37: 135-140.

Díaz, S., S. Lavorel, F. de Bello, F. Quétier, K. Grigulis & T. M. Robson. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences of the United States of America* 104 (52): 20684-20689. DOI:10.1073/pnas.0704716104.

Díaz, S., A. Purvis, J.H. Cornelissen, G.M. Mace, M.J. Donoghue, R.M. Ewers, P. Jordano & W.D. Pearse. 2013. Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution* 3 (9): 2958-2975. DOI:10.1002/ece3.601

Domeier, M. L. 2001. Giant sea bass. *In:* Leet, W.S., C.M. Dewees, R. Klingbeil & E. Larson (eds). *California's marine living resources: a status report*. University of California Press, pp. 209-211.

Dooley, J., B. Collette., K. A. Aiken, J. Marechal, F. Pina-Amargos, R. Robertson, R. Kishore & S. Singh-Renton. 2015. *Chaetodipterus faber*. The IUCN Red List of Threatened Species 2015: e.T16435530A16509752. DOI:10.2305/ IUCN.UK.2015-4.RLTS.T16435530A 16509752.en.

Ekman, S. 1953. *Zoogeography of the sea*. Sigwick and Jackson, 417 p.

Elliott, M., A. K. Whitfield, I. C. Potter, S. J. M. Blaber, D. P. Cyrus, F. G. Nordlie & T. D. Harrison. 2007. The guild approach to categorizing estuarine fish assemblages: a global review. *Fish and Fisheries* 8:241-268. DOI:10.1111/j.1467-2679. 2007.00253.x.

Elton, C. S. 1927. *Animal ecology*. MacMillian Company, 256 p.

Eschmeyer, W. N. & J. Alvarado. 2010. *Scorpaena guttata*. The IUCN Red List of Threatened Species 2010: e.T183715A8163197. DOI:10.2305/ IUCN. UK.2010-3.RLTS.T18371 5A8163197.en.

Eschmeyer, W. N. & J. D. Fong. 2013. *Catalog of Fishes.* http://researcharchive. calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp.

Eschmeyer, W. N., E. S. Herald & H. Hammann. 1983. *A field guide to Pacific coast fishes of North America.* Boston (MA, USA): Houghton Mifflin Company, 336 p.

Escobar-Toledo, F., M. J. Zetina-Rejón, J. Ramos-Miranda & F. Arreguín-Sánchez. 2017. Temporal shifts in functional traits of the fish community in Terminos Lagoon (Mexico) in three periods (1980, 1998, and 2011). *Environmental Biology of Fishes* 100: 1575-1586. DOI:10.1007/s10641-017-0666-2.

Fariña, J. M., J. C. Castilla & F. Patricio Ojeda. 2003. The idiosyncratic effect of a sentinel species on contaminated rocky intertidal communities. *Ecological Applications* 13 (6): 1533-1552. DOI:10.1890/02-5216

Felder, D. L., Jr. J. W. Tunnell & S. A. Earle. 2009. *Gulf of Mexico origin, waters, and biota*. Texas A&M University Press, 17 p.

Ferraro, S. P. 2013. Ecological periodic tables: in principle and practice. *Oikos* 122: 1541-1553. DOI:10.1111/j.1600-0706.2013.00717.x.

Ferraro, S. P. & F. A. Cole. 2010. Ecological periodic tables for nekton usage of four US Pacific Northwest estuarine habitats. *Canadian Journal of Fisheries and Aquatic Sciences* 67: 1957-1967. DOI:10.1139/F10-114.

Field, J. G., K. R. Clarke & R. M. Warwick.1982. A practical strategy for analyzing multispecies distribution patterns. *Marine Ecology Progress Series* 8: 37-52. DOI:10.3354/meps008037.

Floeter, S. R., M. G. Bender, A. C. Siqueira & P. F. Cowman. 2018. Phylogenetic perspectives on reef fish functional traits. *Biological Reviews* 93: 131-151. DOI:10.1111/brv.12336.

Friedman, S. T., S. A. Price, A. S. Howy & P. C. Wainwright. 2016. Ecomorphological convergence in planktivorous surgeonfishes. *Journal of Evolutionary Biology* 29 (5): 965-978. DOI:10.1111/jeb.12837.

Fulton, C. J. 2007. Swimming speed performance in coral reef fishes: field validations reveal distinct functional groups. *Coral Reefs* 26: 217-228. DOI: 10.1007/s00338-007-0195-0.

Gagic, V., I. Bartomeus, T. Jonsson, A. Taylor, C. Winqvist, C. Fischer, E. M. Slade, I. Steffan-Dewenter, M. Emmerson, S. G. Potts, T. Tscharntke, W. Weisser & R. Bommarco. 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B: Biological Sciences* 282: 20142620. DOI:10.1098/rspb.2014.2620.

Galland, G. R., B. Erisman, O. Aburto-Oropeza & P. A. Hastings. 2017. Contribution of cyrytobenthic fishes to estimating community dynamics of sub-tropical reefs. *Marine Ecology Progress Series* 584: 175-184. DOI:10.3354/meps12364:

Garrison, G. 2000. *Peces de la Isla del Coco*. Instituto Nacional de Biodiversidad (INBio), Santo Domingo, Costa Rica,393 p.

Gaston, K. J. 1996. Species-range-size distributions: patterns, mechanisms and implications. *Trends in Ecology and Evolution* 1: 197-201. DOI:10.1016/0169-5347(96)10027-6.

Giller, P. S. & G. O'Donovan. 2002. Biodiversity and ecosystem funtion: do species matter? *Biology and Environment: Proceedings of the Royal Irish Academy* 3:129-139. DOI:10.3318/BIOE.2002.102.3.129.

Gilmore, R. G. 1992. Bigmouth sleeper, *Gobiomorus dormitor. In:* Gilbert, C.R. (ed). *Rare and endangered biota of Florida*, Volume II. Fishes. University Press of Florida, pp. 105-111.

Gracey, A. Y. 2008. The *Gillichthys mirabilis* Cooper array: a platform to investigate molecular basis of phenotypic plasticity. *Journal of Fish Biology* 72: 2118-2132. DOI:10.1111/j.1095-8649. 2008.01903.x:

Grove, J. S., R. J. Lavenberg. 1997. The fishes of the Galápagos Islands. Stanford University Press, 863 p.

Glynn, P. W. & J. S. Ault. 2000. A biogeographic analysis and review of the far Eastern Pacific coral reef region. *Coral Reefs* 19: 1-23. DOI:10.1007/s003380050220.

Halpern, B. S., S. Walbridge, K. A. Selkoe, C.V. Kappel, F. Micheli, C. D'Agrosa, J.F. Bruno, K. S. Casey, C. Ebert, H. E. Fox, R. Fujita, D. Heinemann, H. S. Lenihan, E. M. P Madin, M. T. Perry, E. R. Selig M. Spalding, R. Steneck &

R. Watson. 2008. A global map of human impact on marine ecosystems. *Science* 319: 948-952. DOI:10.1126/science.1149345.

Harrison, I. J. & H. Senou. 1999. Mugilidae. *In:* Carpenter, K. E. & V. H. Niem (eds). *FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific, Volume 4. Bony Fishes, Part 2 (Mugilidae to Carangidae).* Food and Agriculture Organization, Rome, pp. 2069-2108.

Hastings, P. A. 2000. Biogeography of the tropical eastern Pacific: distribution and phylogeny of chaenopsid fishes. *Zoological* Journal *of the Linnean* Society 128: 319-335. DOI:10.1111/j.1096-3642.2000.tb00166.x.

Hawk, H. A. & L. G. Allen. 2014. Age and growth of the giant sea bass, *Stereolepis gigas*. *California Cooperative Oceanic Fisheries Investigations Report* 55: 128-134.

Hawkins, C. P. & J. A. MacMahon. 1989. Guilds: the multiple meanings of a concept. *Annual Review of Entomology* 34: 423-451.

Heenan, A. & I. D. Williams. 2013. Monitoring herbivorous fishes as indicators of coral reef resilience in American Samoa. *PLoS ONE* 8 (11):e79604. DOI:10.1371/journal.pone.0079604.

Hillebrand, H. 2004a. Strength, slope and variability of marine latitudinal gradients. *Marine Ecology Progress Series* 273: 251 267. DOI:10.3354/meps273251.

Hillebrand, H. 2004b. On the generality of the latitudinal diversity gradient. *American Naturalist* 163 (2): 192-211. DOI:10.1086/381004.

Hildebrand, S. F. 1935. An annotated list of fishes of the fresh waters of Puerto Rico. *Copeia* 1935: 49-56. DOI:10.2307/1436106.

Hooper, D. U., M. Solan, A. Symstad, S. Díaz, M.O. Gessner, N. Buchmann, V. Degrange, P. Grime, F. Hulot, F. Mermillod-Blondin, J. Roy, E. Spehn & L. van Peer. 2002. Species diversity, functional diversity and ecosystem functioning. *In:* Loreau, M. S. Naeem & P. Inchausti (eds). *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, pp.195-208.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti & S. Lavorel. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75: 3-35. DOI:10.1890/04-0922**.**

Huang, D. & G. Bernardi. 2001. Disjunct Sea of Cortez-Pacific Ocean *Gillichthys miriabilis* populations and the evolutionary origin of their Sea of Cortez endemic relative, *Gillichthys seta*. *Marine Biology* 138: 421-428. DOI:10.1007/ s002270000454.

Hubbs, C. 1952. A contribution to the classification of blennioid fishes of the family Clinidae, with a partial revision of the eastern Pacific forms. *Standford Ichthyological Bulletin* 4: 41-165.

Hughes, T. P., D. R. Bellwood & S. R. Connolly. 2002. Biodiversity hotspots, centres of endemicity, and the conservation of coral reefs. *Ecology Letters* 5:775-784. DOI:10.1046/j.1461-0248.2002.00383.x.

Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22: 415-427. DOI:10.1101/SQB.1957.022.01.039.

Jacobs, D. K., T. A. Haney & K. D. 2004. Genes, diversity, and geologic process on the Pacific coast. *Annual Review of Earth and Planetary Sciences* 32: 601-652.

Jaksic, F. M. 1981. Abuse and misuse of the term guild in ecological studies. *Oikos* 37: 397-400. DOI:10.2307/3544138.

Jiménez-Prado, P. & P. Béarez. 2004. Peces Marinos del Ecuador Continental II. SIMBIOE, 406 p.

Karpouzi, V. S. & K. I. Stergiou. 2003. The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. *Journal of Fish Biology* 62: 1353-1365. DOI:10.1038/368734a0.

Kieckbusch, K. D., M. S. Koch, J. E. Serafy & W. T. Anderson. 2004. Trophic linkage among primary producers and consumers in fringing mangroves of subtropical lagoons. *Bulletin of Marine Science* 74 (2): 271-285.

Krebs, C. J. 2003. *Ecología: estudio de la distribución y la abundancia*. 2nd ed. Oxford University Press, 753 p.

Lane, E. D. 1975. Quantitative aspects of the life history of the diamond turbot, *Hypsopsetta guttulata* (Girard), in Anaheim Bay. *California Department of Fish and Game, Fish Bulletin* 165: 153-174.

Laureto, L. M. O., M. V. Cianciaruso & D. S. M Samia. 2015. Functional diversity: an overview of its history and applicability. *Natureza & Conservação* 13:112-116. DOI:10.1016/j.ncon.2015.11.001**.**

Lawton, J. H. 1994. What do species do in ecosystems? *Oikos* 71: 367-374. DOI:10.2307/3545824.

Lawton, J. H. & V. K. Brown. 1993. Redundancy in ecosystems. *In:* Schulze, E. D. & H. A. Mooney (eds). *Biodiversity and ecosystem function*. Springer Verlag, pp. 255-270.

Lea, R. N. & R. H. Rosenblatt. 2000. Observations on fishes associated with the 1997-98 El Niño off California. *California Cooperative Oceanic Fisheries Investigations Report* 41: 117-129.

Leis, J. M. 1984. Larval fish dispersal and the East Pacific barrier. *Océanographie Tropicale* 19 (2): 181-192.

Lin, H. C. & P. A. Hastings. 2013. Phylogeny and biogeography of a shallow water fish clade (Teleostei: Blenniiformes). *BMC Evolutionary Biology* 13: 210-227. DOI:10.1186/1471-2148-13-210**.**

Livingston, R. J. 2002. *Trophic Organization in Coastal Systems*. CRC Press, 388 p.

Loiseau, N. & J. C. Gaertner. 2015. Indices for assessing coral reef fish biodiversity: the need for a change in habits. *Ecology and Evoution* 5 (18): 4018-4027. DOI:10.1002/ece3.1619.

López de Casenave, J. 2001. Estructura gremial y organización de un ensamble de aves del desierto del Monte. Tesis de Doctorado en Ciencias, Universidad de Buenos Aires, Argentina. 117 p.

Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M Kidwell, M. X. Kirby, C. H. Peterson & J. B. C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312: 1806-1809. DOI:10.1126/science.1128035.

Love, R. M. 1996. Probably more than you want to know about the fishes of the Pacific Coast, 2nd ed. Really Big Press, 215 p.

Love, M. S., B. Axell, P. Morris, R. Collins & A. Brooks. 1987. Life history and fishery of the California Scorpionfish, *Scorpaena guttata*, within the Southern California Bight. *Fishery Bulletin* 85 (1): 99-116.

Lyons, K. G. C., A. Brigham, B. H. Traut & M. W. Schwarts. 2005. Rare species and ecosystem functioning. *Conservation Biology* 19 (4):1019-1024. DOI:10.1111/ j.1523-1739.2005.00106.x.

Macossay-Cortez, A., A. J. Sánchez, R. Florido, L. Huidobro & H. Montalvo-Urgel. 2011. Historical and environmental distribution of ichthyofauna in the tropical wetland of Pantanos de Centla, southern Gulf of Mexico. *Acta Ichthyologica et Piscatoria* 41 (3): 229-245. DOI:10.3750/AIP2011.41.3.11.

MacPherson, E. 2003. Species range size distributions for some marine taxa in the Atlantic Ocean: effect of latitude and depth. *Biological Journal of the Linnean Society* 80: 437-455. DOI:10.1046/j.1095-8312.2003.00256.x.

Mair, J. M., R. Cipriani, H. M. Guzmán & D. Usan. 2012. Fishery of the Green Jack *Caranx caballus* (Osteichytes: Carangidae) in Las Perlas Archipelago, Pacific Panama. *International Journal of Tropical Biology* 60: 1271-1288. DOI:10.15517 /rbt.v60i3.1806.

Margalef, R. 1972. Biogeografía historica. *In*: H. Ginés & R. Margalef (eds). *Ecología Marina*. Fundación La Salle de Ciencias Naturales, pp. 365-376.

Martín-López, B., J. A. González, S. Díaz, I. Castro & M. García-Llorente. 2007. Biodiversidad y bienestar humano: El papel de la diversidad funcional. *Ecosistemas* 2007 (3). Available on line at: http://www.revistaecosistemas.net/articulo.asp? Id=500&Id_ Categoria= 1&tipo=portada.

McBride, R. S. & A. Z. Horodysky. 2004. Mechanisms maintaining sympatric distributions of two ladyfish (Elopidae: *Elops*) morphs in the Gulf of Mexico and western North Atlantic Ocean. *Limnology and Oceanography* 4 (49): 1173-1181. DOI:10.4319/lo.2004.49.4.1173.

McBride, R. S., C. R. Rocha, R. Ruiz-Carus & B. W. Bowen. 2010. A new species of ladyfish, of the genus *Elops* Elopiformes: Elopidae), from the western Atlantic Ocean. *Zootaxa* 2346: 29-41.

McCosker, J. E. & R. H. Rosenblatt. 1975. Fishes collected at Malpelo Island. *Smithsonian Contributions to Zoology* 176: 91-93.

McEachran, D., J. D. Fechhelm. 2005. *Fishes of the Gulf of Mexico. Vol. 2: Scorpaeniformes to Tetraodontiformes.* The University of Texas Press, 1004 p.

Miller, D. J. & R. N. Lea. 1972. Guide to the coastal marine fishes of California. *Fish Bulletin* 157: 1-249.

Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios, C. M. McCain, A. R. McCune, L. A. McDade, M. A. McPeek, T. J. Near, T. D. Price, R. E. Ricklefs, K. Roy, D. F. Sax, D. Schluter, J. M. Sobel & M. Turelli. 2007. Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecology Letters* 10:315-331. DOI: 10.1111/j.1461-0248.2007.01020.x.

Moffat, N. M. & D. A. Thomson.1975. Taxonomic status of the Gulf grunion (*Leuresthes sardina*) and its relationship to the California grunion (*L. tenuis*). *Transactions of the San Diego Society of Natural History* 18: 75-84.

Mora, C. & D. R. Robertson. 2005. Causes of latitudinal gradients in species richness: a test with the endemic shorefishes of the Tropical Eastern Pacific. *Ecology* 86: 1771-1782. DOI:10.1890/04-0883.

Mora, C., D. P. Tittensor, S. Adl, A. G. B. Simpson & B. Worm. 2011. How many species are there on Earth and in the ocean? *PLoS Biol* 9 (8): e1001127. DOI:10.1371/journal.pbio.1001127.

Morrone, J. J. 2002. El espectro del dispersalismo: de los centros de origen a las áreas ancestrales. *Revista de la Sociedad Entomológica Argentina* 61 (3-4): 1-14. Moser, H. G. 1971. Development and geographic distribution of the rockfish, *Sebastes macdonaldi* (Eigenmann & Beeson, 1893), family Scorpaenidae, off southern California and Baja California. *Fishery Bulletin* 70: 941-958.

Mouillot, D., D. R. Bellwood, C. Baraloto, J. Chave, R. Galzin, M. Harmelin-Vivien, M. Kulbicki, S. Lavergne, S. Lavorel, N. Mouquet, C. E. T. Paine, J. Renaud & W. Thuiller. 2013. Rare species support vulnerable functions in high-diversity ecosystems. *PLoS ONE* 115:e1001569. DOI:10.1371/journal.pbio.1001569.

Mouillot, D. S. Villéger, V. Parravicibni, M. Kulbicki, J. E. Arias-González, M. Bender, P. Chababet, S. R. Floeter, A. Friedlander, L. Vigliola & D. R. Bellwood. 2014. Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences of United States of America* 111 (38): 13757-13762. DOI:10.1073/pnas.1317625111.

Naeem, S. 1998. Species redundancy and ecosystem reliability. *Conservation Biology* 12: 39-45. DOI:10.1111/j.1523-1739.1998.96379.x.

Naeem, S. 2002. Biodiversity equals instability? *Nature* 416: 23-24. DOI:10.1038/416023a.

Naeem, S. & S. Li. 1997. Biodiversity enhances ecosystem reliability. *Nature* 390: 507-509. DOI:10.1038/37348.

Naeem, S. F., J. Thompson, S. P. Lawler, J. H. Lawton & R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368: 734-737. DOI:10.1038/368734a0.

Naeem, S. F., M. Loreau & P. Inchausti. 2002. Biodiversity an ecosystem functioning: the emergence of a synthetic ecological framework. *In:* Loreau, M. S. Naeem & P. Inchausti (eds). *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, pp. 3-11.

Naeem, S. & J. P. Wright. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters* 6: 567-579. DOI:10.1046/ j.1461-0248.2003.00471.x.

Nielsen, J. G., T. Munroe & J. Tyler. 2010. *Balistes polylepis*. The IUCN Red List of Threatened Species 2010: e.T183532A8129809. DOI:10.2305/IUCN. UK.2010-3.RLTS. T183532A8129809.en.

