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DEMOGRAFÍA E HISTORIA DE VIDA DEL ISÓPODO *Excirolana braziliensis*: UN ANÁLISIS A MACROESCALA

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ÍNDICE GENERAL

RESUMEN GENERAL

Las reglas ecogeográficas describen tendencias generales en los rasgos biológicos generadas por la acción de mecanismos ecológicos y evolutivos. Consecuentemente, el análisis de estas reglas a distintos niveles de organización, así como los vínculos entre ellas, constituye un tema central en Ecología. Esta tesis se enfoca en tres reglas ecográficas a nivel intraespecífico, utilizando al isópodo cirolánido *Excirolana braziliensis* Richardson 1912 como modelo de estudio. La primera regla considerada refiere a la hipótesis de la abundancia central (ACH), según la cual las mejores condiciones ambientales se darían en el centro del rango de distribución de las especies y por tanto la abundancia sería máxima en estas regiones. Se evaluó aquí tanto la predicción general como las hipótesis auxiliares que la sustentan, representando una evaluación integral de la misma. Las hipótesis auxiliares involucran la disponibilidad de hábitat (playas arenosas en este caso), variables oceanográficas (producción primaria, temperatura superficial del agua y salinidad), y las características del hábitat (tamaño de grano y rango mareal). La regla temperatura-tamaño corporal fue la segunda regla considerada, relacionándola con los parámetros de historia de vida. Por último, se analizó la relación densidad-tamaño corporal, incorporando el potencial papel de los gradientes espaciales en temperatura y tamaño corporal como parte del fenómeno general analizado.

El modelo de estudio, el isópodo cirolánido *Excirolana braziliensis* es un consumidor primario que se distribuye en playas arenosas en ambos lados de América tropical a templada, desde Baja California hasta el sur de Chile en el Pacífico (3 provincias biogeográficas) y desde el sur del Golfo de México a Uruguay en el Atlántico (4 provincias biogeográficas). Esta especie habita tanto en zonas supralitorales como intermareales de playas de arena fina y gruesa. Hallazgos recientes sugieren que *E. braziliensis* podría ser un grupo de especies crípticas, agrupados en tres clados monofiléticos, con varios linajes divergentes y geográficamente restringidos en el Atlántico y Pacífico. Este complejo constituiría un grupo cercanamente emparentado y funcionalmente muy similar. De hecho, la clasificación en base a atributos morfológicos realizado anteriormente ha indicado que *E. braziliensis* constituiría una sola especie. Se realizó una recopilación

bibliográfica de datos que cubrió 139 playas a lo largo de un gradiente geográfico de 73° de latitud en ambas costas de América.

La abundancia de *E. braziliensis* alcanzó su punto máximo en los dos bordes de su área de distribución en la costa atlántica y hacia el centro de su área de distribución en la costa del Pacífico. Las desviaciones o la congruencia con las expectativas de la ACH podrían deberse a las tendencias en los mecanismos que respaldan la ACH, como por ejemplo, las variables oceanográficas, la disponibilidad del hábitat y la morfodinámica de las playas. Los patrones de abundancia de *E. braziliensis* mostraron tendencias opuestas entre océanos. *E. braziliensis* siguió la regla de temperatura-tamaño corporal, registrándose individuos más grandes hacia latitudes altas con menores temperaturas. Asimismo, se reportaron cambios latitudinales significativos en los parámetros de historia de vida con menores tasas de crecimiento, mayor longitud de madurez sexual, longevidad y fecundidad a mayores latitudes. El análisis del escalamiento del tamaño corporal-densidad fue congruente con un uso de energía equivalente en todas las clases de tamaño corporal. Si bien se encontraron diferencias entre clados filogenéticos, las mismas fueron explicadas por los patrones latitudinales en tamaño y densidad de individuos. El análisis conjunto de ambas reglas mostró una tendencia similar, donde la temperatura superficial del agua fue el principal impulsor de la conexión causal entre la latitud, el tamaño del cuerpo y la densidad. Esto implica encontrar un mayor tamaño corporal y menores densidades en latitudes más altas, patrón guiado por las tendencias en temperatura.

Las abundancias más altas registradas, en áreas de surgencia, altas temperaturas del agua y en playas disipativas (grano de arena fino, baja pendiente y alta producción primaria local), indican que los efectos combinados de las condiciones regionales y locales son más determinantes que la ubicación geográfica. Los patrones de abundancia de E*. braziliensis* estarían más relacionados con un centro de nicho ambiental que con un centro de distribución geográfica. En el escenario de constituir especies crípticas, aunque muy parecidas morfológicamente, lo anterior implica que las mismas probablemente respondan de manera similar a las condiciones ambientales al vivir en simpatría en latitudes similares. Estas respuestas son en su mayoría impulsadas por presiones de selección hacia formas morfológicas similares, independientemente del aislamiento reproductivo entre ellas, debido a las necesidades de adaptarse a ambientes estresantes como son las playas arenosas.