Nordlie, F. G. 2012. Life-history characteristics of eleotrid fishes of the western hemisphere, and perils of life in a vanishing environment.

*Reviews in Fish Biology and Fisheries* 22: 189-224. DOI:10.1007/s11160-011-9229-3.

O'Dea, A., H.A. Lessios, A.G. Coates, R.I. Eytan, S.A. Restrepo-Moreno, A.L. Cione, L. S. Collins, A. de Queiroz, D.W. Farris, R.D. Norris, R.F. Stallard, M.O. Woodburne, O. Aguilera, M.P. Aubry, W. A. Berggren, A.F. Budd, M.A. Cozzuol, S.E. Coppard, H. Duque-Caro, S. Finnegan, G.M. Gasparini, E.L. Grossman, K.G. Johnson, L.D. Keigwin, N. Knowlton, E. G. Leigh,J.S. Leonard-Pingel, P.B. Marko, N.D. Pyenson, P.G. Rachello-Dolmen, E. Soibelzon, L. Soibelzon, J. A. Todd, G.J. Vermeij & J.B.C. Jackson. 2016. Formation of the Isthmus of Panama. *Science Advance* 2 (8), e1600883. DOI: 10.1126/sciadv.1600883.

Odum, E. P. & G. W. Barrett. 2006. *Fundamentos de ecología*. 5th Ed. Cengage-Learning Editores, 614 p.

Orton, R. D. & D. G. Buth. 1984. Minimal genetic differentiation between *Girella nigricans* and *Girella simplicidens* (Perciformes: Kyphosidae). *Isozyme Bulletin* 17: 66.

Page, L. M. & B. M. Burr. 2011. *Peterson field guide to freshwater fishes of North America north of Mexico*. 2nd Ed. Boston Houghton Mifflin Harcourt, 663 p.

Parravicini, V., S. Villéger, T. R. McClanahan, J. E. Arias-González, D. R. Bellwood, J. Belmaker, P. Chabanet, S. R. Floeter, A. M. Friedlander, F. Guilhaumon, L. Vigliola, M. Kulbicki & D. Mouillot. 2014. Global mismatch between species diversity and vulnerability of reef fish assemblages. *Ecology Letters* 17: 1101-1110. DOI:10.1111/ele.12316.

Pecuchet, L., A. Törnroos & M. Lindegren. 2016. Patterns and drivers of fish community assembly in a large marine ecosystem. *Marine Ecology Progress Series* 546: 239-248. DOI:10.3354/meps11613.

Pecuchet, L., M. Lindegren, M. Hidalgo, M. Delgado, A. Estaban, H. O. Fock, L. G. de Sola, A. Punzpón, J. Sólmundsson & M. R. Payne. 2017. From traits to life-history strategies: deconstructing fish community composition across European seas. *Global Ecology and Biogeography* 26: 812-822. DOI:10.1111/geb.12587.

Petchey, O. L. & K. J. Gaston. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* 5: 402-411. DOI:10.1046/j.1461-0248. 2002.00339.x.

Petchey, O. L. & K. J. Gaston. 2006. Functional diversity: back to basics and looking forward. *Ecology Letters* 9: 741-758. DOI:10.1111/j.1461-0248.2006.00924.x.

Pezold, F., J. Van Tassell, K.A. Aiken, L. Tornabene & J.L. Bouchereau. 2015. *Gobiomorus dormitor*. The IUCN Red List of Threatened Species 2015: e.T186008A1803224. DOI:10.2305/IUCN.UK.2015-2.RLTS.T18600 8A1 803224.en.

Pianka, E. R. 1980. Guild structure in desert lizards. *Oikos* 35:194-201. DOI: 10.2307/3544427.

Pianka, E. R. 2000. *Evolutionary Biology.* 6th Ed. Benjamin/Cummings, 512 p.

Pianka, E. R., L. J. Vitt, N. Pelegrin, D. B. Fitzgerald & K. O. Winemiller. 2017. Toward a periodic table of niches, or exploring the lizard niche hypervolume. *American Naturalist* 190 (5): 601-616. DOI: 10.1086/693781.

Poortvliet, M., G. C. Longo, K. Selkoe, P. H Barber, C. White, J. E. Caselle, A. Perez-Matus, S. D. Gaines & G. Bernardi. 2013. Phylogeography of the California sheephead, *Semicossyphus pulcher*: the role of deep reefs as stepping stones and pathways to antitropicality. *Ecology and Evolution* 3 (13): 4558-4571. DOI:10.1002/ece3.840.

Pratchett, M. S., A. S. Hoey, S. K. Wilson, V. Messemer & N. A. J. Graham. 2011. Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. *Diversity* 3: 424-452. DOI:10.3390/d3030424.

Pratchett, M. S., P. L. Munday, S. K. Wilson, N. A. J. Graham, J. E. Cinner, D. R. Bellwood, G. P. Jones, N. V. C. Polunin & T. R. McClanahan. 2008. Effects of climate-induced coral bleaching on coral-reef fishes ecological and economic consequences. *In*: R. N. Gibson, R. J. A. Atkinson, J. D. Gordon (eds). *Oceanography and Marine Biology: An Annual Review* 46, CRC Press, pp. 251-296. DOI:10.1201/9781420065756.ch6

Present, T. 1987. Genetic differentiation of disjunct Gulf of California and Pacific outer coast populations of *Hypsoblennius jenkinsi*. *Copeia* 1987: 1010-1024. DOI:10.2307/1445565.

Robertson, D. R. & G. R. Allen. 1996. Zoogeography of the shorefish fauna of Clipperton Atoll. *Coral Reefs* 15: 121-131. DOI:10.1007/BF01771902.

Robertson, D. R. & G. R. Allen. 2002. *Shore fishes of the tropical Eastern Pacific: An Information System*. CD- ROM. Smithsonian Tropical Research Institute, Balboa, Panamá.

Robertson, D. R. & G. R. Allen. 2008. Shore fishes of the Tropical Eastern Pacific. Panamá: Smithsonian Tropical Research Institute. Available online at: http://www.neotropicalfishes.org/sftep; www.stri.org/sftep

Robertson, D. R. & K. L. Cramer. 2009. Shore fishes and biogeographic subdivisions of the Tropical Eastern Pacific. *Marine Ecology Progress Series* 380: 1-17. DOI:10.3354/meps07925.

Robertson, D. R., J. S. Grove & J. E. McCosker. 2004.Tropical transpacific shore fishes. *Pacific Science* 58 (4): 507-565. DOI:10.1353/psc.2004.0041.

Robins, C. R., G. C. Ray & J. Douglass. 1986. *A field guide to Atlantic coast fishes of North America*. Houghton Mifflin Company, 354 p.

Rodrigues-Filho, C. A., R. C. Gurgel-Lourenco, S. M. Q. Lima, E. F. de Oliveira & J. I. Sánchez-Botero. 2017. What governs the functional diversity patterns of fishes in the headwater streams of the humid forest enclaves: environmental conditions, taxomimic diversity or biotic interactions? *Environmental Biology of Fishes* 100 (9): 1023-1032. DOI:10.1007/s10641-017-0603-4.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65: 514-527. DOI:10.2307/3545569.

Ronquist, F. 1997. Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology* 46 (1): 195-203. DOI:10.1093/sysbio/46.1.195.

Root, R. B. 1967. The niche exploitation pattern of the Blue-Gray Gnatcatcher. *Ecological* Monographs 374: 317-350. DOI:10.2307/1942327.

Root, R. B. 2001. Guilds. *In:* Levin, S.A. (ed). *Encyclopedia of Biodiversity*. Academic Press, pp. 295-302.

Rosenblatt, R. H. 1967. The zoogeographic relationships of the marine shore fishes of the tropical America. *Studies in Tropical Oceanography, University of Miami* 5: 579-592.

Rosenfeld, J. S. 2002. Functional redundancy in ecology and conservation. *Oikos* 98: 156-162. DOI:10.1034/j.1600-0706.2002.980116.x.

Rosenweig, M. L. 1992. Species Diversity gradients: we know more and less than we thought. *Journal of Mammalogy* 73 (4): 715-730. DOI:10.2307/1382191.

Ruggiero, A. 2001. Interacciones entre la biogeografía ecológica y la macroecología: aportes para comprender los patrones espaciales en la diversidad biológica. *In:* Llorente, J. & J. J. Morrone (eds). *Introducción a la biogeografía en Latinoamérica: teorías, conceptos, métodos y aplicaciones*. Las Prensas de Ciencias, pp. 81-94.

Ruggiero, M. A., D. P. Gordon, T. M. Orrell, N. Bailly, T. Bourgoin, R. C. Brusca, T. Cavalier-Smith, M. D. Guiry & P. M. Kirk. 2015. A higher level classification of all living organisms. *PLoS ONE* 10 (6): e0130114. DOI:10.1371/journal.pone.0119248.

Sazima, I. 1986. Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities. *Journal of Fish Biology* 29: 53-65. DOI:10.1111/j.1095-8649.1986.tb04926.x.

Scheltema, R. S. 1988. Initial evidence for the transport of teleplanic larvae of benthic invertebrates across the east Pacific barrier. *Biology Bulletin* 174: 1445-1452. DOI:10.2307/1541781

Scherer-Lorenzen, M. 2005. Biodiversity and ecosystem functioning: basic principles. *In:* Barthlott W, K. E. Linsenmair & S. Porembski (eds). *Biodiversity: structure and function*. Encyclopedia of life support systems (EOLSS). Available omline at: http://www.eolss.net.

Schluter, D. & R. E. Ricklefs. 1993. Species diversity: an introduction to the problem. *In:* Ricklefs, R. E. & D. Schluter (eds). Species diversity in ecological communities historical and geographical perspectives. The University of Chicago Press, pp. 1-10.

Schulze, E. D. & H. A. Mooney (Eds.). 1994. Biodiversity and Ecosystem Function. Springer Publishing, 525 p.

Silva-Júnior, C.A.B., B. Mérigot, F. Lucena-Frédou, B. P. Gerreira, M. S. Coxey, S. M. Rezende & T. Frédou. 2017. Functional diversity of fish in tropical estuaries: a traits-based approach of communities in Pernambuco, Brazil. *Estuarine, Coastal and Shelf Science* 198: 413-420. DOI:10.1016/j.ecss.2016.08. 030.

Silvestre, R., C. R. F. Brandão & R. R. Silva. 2003. Grupos funcionales de hormigas: el caso de los gremios del Cerrado. *In:* Fernández, F. (ed). *Introducción a las hormigas de la Región Neotropical*. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, pp. 113-148.

Simberloff, D. & T. Dayan. 1991. The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematic* 22: 115-143.

Smith, R. O. & T. Smith. 2001. *Elements of Ecology*. 6th ed. Pearson Education, Inc.

Smith-Vaniz, W. F. & I. Williams. 2015. *Uraspis helvola*. The IUCN Red List of Threatened Species 2015:e.T50902942A50912682. DOI:10.2305/IUCN. UK.2015-4. RLTS.T50 902942A50912682.en.

Sodhi, N. S., B. W. Brook & C. Bradshaw. 2009. Causes and consequences of species extinctions. *In:* Levin, S. A., S. R. Carpenter, H. C. J. Godfray, A.P. Kinzing, M. Loreau, J. B. Losos, B. Walker & D. S. Wilcove (eds). Princeton University Press, pp 514-520.

Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46: 337-365. DOI:10.2307/3817.

Springer, V. G. 1959. Systematics and zoogeography of the clinid fishes of the subtribe Labrisomini Hubbs. *Publications of the Institute of Marine Science, University of Texas* 5: 417-492.

Steneck, R. S. 2001. Functional groups. *In:* Levin, S.A. (ed). *Encyclopedia of Biodiversity*. Academic Press, pp. 121-139.

Stephens, J. S. Jr. 1963. A revised classification of the blennioid fishes of the American family Chaenopsidae. *University of California Publications in Zoology* 68: 1-165.

Stepien, C. A., R. H. Rosenblatt & B. A. Bargmeyer. 2001. Phylogeography of the spotted sand bass, *Paralabrax maculatofasciatus*: divergence of Gulf of California and Pacific coast populations. *Evolution* 55 (9): 1852-1862. DOI:10.1111/j.0014-3820.2001.tb00834.x.

Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* 133: 240-256.

Stevens, G. C. 1996. Extending Rapoport's rule to Pacific marine fishes. *Journal of Biogeography* 23: 149-154. DOI:10.1046/j.1365-2699.1996.00977.x.

Stuessy, T. F. & E. Hoerandl. 2014. The importance of comprehensive phylogenetic (evolutionary) classification -a response to Schmidt-Lebuhn's commentary on paraphyletic taxa. *Cladistics* 30: 291-293. DOI:10.1111/cla.12038.

Tavera-Vargas, J. J. 2006. Analisis filogenetico y biogeografico del género *Anisotremus* Gill, 1861 (Perciformes: Haemulidae). Tesis Maestría en Ciencias, Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, México, 96 p.

Terborgh, J. & S. Robinson. 1986. Guilds and their utility in ecology. *In:* Kikkawa, J. & D. J. Anderson (eds). *Community ecology: pattern and process*. Blackwell Scientific Publications, pp. 65-90.

Thibaut, L. M. & S. R. Connolly. 2012. Understanding diversity-stability relationships: toward a unified model of portafolio effects. *Ecology Letters* 16:140-150. DOI:10.1111/ele.12019

Thomson, D. A., L. T. Findley & A. N. Kerstitch. 2000. Reef fishes of the Sea of Cortez. The rocky-shore fishes of the Gulf of California. The University of Texas Press, 353 p.

Tilman, D. 2001. Functional diversity. *In:* Levin S.A. (ed). *Encyclopedia of Biodiversity*. Academic Press, pp 109-120.

Tilman, D., J. Knops & D. Wedin. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277: 1300-1302. DOI:10.1126/science.277.5330.1300.

Tilman, T., F. Isbell & J. M. Cowles. 2014. Biodiversity and ecosystem functioning. *Annual Review of Ecology and Systematic* 45: 471-493. DOI:10.1146/ annurev.ecolsys.120213-091917.

Tittensor, D. P., C. Mora, W. Jetz H. K. Lotze, D. Ricard, E. V. Berghe & B. Worm. 2010. Global patterns and predictors of marine biodiversity across taxa. *Nature* 466:1098-1101. DOI: 10.1038/nature09329**.**

Van Tassell, J. 2010a. *Gobiomorus maculatus*. The IUCN Red List of Threatened Species 2010: eT183466A8118095. DOI:10.2305/IUCN.UK.2010-3.RLTS. T183466A8118 095.en. Downloaded on 18 October 2017.

Van Tassell, J. 2010b. *Dormitator latifrons*. The IUCN Red List of Threatened Species 2010:e.T183257A8081686. DOI:10.2305/IUCN.UK.2010-3.RLTS.T183 257A80816 86.en. Downloaded on 19 October 2017.

Van Tassell, J., R. Lea & P. Bearez. 2010c. *Lythrypnus dalli*. The IUCN Red List of Threatened Species2010:e.T183363A8100277. DOI:10.2305/ IUCN.UK. 2010-3.RLTS.T183363A8100277.en. Downloaded on 6 October 2017.

Vilà, M. 1998. Efectos de la diversidad de especies en el funcionamiento de los ecosistemas. *Orsis* 13: 105-117.

Villéger, S., J. Miranda, D. F. Hernández & D. Mouillot. 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications* 20: 1512-1522. DOI:10.1890/09-1310.1.

Villéger, S., G. Grenouillet & S. Brosse. 2013. Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. *Global Ecology and Biogeography* 22: 671-681. DOI:10.1111/geb.12021.

Villéger, S., G. Grenouillet & S. Brosse. 2014. Functional homogenation excedes taxonomic homogenization among European fish assemblages. *Global Ecology and Biogeography* 23: 1450-1460. DOI:10.1111/geb.12226.

Villéger, S., J. R. Miranda, D. F. Hernandez & D. Mouillot. 2012. Low functional β-diversity among tropical estuarine fish communities. *PLoS ONE* 7 (7):e40679. DOI:10.1371/journal.pone.0040679.

Villéger, S., S. Brosse, M. Mouchet & M. J. Vanni. 2017. Functional ecology of fishes: current approaches and future challenges. *Aquatic Sciences* 79 (4): 783-801. DOI:10.1007/s00027-017-0546-z.

Violle, C., M. L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel & E. Garnier. 2007. Let the concept of trait be functional. *Oikos* 116: 882-892. DOI:10.1111/j.0030-1299.2007.15559.x.

Vitousek, P. M., H. A. Mooney, J. Lubchenco & J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* 277: 494-499. DOI:10.1126/science.277.5325.494.

Walker, B. W. 1952. A guide to the Grunion. *California Fish and Game* 38: 409-420.

Walker, B. H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6: 18-23. DOI:10.1046/j.1523-1739.1992.610018.x.

Walker, B. H., A. Kinzing & J. Langridge. 1999. Plant attribute diversity, resilience, and ecosystemfunction: the nature and significance of dominant and minor species. *Ecosystems* 2:95-113. DOI:10.1007/s100219900062**.**

Wellnitz, T. & N. L Poff. 2001. Functional redundancy in heterogeneous environments: implications for conservation. *Ecology Letters* 4: 177-179. DOI:10.1046/j.1461-0248.2001.00221.x.

Westneat, M. W., M. E. Alfaro, P. C. Wainwright, J. R. Grubich, J. L. Fessler, K. D. Clements & L. L. Smith. 2005. Local phylogenetic divergence and global evolutionary convergence of skull function in reef fishes of the family Labridae. *Proceedings of the Royal Society B: Biological Science* 252: 993-1000. DOI:10.1098/rspb.2004.3013.

Whittaker, R. H. & S. A. Levin (eds). 1975. Niche: theory and application. Dowden, Hutchinson and Ross, Inc, 448 p.

Wiley, J. W. 1976. Life histories and systematics of the western North American Gobies *Lythrypnus dalli* (Gilbert) and *Lythrypnus zebra* (Gilbert). *Transactions of San Diego Society of Natural History* 18: 169-184.

Williams, J. T. 2014. *Ophioblennius macclurei*. The IUCN Red List of Threatened Species 2014:e.T46104090A48344385. DOI:10.2305/IUCN.UK.2014-3. RL TS.T46104090 A48344385.en.

Willig, M. R. & C. P. Bloch. 2006. Latitudinal gradients of species richness: a test of the geographic area hypothesis at two ecological scales. *Oikos* 112: 163-173. DOI:10.1111/j.0030-1299.2006.14009.x.

Willig, M. R. & S. J. Presley. 2017. Latituidinal gradients of biodiversity. *In: Reference Module in Life Sciences*. DOI:10.1016/B978-0-12-809633-8.02174-9

Willig, M. R., D. M. Kaufman & R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics* 34: 273-309. DOI:10.1146/annurev.ecolsys.34.012103.144032.

Wilson, S. K., N. A. J Graham, M. S. Pratchett, G. P. Jones & N. V. C. Polunin. 2006. Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology* 12: 2220-2234. DOI:10.1111/j.1365-2486.2006.01252.x.

Winemiller, K. O., D. B. Fitzgerald, L. M. Bowe & E. R. Pianka. 2015. Functional traits, convergent evolution, and periodic table of niches. *Ecology Letters* 18: 737-751. DOI:10.1111/ele.12462.