El análisis de las 3 reglas ecogeográficas mostraron que el gradiente geográfico (e.g. latitud), el tamaño corporal, y la abundancia y sus patrones de distribución geográfica pueden conformar un triángulo de inter-relaciones. En este sentido, los patrones geográficos de la abundancia de *E. braziliensis* estarían determinados por: 1) los centros de nicho ambiental y gradientes morfodinámicos locales; y 2) la tasa metabólica debido a su dependencia térmica y su efecto en la demanda de recursos, conectando las reglas temperatura-tamaño corporal (TSR) y el escalamiento densidad-tamaño corporal. El análisis de las 3 reglas ecogeográficas y sus hipótesis auxiliares resultaron fundamentales para la comprensión de los patrones de abundancia de este isópodo, así como para entender las causas de su amplia distribución geográfica en ambos océanos de América.

Las reglas ecogeográficas representan principios generales, regularidades biológicas, que sugieren la existencia de mecanismos comunes organizando la diversidad en diferentes grupos biológicos. Consecuentemente, la identificación de los mecanismos subyacentes representa una meta central en Ecología. El presente enfoque, con una especie de gran distribución y conocimiento biológico permitió avanzar en estos mecanismos en dos aspectos centrales pero poco atendidos. Uno de ellos corresponde al papel de los mecanismos auxiliares en la emergencia o no de los patrones biogeográficos y el otro, en la interconexión mecanicista entre reglas. La evaluación de hipótesis auxiliares y la unificación de mecanismos y teorías, es un paso esencial en la consolidación del marco teórico. La presente tesis intenta ser una contribución en esta dirección.

1. INTRODUCCIÓN GENERAL

1.1 Antecedentes y marco teórico

1.1.1 Biogeografía ecológica y reglas ecogeográficas

Dentro de las raíces más importantes de la ecología contemporánea están las campañas de investigación de Alejandro V. Humbolt, a partir de las cuales las investigaciones naturales tomaron escala planetaria, constituyendo un paso fundacional de la biogeografía (Lomolino et al. 2010). Tanto el desarrollo de la Ecología como ciencia, como los estudios y modelos matemáticos desarrollados sobre la teoría de islas (Foster 1964, MacArthur y Wilson 1967, MacArthur 1972), contribuyeron fuertemente para la generación de líneas de investigación vinculadas a la biogeografía ecológica o ecología geográfica (Deleáge 1991, Arita y Rodriguez 2001, Lomolino et al. 2010). La misma trata de explicar la distribución actual de las especies y la variación geográfica en la diversidad en términos de dispersión de organismos, interacciones bióticas y sus entornos físicos (Lomolino et al. 2010). Dentro de esta se pueden distinguir dos tipos principales de investigaciones: las vinculadas a la ecología de poblaciones y la macroecología, cuyas investigaciones están dirigidas al análisis de los patrones de ensamblaje de especies a grandes escalas espaciales y temporales (Arita y Rodriguez 2001, Lomolino et al. 2010). En ambos casos la búsqueda de mecanismos generales y unificados representa la meta principal de sus programas de investigación (Scheiner y Willig 2008, Marquet et al. 2014).

Un debate persistente en Ecología ha sido la existencia o no de leyes o reglas similares a las de otras disciplinas (e.g. leyes de termodinámica) (Lawton 1999, Colyvan y Guinzburg 2003, O'Hara y Benton 2005). En este sentido, se propusieron cuatro definiciones alternativas sobre los requerimientos que debe cumplir un patrón para constituirse en 'regla ecogeográfica': 1) patrones generalizados y repetibles en la naturaleza, aunque no universalmente ciertos (Lawton 1999); 2) cuando las tendencias particulares son comunes y las excepciones parecen ser lo suficientemente escasas (Gaston et al. 2008); 3) tendencias generales en morfología y rasgos relacionados a lo largo de gradientes geográficos (Lomolino et al. 2006); y/o 4) cuando un patrón fue mostrado por más del 50% de las especies estudiadas (Mayr 1956). En estas definiciones, hay un consenso respecto a la generalidad de una tendencia y que a su vez pueda presentar excepciones puntuales. A partir de revisiones realizadas en esta temática, existirían unas 15 reglas ecogeográficas (ver Tabla 1.1) que presentan cierto grado de aceptación y/o que se viene discutiendo fuertemente sobre ellas en Ecología; seis de estas reglas se refieren o incluyen invertebrados (Gastón y Blackburn 1999, Lomolino et al. 2006, McDowall 2008, Gastón et al. 2008, Boyer et al. 2010, Lomolino et al. 2010). A nivel intraespecífico, existen muchos trabajos mostrando tendencias geográficas en el tamaño del cuerpo, fisiología, historia de vida, dinámica poblacional, abundancia y variación genética (ver revisión en Gastón et al. 2008). No obstante, solo algunos de ellos han llegado a considerarse como reglas ecogeográficas (Lawton 1999). La aplicabilidad de estas reglas en diferentes niveles de organización o de grupos taxonómicos ha motivado fuertes debates en Ecología (e.g. What et al. 2010, Meiri 2011) debido, en parte, a que las mismas fueron desarrolladas y discutidas en diferentes marcos teóricos (Gastón y Blackburn 1999).