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# NOTA CIENTÍFICA

## First rrecord of the fin whal whale *Balaenoptera physalus* in the Mexican Caribbean

## Primer registro de la ballena de aleta *Balaenoptera physalus* para el Caribe mexicano

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## ABSTRACT

**Background.** Until 2015, the aquatic mammal's biodiversity in the Mexican Caribbean was unknown, but that year 18 species were confirmed to be distributed in this region, none of them a Rorcual species. **Goals.** The aim of this study is to report on the first record of a Balaenopteridae whale in the Mexican Caribbean. **Methods.** The CONANP and RVMMEQR attended a stranding event at the Isla Contoy National Park. **Results.** On August 2, 2018, a stranded alive whale was found. The animal was identified as a ~18m (in length) fin whale *Balaenoptera physalus*. It was guided to deep waters and released. **Conclusions.** This note is the first confirmed record of this species in the Mexican Caribbean increasing the list of confirmed aquatic mammal species distributed in this region.

**Keywords:** common rorcual, Isla Contoy, new record, Quintana Roo, stranded, Western Caribbean

## RESUMEN

**Antecedentes.** Hasta 2015 la biodiversidad de los mamíferos acuáticos en el Caribe mexicano era desconocida, pero en ese año se confirmó la distribución de 18 especies en esta región, ninguna de ellas una especie de Rorcual. **Objetivos**. El objetivo de este trabajo es registrar el primer avistamiento de una ballena Balaenopteridae en el Caribe mexicano. **Métodos.** La CONANP y la RVMMEQR atendieron un evento de varamiento en el Parque Nacional Isla Contoy. **Resultados.** El 2 de agosto de 2018, se encontró varada una ballena de aleta o rorcual común *Balaenoptera physalus* de ~18m (en longitud), ésta fue guiada a aguas profundas y liberada. **Conclusiones.** Esta nota es el primer registro confirmado de esta especie en el Caribe mexicano y aumenta la lista de especies de mamíferos acuáticos distribuidas en esta región.

**Palabras clave:** Caribe oriental, Isla Contoy, nuevo registro, Quintana Roo, rorcual común, varamiento

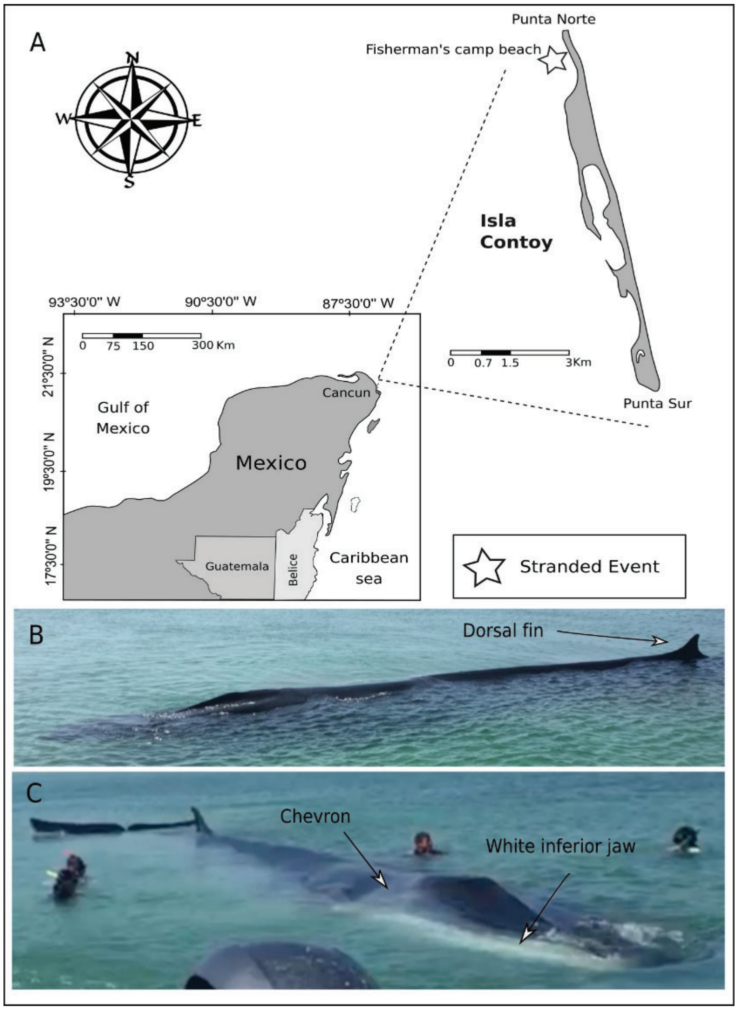
The fin whale *Balaenoptera physalus* (Linnaeus, 1758), is the second-largest whale; the average length of fin whales in the Northern Hemisphere is 22 m for males and 24 m for females (Gamble, 1985).The body is elongated and slender, brownish-gray in the dorsal portion and paler in the ventral area (Notarbartolo-Di-Sciara *et al.,* 2003). This whale has a characteristic asymmetric color in the anterior-ventral portion, being white/cream in the right lower jaw, whereas the left portion is black/dark. The dorsal fin is tall and bigger in size compared with other Balaenopterids; it is located at the third body portion, portion, with white cream a V grey-light shape pattern (called chevron) which extends over the dorsal portion and flanks behind the head (Notarbartolo-Di-Sciara *et al.,* 2003; Perrin, 2018). The species has a cosmopolitan distribution occurring principally in temperate and cold waters (Rice, 1998). Currently, three subspecies are recognized. The species also has a V grey-light two in the Southern Hemisphere, and *B. p. physalus* in the Northern Hemisphere (Committee-on-Taxonomy, 2018). Similar to all other large whales, the fin whale was profusely hunted during the

20th century, resulting in a drastic reduction of their populations. This species is considered internationally as an Endangered species (Reilly *et al.,* 2013), and is subject to special protection in Mexico (SEMARNAT, 2010). Additionally, the International Whaling Commission (IWC) issued a moratorium on commercial hunting of this species, and was listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (UNEP-WCMC, 2018).

The Mexican Caribbean is recognized as one of the principal Mexican marine eco-regions (Lara-Lara *et al.,* 2008; Niño-Torres *et al.,* 2015). Currently, for the Mexican Caribbean, there are reported 18 aquatic mammal species (Niño-Torres *et al.,* 2015), none of them, a Rorcual species (Balaenopteridae Gray, 1864 ).

As part of the activities of the Comisión Nacional de Áreas Naturales Protegidas (CONANP) and the Marine Mammal Stranding Network of Quintana Roo (RVMMEQR), a stranded alive whale was aided on August 2, 2018, near to the fishermen's camp beach (21° 31´31.03" N; 86° 48´11.26" W, fig. 1a) at the northern section of the Isla Contoy National Park. The stranded animal was an adult fin whale, B. physalus, of ~ 18 m in length. Species identification was based on the form of the dorsal fin, the chevron, and the right lower jaw coloration ("white-lip") characteristic of this species (Notarbartolo-Di-Sciara *et al.,* 2003; Perrin, 2018) (fig. 1b-c). After some maneuvers, the fin whale was towed to deep waters and released. Sex was not determined.

Stranding records are of outstanding importance, especially when they concern species that are difficult to observe in the wild. The stranded event reported here represents the first record of a fin whale *B. physalus* in the Mexican Caribbean, and the second for the Western Caribbean Sea (Ramos *et al.,* 2016). The first case was reported in Belize on the April 28, 1986, in which a single adult female stranded alive near to Placencia (Sanders *et al.,* 1997; Ramos *et al.,* 2016). Other fin whales records in the Caribbean Sea have been reported in Venezuela at Margarita Island and Paraguana Peninsula on August 1953 and February-May 1959 (Agudo, 1995; Romero *et al.,* 2001), and Colombia (Muñoz-Hincapié *et al.,* 1998). Live groups of this species have been documented in Puerto Rico (Mignucci-Giannoni, 1998).



Figures 1a-c. a) Location of region in the Mexican Caribbean, where the stranded whale *Balaenoptera physalus* (Linnaeus, 1758) was found, at the fishermen's camp beach; b) Detail of the dorsal fin; c) Chevron and right lower jaw coloration in the stranded whale (Photography by: Caribbean Connection Cia.).

We should highlight that this stranding event occurred during the summer season (August), which is unexpected. Gamble (1985) described that the breeding season for western North Atlantic fin whales takes place in Florida, Gulf of Mexico, and the Caribbean Sea waters during the winter, whereas they spend spring and summer at higher latitudes (north) at their feeding grounds. An interesting hypothesis is that this individual could belong to the Southern population. Unfortunately, it wasn't possible to take DNA samples to determine its place of origin.

This stranding event represents an important record of the marine mammal species richness in the Mexican Caribbean, increasing the number of confirmed species from 18 (Niño-Torres *et al.,* 2015) to 19. Characterizing the species occurrence, abundance, and distribution is relevant to create and implement adequate management and conservation plans (Ramos *et al.,* 2016), that help to preserve the natural resources and biodiversity. In the Mexican Caribbean ~98% of the marine ecosystems are protected under different categories of "natural protected areas."

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## REFERENCES

Agudo, I. 1995. Sobre la ocurrencia de la ballena barbada *Balaenoptera physalus* (Linnaeus) 1758 (Cetacea: Mysticeti: Balaenopteridae) en Venezuela. *Revista de Ecología Latinoamericana* 4 (1-3):7-10.

Committee-on-Taxonomy. 2018. *List of marine mammal species and subspecies*. Society for Marine Mammalogy. Available online at: www.marinemammalscience.org (downloaded January 4th, 2019).

Gamble, R. 1985. Fin Whale: *Balaenoptera physalus*. *Handbook of Marine Mammals* 3: 171-192.

Lara-Lara, J. R., V. Arenas Fuentes, B. G. V, V. Díaz Castañeda, E. E. Briones, M. D. L. C. G. Abad, G. G. Castro, G. R. Jarero, R. S. Ávalos, L. A. S. González, M. Tapia García & J. E. Valdez-Holguín. 2008. Los ecosistemas marinos. *In* Soberón, J., G. Halffter & J. Llorente-Bousquets (Eds.). *Capital natural de México. Conocimiento actual de la biodiversidad. Vol. 1.* Comisión Nacional Para el Conocimiento y Uso de la Biodiversidad. Pp. 135-159.

Mignucci-Giannoni, A. A. 1998. Zoogeography of cetaceans off Puerto Rico and the Virgin Islands. *Caribbean Journal of Science* 34 (3-4): 173-190.

Muñoz-Hincapié, M., D. Mora-Pinto, R. Montoya-Ospina & A. Mignucci-Giannoni. 1998. Records of cetacean mortality and strandings from the Colombian Caribbean. En: *Abstracts, The World Marine Mammal Science Conference*. Pp. 20-24.

Niño-Torres, C. A., M. d. C. García-Rivas, D. N. Castelblanco-Martínez, J. A. Padilla-Saldívar, M. d. P. Blanco-Parra & R. De la Parra-Venegas. 2015. Aquatic mammals from the Mexican Caribbean; a review. *Hidrobiológica* 25 (1): 127-138.

Notarbartolo-Di-Sciara, G., M. Zanardelli, M. Jahoda, S. Panigada & S. Airoldi. 2003. The fin whale *Balaenoptera physalus* (L. 1758) in the Mediterranean Sea. *Mammal Review* 33 (2): 105-150. DOI: 10.1046/j.1365-2907.2003.00005.x

Perrin, W. F. 2018. *Balaenoptera physalus*. World Cetacea Database. Available online at: http://www.marinespecies.org/cetacea/aphia.php?p=taxdetails&id=137091 (downloaded August 4th, 2018).

Ramos, E. A., D. N. Castelblanco-Martínez, C. A. Niño-Torres, K. Jenko & N. A. Gomez. 2016. A review of the aquatic mammals of Belize. *Aquatic Mammals* 42 (4): 476-493. DOI: 10.1578/am.42.4.2016.476

Reilly, S. B., J. L. Bannister, P. B. Best, M. Brown, R. L. Brownell Jr., D. S. Butterworth, Clapham, J. Cooke, G. P. Donovan, J. Urbán & A. N. Zerbini. 2013. *Balaenoptera physalus*. The IUCN Red List of Threatened Species. Available online at: http://www.iucnredlist.org/details/2478/0 (downloaded August 4th, 2018).

Rice, D. W. 1998. *Marine mammals of the world*. Systematics and distribution. The Society for Marine Mammalogy. 231 p..

Romero, A., A. I. Agudo, S. M. Green & G. N. di Sciara. 2001. Cetaceans of Venezuela: Their distribution and conservation status. FALTA LA FUENTE

Sanders, A. M., B. A. Bilgre & H. Markowitz. 1997. *Annotated checklist of cetaceans in Belize, Central America*. Oceanic Society Tecnical Report. Belize City. páginas

SEMARNAT (Secretaría del Medio Ambiente y Recursos Naturales). 2010. *Norma Oficial Mexicana de Protección ambiental. Especies nativas de México de flora y fauna silvestres. Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio. Lista de especies en riesgo (NOM-059)*. Diario Oficial de la Federación. México D.F., December 30: 78 p..

UNEP-WCMC. 2018. The checklist of CITES species website. Available online at: www.checklist.cites.org (downloaded August 4th, 2018).

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# NOTA CIENTÍFICA

## Translocación de *Chapalichthys encaustus* (Actinopterygii: Goodeidae) en el río Teuchitlán, Jalisco, México

## Translocation of *Chapalichthys encaustus* (Actinopterygii: Goodeidae) in the Teuchitlán River, Jalisco, Mexico

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## RESUMEN

**Antecedentes y objetivo.** Se reporta por primera vez la translocación del pintito de Ocotlán *Chapalichthys encaustus* (Goodeidae) en el río Teuchitlán, ubicado en la cabecera de la cuenca del río Ameca en el centro del estado de Jalisco. **Métodos.** El registro se obtuvo aproximadamente a 1 km del inicio del río. El organismo fue depositado en la Colección de Peces de la Universidad Michoacana de San Nicolás de Hidalgo (CPUM). **Resultados.** Se describe e ilustra un ejemplar hembra adulto, con una longitud total de 65 mm, recolectado el día 17 de julio del 2015. En recolectas posteriores fue obtenido también un ejemplar macho de la misma especie. **Conclusión.** El pintito de Ocotlán es uno de los pocos casos documentados de ictiofauna nativa translocada para México y su posible impacto en el río Teuchitlán no ha sido determinado.

**Palabras clave:** Antropización, centro de México, especies no nativas, introducción de fauna.

## ABSTRACT

**Background and goal.** The translocation of the Barred Splitfin *Chapalichthys encaustus* (Goodeidae) in the Teuchitlán River, located at the headwaters of the Ameca river basin in the center of the state of Jalisco, is reported for the first time. **Methods.** The fish record was obtained approximately 1 km from the origin of the river. Fish were deposited in the ichthyology collection of the Universidad Michoacana de San Nicolás de Hidalgo (CPUM). **Results.** On July 17, 2015 an adult female specimen of this species with a total length of 65 mm was collected. The specimen is described and illustrated. In subsequent collections a male specimen of the same species was also obtained. **Conclusion.** The Barred Splitfin is one of the few documented cases of native translocated ichthyofauna for Mexico and its possible impact on the Teuchitlán River has not been determined.

**Key word:** Anthropization, Central Mexico, introduction of fauna, non-native species.

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En julio de 2015 durante recolectas para evaluar la ictiofauna del río Teuchitlán, se capturó un ejemplar con el uso de electropesca (Electropesca de mochila DC modelo ABP-3, ETS Electrofishing Systems LLC. Energía promedio ~200 watts, voltaje máx. ~250 V, corriente máx. ~10 amp. Cap. Energía de pulso 30 jules. Batería ácida 12 V, 18 amp) que fue identificado como un goodeido, el cual era una hembra grávida que peso 3.17 gr y midió 54.1 mm de longitud patrón. La recolecta se realizó en el río Teuchitlán, a 1 km de su inicio (20º 41.111' N, 103º 50.581' O), en el municipio del mismo nombre. Utilizando las claves propuestas por Miller *et al.* (2009), el espécimen fue identificado como *Chapalichthys encaustus* (Jordan & Snyder, 1899) (Fig. 1).

El ejemplar fue fijado utilizando una solución de formol al 5% y posteriormente fue transferido a alcohol etílico al 70%. Fue depositado en la Colección Ictiológica del Laboratorio de Biología Acuática "J. Javier Alvarado Díaz" de la Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo (CPUM Registro de Colección Científica: MICH.-PEC-227-07-09), con el número de catálogo CPUM-13753.

En muestreos sucesivos realizados durante dos años en el río Teuchitlán se recolectó adicionalmente un macho de una longitud patrón de 54.38 mm y un peso de 3.39 gr, por lo que se considera que la abundancia de la especie en el sitio es menor. Sin embargo, en la presa de la Vega, adyacente al Río Teuchitlán, en enero del 2015 se capturaron dos especímenes con un peso total de 2.57 g. En febrero del 2016 se encontró un ejemplar más con un peso de 1.5 g, por lo que su abundancia podría ser mayor en el embalse.

El pintito de Ocotlán, *Chapalichthys encaustus*, pertenece a la subfamilia Goodeinae (Goodeidae), cuyas especies son endémicas del centro de México. Su ámbito de distribución natural es la vertiente del Pacífico, especie endémica del bajo río Lerma y el lago de Chapala (*sensu* Domínguez-Domínguez *et al.*, 2006). Los registros históricos de la ictiofauna de la cuenca del río Ameca (Webb & Miller, 1998; López-López & Paulo-Maya, 2001), así como los registros de recolectas en el río Teuchitlán de la CPUM de la Universidad Michoacana de San Nicolás de Hidalgo, México, y de la Colección de Peces de la Universidad de Michigan, Estados Unidos, no reportan a la especie en la región. Por lo que el pintito de Ocotlán es una especie introducida en el río Teuchitlán.

Aunque no se sabe con certeza la causa o el medio de introducción de esta especie al río Teuchitlán, una posibilidad es la movilidad entre la siembra de tilapias procedentes de granjas en la región de Chapala. Esta especie presenta tolerancia a la degradación ambiental (Soto-Galera *et al.*, 1998). En el lago de Chapala *C. encaustus* alcanza una densidad máxima de 12.28 ind/m$^{-3}$, en sitios con influencia de aguas contaminadas procedentes de las descargas municipales (Becerra-Muñoz *et al.*, 2003). Por su intestino largo, sus dientes bífidos y presencia de branquiespinas delgadas, se ha considerado como un pez herbívoro (Miller *et al.*, 2009). Estas características de su historia de vida podrían ser clave en su posible establecimiento en el río Teuchitlán, donde el represamiento y la modificación del sistema lótico, han provocado que la dinámica del río tienda a ser léntica (de la Mora-Orozco, 2013), y por tanto se presente acumulación de materia orgánica y restos vegetales en el sedimento del lecho del río, particularmente en la desembocadura a la presa de La Vega.

El pintito de Ocotlán es uno de los pocos casos documentados de peces goodeinos nativos introducidos fuera de su distribución natural en México. Se considera que uno de los principales agentes de cambio en los sistemas acuáticos de agua dulce es la invasión de especies introducidas (Havel *et al.,* 2015). Una especie introducida puede afectar las poblaciones nativas por depredación (Weyl & Lewis 2006), por competencia (Blanchet *et al.,* 2007) o al introducir enfermedades (Gozlan *et al.*, 2006). La translocación de especies entre cuencas es un riesgo de invasión biológica y sus consecuencias pueden ser tan graves como aquellas derivadas de la introducción de una especie exótica a un país o región distante (Simberloff *et al.*, 2012; Nackley *et al.*, 2017). De esta forma la translocación y cualquier otra forma de introducción de especies es un proceso que puede ser perjudicial y por tanto es una pr**á**ctica que debe ser evitada.