Lomolino et al. (2006) señalaron la necesidad de deconstruir los patrones ecogeográficos primarios para diferentes grupos de especies, escalas espaciales y temporales, y que el programa de investigación en biogeografía debería ampliarse con relación al enfoque tradicional en mamíferos y aves insulares, a otros vertebrados, a invertebrados y a plantas. Recientemente los investigadores han comenzado a explorar los vínculos entre ellas a nivel teórico (Kingsolver y Huey 2008), poblacional (Virgos et al. 2011, VanderWerf 2012, Gutierrez-Pinto et al. 2014, Cardilini et al. 2016) y en ensamblajes (Smith y Gaines 2003, McDowall 2008, Boyer et al. 2010, Gouveia et al. 2013), teniendo en cuenta que se convirtió en un tema central para la biogeografía ecológica (Gastón y Blackburn 2000, Lomolino et al. 2006, Gaston et al. 2008). A pesar de lo anterior, las interacciones entre los diferentes patrones espaciales o reglas ecogeográficas a nivel intraespecífico siguen siendo poco conocidas, al igual que la variación latitudinal en la dinámica de poblaciones a lo largo de un amplio rango latitudinal (Gaston et al. 2008). En este sentido, esta tesis se enfoca en tres de estas reglas, con un análisis intraespecífico: (1) la hipótesis de la abundancia central o "abundance centre hipothesis "(ACH por sus siglas en inglés); (2) la regla de la temperatura-tamaño corporal (TSR por sus siglas en inglés) y su relación con los parámetros de historia de vida; y (3) la relación densidad-tamaño corporal.

La hipótesis de la abundancia central (ACH) proporciona una explicación mecanicista de las tendencias geográficas en la abundancia de especies (Brown 1984). La ACH establece que la abundancia de especies es mayor en el centro del rango de la distribución y disminuye hacia los límites en respuesta a las tendencias espaciales en el rendimiento fisiológico (por ejemplo, térmico) y ecológico (por ejemplo, interacciones biológicas) (Brown 1984, Sagarin y Gaines 2002b). Sin embargo, las especies exhiben patrones de distribución variable en sus rangos geográficos (Sagarin y Gaines 2002a). De las 34 especies estudiadas en ecosistemas costeros, solo 8 mostraron modelos normales o cuadráticos inversos de abundancia como predice la ACH (Sagarin y Gaines 2002b, Samis y Eckert 2007, Tuya et al. 2008, Rivadeneira et al. 2010, Fenberg y Rivadeneira 2011, Tam y Scrosati 2011, Baldanzi et al. 2013, Soria et al. 2017). Este apoyo contradictorio para la ACH podría reflejar la aparición de condiciones óptimas para que la abundancia máxima esté cerca de los límites de las especies (modelos en rampa, 13 especies). Sin embargo, para algunas especies (13), no se encontraron patrones, aunque algunos patrones pueden haber sido enmascarados por un patrón de pico y cola (McGill y Collins 2003). El fracaso de las hipótesis auxiliares relacionadas con la disponibilidad de hábitat (Samis y Eckert 2007) o los rasgos de la historia de vida (Rivadeneira et al. 2010) también podría explicar las desviaciones en las predicciones de la ACH (Brown 1984, Martínez-Meyer et al. 2013). De hecho, se han encontrado distribuciones discontinuas asociadas con las condiciones ambientales y las interacciones entre especies (Sagarin et al. 2006).