Es necesario implementar un diseño de muestreo para establecer su dinámica poblacional y así poder determinar su posible impacto so-

Figura 1. Hembra grávida de *Chapalichthys encaustus* recolectada en el Río Teuchitlán, Jalisco, México. Fotografía de Sesangari Galván Quesada.

bre la estructura y funcionamiento del ecosistema y su potencial como especie invasora en el río Teuchitlán. Así mismo, es fundamental revisar las prácticas de transporte para especies de acuicultura para evitar el riesgo de introducción accidental de organismos, que debe ser evitado por los potenciales efectos nocivos sobre la fauna nativa.

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## REFERENCIAS

Becerra-Muñoz, S., H. R. Buelna-Osben & J. M. Catalán-Romero. 2003. Spatial patterns of ARIMA modeled rates of change of atherinids (*Chirostoma* spp.) and goodeid *Chapalichthys encaustus* from Lake Chapala, México. *Ecological Modelling* 165 (2): 237-250. DOI: 0.1016/S0304-3800(03)00073-5

Blanchet, S., G. Loot, G. Grenouillet & S. Brosse. 2007. Competitive interactions between native and exotic salmonids: a combined field and laboratory demonstration. *Ecology of Freshwater Fish* 16: 133–143. DOI: 10.1111/j.1600-0633.2006.00205.x

De La Mora-Orozco, C; Flores-López H. E., Durán-Chávez, A. A. 2013. Calidad del agua del embalse de la presa La Vega y su impacto en las tierras agrícolas bajo riego. Libro técnico Núm. 6. INIFAP. 171 p.

Domínguez-Domínguez, O., I. Doadrio & G. Pérez-Ponce de León. 2006. Historical biogeography of some river basins in central Mexico evidenced by their goodeine freshwater fishes: a preliminary hypothesis using secondary Brooks parsimony analysis. *Journal of Biogeography* 33 (8): 1437-1447. DOI: https://doi.org/10.1111/j.1365-2699.2006.01526.x

Gozlan, R. E., E. J. Peeler, M. Longshaw, S. St-Hilaire & S. W. Feist. 2006. Effect of microbial pathogens on the diversity of aquatic populations, notably in Europe. *Microbes and Infection* 8: 1358-1364. DOI: https://doi.org/10.1016/j.micinf.2005.12.010

Havel, J. E., K. E. Kovalenko, S. M. Thomaz, S. Amalfitano & L.B. Kats. 2015. Aquatic invasive species: challenges for the future. *Hydrobiologia* 750 (1): 147-170. DOI: 10.1007/s10750-014-2166-0

López López, E. & J. Paulo-Maya. 2001. Changes in the fish assemblages in the upper río Ameca, México. *Journal of Freshwater Ecology* 16 (2): 179-187. DOI: 10.1080/02705060.2001.9663803

Miller, R. R., W. L. Minckley & S. M. Norris. 2009. *Peces dulceacuícolas de México*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Sociedad Ictiológica Mexicana A.C., El Colegio de la Frontera Sur, Consejo de los Peces del Desierto, Ciudad de México. 559 p.

Nackley, L. L., A. G. West, A. L. Skowno & W. J. Bond. 2017. The Nebulous Ecology of Native Invasions. *Trends in Ecology & Evolution* 32 (11): 814-824. DOI: /10.1016/j.tree.2017.08.003

Simberloff, D., L. Souza, M. A. Nuñez, M. N Barrios-Garcia & W. Bunn. 2012. The natives are restless, but not often and mostly when disturbed. *Ecology* 93 (3): 598-607. DOI: 10.1890/11-1232.1

Soto-Galera, E., E. Díaz-Pardo, E. López-López & J. Lyons.1998. Fish as indicators of environmental quality in Río Lerma Basin, México. *Aquatic Ecosystem Health Manage* 1: 267– 276. DOI: 10.1016/S1463-4988(98)00012-8

Webb, S. A. & R. R. Miller. 1998. *Zoogoneticus tequila*, a new goodeid fish (Cyprinodontiformes) from the Ameca drainage of Mexico, and a rediagnosis of the genus. *Occasional Papers of the Museum of Zoology the University of Michigan* 725: 1-23.

Weyl, O. L. F. & H. Lewis. 2006. First record of predation by the alien invasive freshwater fish *Micropterus salmoides* L. (Centrarchidae) on migrating estuarine fishes in South Africa. *African Zoology* 41: 294-296. DOI: 10.1080/15627020.2006.11407365

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# NOTA CIENTÍFICA

## Earthquake induces mass-spawning event in two coral-reef sea cucumber species in Belize

## Terremoto induce evento de desove masivo en dos especies de pepino de mar en arrecifes de coral en Belice

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## ABSTRACT

**Background.** Electromagnetic pulses that precede earthquakes, and the ensuing crust deformations and vibrations, have been associated with unusual animal behavior (UAB), most commonly in terrestrial species but also in certain marine species, chiefly in the Chordata phylum (e.g. fish, cetaceans).**Goals**. This study explored the occurrence of earthquake-related UAB in an entirely new marine phylum, the Echinodermata. **Methods.** Formal and informal surveys conducted by fishing vessels pre- and post-earthquake along the southern coast of Belize (Central America) were collated. **Results.** The first cases of post-earthquake UAB in echinoderms were documented. They involved thousands of individuals of the holothuroids *Isostichopus badionotus* and *Holothuria mexicana* spawning on May 29, 2009 and January 10, 2018. These rare accounts represent the first direct correlation between an earthquake and spawning activity, which occurred outside the normal spawning season and at an unusual time of day. **Conclusions.** While a growing number of reports indicate that many terrestrial and a smaller number of marine species can change their behavior before and during an earthquake, post-earthquake effects related to reproduction have apparently never been reported before in the animal kingdom. While underlying mechanisms remain unclear, holothuroid echinoderms may be reacting directly or indirectly to seismic activity, or the pressure change generated by it.

**Keywords***:* disturbance, echinoderm, *Holothuria mexicana, Isostichopus badionotus,* reproduction, unusual animal behavior

## RESUMEN

**Antecedentes.** Los pulsos electromagnéticos que preceden a los terremotos y las consiguientes deformaciones y vibraciones de la corteza de la tierra han sido asociados con el comportamiento animal inusual (CAI), más comúnmente en especies terrestres sino también en ciertas especies marinas, principalmente en el filo Chordata (por ejemplo, peces, cetáceos). **Objetivos.** El presente estudio exploró la ocurrencia de CAI relacionada con terremotos en un filo marino completamente nuevo, el Echinodermata. **Métodos**. Se recopilaron encuestas formales e informales realizadas por barcos pesqueros antes y después del terremoto a lo largo de la costa sur de Belice (América Central). **Resultados.** Se document**ó** el primer caso de CAI post-terremoto en equinodermos. El caso involucró a miles de individuos de los holothuroidea*Isostichopus badionotus* y *Holothuria mexicana* desovando el 28 de mayo de 2009 y el 10 de enero de 2018, respectivamente. Estas ocurrencias raras representan la primera correlación directa entre un terremoto y la actividad de desove, que ocurrió fuera de la temporada de desove normal y en un momento del día inusual. **Conclusiones.** Mientras que un número creciente de informes indica que muchas especies terrestres y un número menor de especies marinas pueden cambiar su comportamiento antes y durante un terremoto, los efectos posteriores al terremoto relacionados con la reproducción, aparentemente nunca se han reportado antes en el reino animal.

Si bien los mecanismos subyacentes siguen sin estar claros, los equinodermos holoturoideos pueden estar reaccionando directa o indirectamente a la actividad sísmica, o al cambio de presión generado por ella.

**Palabras clave***:* comportamiento inusual, equinodermo, *Holothuria mexicana*, *Isostichopus badionotus,* perturbación, reproducción

Perturbations associated with earthquakes, such as changes in atmospheric pressure and gravity, ground deformations, acoustic signals and vibrations due to micro-crack generation, and the concurrent emission of gases and chemical substances, have been documented to cause unusual animal behaviors or UABs (Hayakawa, 2013). Moreover, Freund & Stolc (2013) showed that electronic charge carriers (called positive holes) were activated during the build-up of stress deep in the Earth before earthquakes. These positive holes can travel fast and far into the surrounding rocks, generating ultralow frequency electromagnetic waves, which may ionize air and generate hydrogen peroxides at the sea surface (Freund & Stolc, 2013). The latter authors suggested that the momentary disappearance of the toad *Bufo bufo* Linnaeus, 1758 in central Italy about 5 days before the L'Aquila earthquake of April 2009 (Grant *et al*. 2011) was triggered by chemical cues in the water, such as the release of hydrogen peroxide products resulting from an influx of hydron (cationic form of atomic hydrogen). Other variables related to earthquakes may be at play in the ocean, such as telluric currents produced through electromagnetic induction by the geomagnetic field or whenever a conducting body (e.g. seawater) moves because of tides or other processes across the Earth's permanent magnetic field (Lanzerotti & Gregori, 1986). These low-frequency currents travel large distances near the surface of the Earth (Lanzerotti & Gregori, 1986). In addition, amplitude anomalies of the telluric field have been detected before shallow earthquakes with magnitudes ≥ 4.5. These amplitude anomalies reached about 100-300 mv km$^{-1}$ 3-16 days before the earthquake (Myachkin *et al*. 1972). All the above-mentioned earthquake-related changes (Nagao *et al*. 2002) have been identified as sources of UAB (Freund & Stolc, 2013), including in aquatic animals (Tributsch, 1982). For instance, geomagnetic sensitivity was related to stranding of dolphins and whales (Kirschvink, 1990), and of Humboldt squids (Than, 2009).

Here we describe for the first time an UAB in a member of the Echinodermata phylum and a side effect recorded post-earthquake. Monitoring the seafloor down to 5 m occurred during daily fishing activities in Belize (Central America) that included sea-cucumber harvests south of Laughing Bird Cay and in Port Honduras in 2009 and 2018, respectively. On January 9, 2018 at 21:51, an earthquake of magnitude 7.6-7.8 was recorded 200 km off the Caribbean coast of Belize. Aftershocks of magnitude 4.2-5.0 followed in the evening and early the following day. The earthquake had a shallow focus (~10 km) which amplified its effects, i.e., increased shaking/vibration levels (USGS, 2018). No tsunami was generated. In the morning of January 10, around 07:00, two species of coral-reef sea cucumbers, *Isostichopus badionotus* Selenka, 1867 and *Holothuria mexicana* Ludwig, 1875, underwent a mass-spawning event involving thousands of individuals (from the shore to ~5 m depth) in the entire Fore Reef (about 3.2 km$^2$). This spawning was uncharacteristic in that it was outside the normal reproductive season and occurred at sunrise rather than at sunset, as is usually the case (Mercier *et al*. 2007). While these sea cucumbers normally shelter in sand, seagrass, or among corals (especially from early morning to late afternoon), most individuals had emerged and displayed their typical spawning posture while broadcasting gametes in the water column (Fig. 1) in full daylight (the inverse of normal behavior). Inside a shoal area measuring 3.2 km$^2$ long by about 1 km wide (16°12'05.61" N; 88°40'04.97" W), which was composed of patch reef and seagrass, nearly 100% of females and males (representing a maximum of 1-3 ind m$^{-2}$) spawned simultaneously for a duration of about 2 h (sexes determined based on the distinct appearance of male and female gametes in the water column). The water temperature was 30.9 °C, the salinity 33.6, with a recorded rainfall of 34.5 mm over the previous 24 h. There was no correlation with the full or new moon (as spawning after the earthquake occurred 2 days after the third moon quarter), or with the low or high tide or any

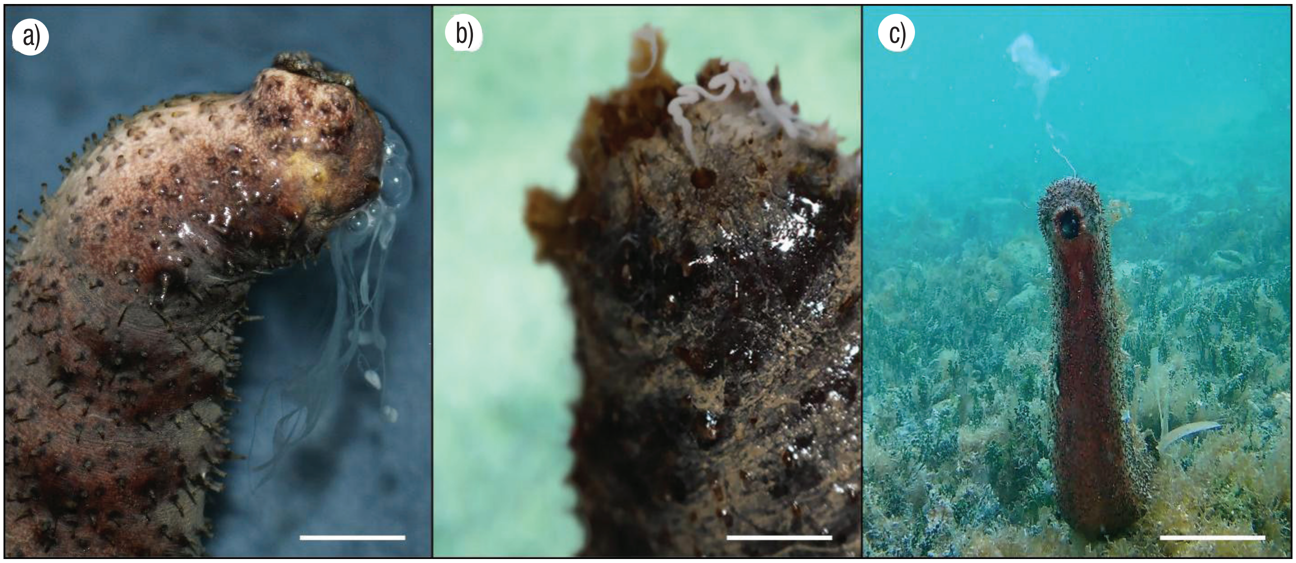

**Figure 1** Close-up view of a spawning **a** male and **b** female of *H. mexicana* Ludwig, 1875 (photos Arlenie Rogers); **c** broader view of a spawning male of *H. mexicana* (photo Víctor Alamina). Scale bar: 3 cm in **a**, 1.7 cm in **b**, 5 cm in **c**

broad environmental factor known to coincide with the spawning period of those species in the study region, including a phytoplankton bloom (Rogers *et al*. 2018).

Despite a growing number of reports indicating that certain terrestrial and marine species can display unusual behaviors before and during earthquakes (Bhargava, 2009), to our knowledge no impact on the timing of reproduction has ever been documented in the animal kingdom. The present observation may also be the first to show the influence of an earthquake on a non-vertebrate marine benthic taxon. While explaining correlations of this magnitude is complex, it may be suggested that sea cucumbers are able to detect seismic events directly or indirectly, through anomalous telluric current changes, changes in atmospheric pressure, and changes in gravity, acoustic signals, vibrations, or ultralow frequency electromagnetic waves generated by earthquakes (Hayakawa, 2013). Exposure to physical stress is a common technique used to artificially induce sea cucumbers to spawn in captivity, especially in aquaculture facilities (Mercier & Hamel, 2009), and it can be assumed that earthquakes generate similar stressors. Despite the present spawning event was only confirmed from one area of the extensive coral reef system of Belize, it is not impossible that the phenomenon occurred in other locations along the coast. An anecdotal correlation between mass spawning of the same sea cucumber species and an earthquake was observed in Belize ~4 hours after the 7.3 magnitude earthquake that occurred at 03:24 on May 28, 2009 (Héctor Saldívar, pers. comm., September 2011), supporting this assertion and the potential disruptive impact of earthquakes on sea cucumber reproduction. If non-mature gametes are released in full daylight under out-of-phase conditions, development failure and higher predation pressure are likely to exacerbate propagule mortality rates.

Overall, the reaction to earthquake documented here may be interpreted as a strategy developed by slow-moving species to survive dangers by releasing dispersive pelagic propagules. It remains unclear how sea cucumbers might detect seismic events, although electric or electromagnetic sensitivity are probable candidates.

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## REFERENCES

Bhargava, N., V. K. Katiyar, M. L. Sharma & P. Pradhan. 2009. Earthquake prediction through animal behavior: A review. *Indian Journal of Biomechanics: Special Issue NCBM* 7-8: 159-165.

Freund, F. & V. Stolc. 2013. Nature of pre-earthquake phenomena and their effects on living organisms. *Animals* 3: 513-531.

Grant, R. A., T. Halliday, W. P. Balderer, F. Leuenberger, M. Newcomer, G. Cyr& F. T. Freund. 2011. Ground Water Chemistry Changes before Major Earthquakes and Possible Effects on Animals. *International Journal of Environmental Research and Public Health* 8: 1936-1956.

Hayakawa, M. 2013. Possible electromagnetic effects on abnormal animal behavior before an earthquake. *Animals* 3: 19-32.

Kirschvink, J. L. 1990. Geomagnetic sensitivity in cetaceans: an update with the U.S. live stranding records. *In*: Thomas, J. A. & R. Kastelein (eds.). *Sensory Abilities of Cetaceans.* Plenum Press, New York, pp. 639-649.

Lanzerotti, L. & G. P. Gregori. 1986. Telluric currents: the natural environment and interactions with man-made systems. *In:* Krider, E. P., R. G. Roble & T. M. Usselman (eds.). *Studies in Geophysics.* National Academies Press, Washington D.C., pp. 232-257.

Mercier, A., R. H. Ycaza & J. F. Hamel. 2007. Long-term study of gamete release in a broadcast-spawning holothurian: predictable lunar and diel periodicities. *Marine Ecology Progress Series* 329: 179–189.

Mercier, A. & J. F. Hamel. 2009. Endogenous and exogenous control of gametogenesis and spawning in echinoderms. *Advances in Marine Biology* 55: 1–302.

Myachkin, V. I., G. A. Sobolev, N. A. Dolbikina, V. N. Morozow, & V.B. Preobrazensky. 1972. The study of variations in geophysical fields near focal zones of Kamchatka. *Tectonophysics* 14(3-4): 287-293.

Nagao, T., Y. Enomoto, Y. Fujinawa, M. Hayakawa, Q. Huang, J. Izutsu, Y. Kushida, K. Maeda, K. Oike, S. Uyeda & T. Yoshino. 2002. Electromagnetic anomalies associated with the 1995 Kobe earthquake. *Journal of Geodynamics*33(4–5): 401–411.

Rogers, A., J. F., Hamel, & A. Mercier. 2018. Population structure and reproductive cycle of the commercial sea cucumber *Holothuria mexicana* (Echinodermata: Holothuroidea) in Belize. *Revista de Biología Tropical* 66(4): 1629-1648.

Than, K. 2009. Dozens of Jumbo Squid Beached after Quake-Coincidence? National Geographic News. Available online at: https://news.nationalgeographic.com/news/2009/07/090714-giant-squid-earthquake/ (downloaded July, 2018).

Tributsch, H. 1982. *When the snakes awake: animals and earthquake prediction*. MIT Press, Cambridge, MA. 248 p.

USGS. 2018. M 7.5 44 km E of Great Swan Island, Honduras. Available online at: https://earthquake.usgs.gov/earthquakes/eventpage/us1000c2zy#executive (downloaded August 8, 2018).

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