El tamaño corporal, que forma parte de las 2 siguientes reglas, constituye uno de los rasgos más notorios para casi todas las especies y está vinculado a los principales parámetros demográficos y de historia de vida de las mismas (Glazier 2005). La regla de Bergmann se refiere a la tendencia de los organismos a ser más pequeños a altas temperaturas y, por consiguiente, en latitudes bajas (Bergmann, 1847; Rensch, 1938; Mayr, 1942; 1956; Meiri, 2011). Originalmente destinada a las endotermos, esta regla también se ha aplicado a los ectotermos (Rensch, 1938; Mayr, 1942) y para explicar las variaciones intraespecíficas en el tamaño corporal (James, 1970; Stelzer, 2002; Virgós et al., 2011; Forster et al., 2012). Revisiones recientes informaron que el 61% de las especies de ectotermos conforman este patrón (Watt et al., 2010). Dada la variabilidad de grupos taxonómicos que implican a los ectotermos (anfibios, reptiles, peces e invertebrados), se sugiere que, además del mantenimiento de la temperatura, otros mecanismos pueden ser determinantes de las variaciones geográficas del tamaño corporal (Anguilletta et al. 2004b). La TSR describe los efectos de la temperatura en el crecimiento intraespecífico y la edad de madurez (Atkinson y Sibly 1997) y afirma que los individuos de latitudes más frías alcanzan la madurez en un tamaño mayor (Atkinson 1994). Todas las asociaciones entre latitud y tamaño corporal están mediadas por las tendencias geográficas de la temperatura y, por lo tanto, la regla de Bergmann y la TSR podrían unificarse (Horne et al. 2015). La correlación negativa entre el tamaño corporal y la temperatura también determina las tendencias en los parámetros de la historia de vida (Enquist et al., 1998; Brown et al. 2004). En consecuencia, la asociación entre la temperatura y el tamaño corporal también puede estar relacionada con las estrategias de historia de vida y las variaciones en la densidad de la población (Brown et al. 2004, White et al. 2007).

La relación entre el tamaño corporal y la densidad se ha analizado mediante varios enfoques complementarios (revisado en White et al. 2007 y Arim et al. 2011). Una disminución de la densidad con el tamaño corporal, que equilibra el aumento de la demanda metabólica ($D \alpha BS^{-0.75}$) es congruente con el papel principal de la demanda energética en la densidad de la población (Cyr et al. 1997). Sin embargo, la suposición implícita de una cantidad constante de recursos para todos los tamaños corporales es difícil de respaldar (Isaac et al. 2010, Arim et al. 2011). De hecho, la relación densidad-tamaño presenta una importante variabilidad entre especies, lo que sugiere que se pueden considerar mecanismos adicionales (Isaac et al. 2010). La temperatura puede afectar el escalamiento entre el tamaño del cuerpo y la densidad a través de la TSR, pero también puede determinar el metabolismo individual, y por consiguiente afectar la densidad de la población (Allen et al., 2002; Brown et al., 2004).

Tabla 1.1. Reglas ecogeográficas en Ecología, con su predicción y el taxón de aplicación, y los niveles de organización donde se han estudiado.

Regla	**Predicción**	**Taxón aplicación**	**Nivel de organización**
Bergmann (1847) - TSR (Atkinson 1994)	Aumento de tamaño corporal con la latitud	Vertebrados-Invertebrados	Intra-inter-ensamblajes
Jordan (1892)	Aumento de número de vertebras con la latitud	Peces	Interespecífico
Lindsey (1975)	Peces mas grandes tienen más vertebras	Peces	Interespecífico
Williston (Lindsey 1975)	Reducción en el número vertebras con avance filético	Peces	Interespecífico
Rapoport (1975)	Aumento en el tamaño del rango de especies con la latitud o la elevación.	Vertebrados-Invertebrados	Interespecífico
Gradiente de diversidad latitudinal (Wallace 1905)	Número de especies aumenta hacia el trópico.	Vertebrados-Invertebrados	Interespecífico
Gloger (1883)	Individuos que viven en zonas cálidas y húmedas son de color más oscuro que las que viven en zonas frías y secas.	Aves, mamíferos e insectos	Interespecífico
Allen (1878)	Tamaño de los apéndices se reduce en los climas fríos	Aves, mamíferos	Interespecífico
Regla de islas (Foster 1964)	Mamíferos pequeños tienden a mas grandes en islas pequeñas y mamíferos grandes tienden a ser más pequeños.	Mamíferos	Interespecífico
Lack (1947)	Número de huevos aumenta con la latitud.	Aves	Intra-interespecífico
Calder (1984)	Aumento del número de huevos con el tamaño corporal.	Aves	Intra-interespecífico
Thorson (1936)	Aumento del tamaño del huevo y desarrollo no planctónico con la latitud y la profundidad del agua.	Crustáceos, caracoles y peces	Intra-interespecífico
Hipótesis de la abundancia central ACH (Brown 1984)	Máxima abundancia en el centro del rango	Especies	Intraespecífico
Escalamiento tamaño corporal-densidad	La densidad disminuye con el aumento del tamaño corporal.	Vertebrados-Invertebrados	Intra-inter-ensamblajes
Hipótesis de la escalada de depredación (Vermej 1978)	La presión de la predación aumenta hacia los trópicos.	Invertebrados marinos	Interespecífico

1.1.2 Reglas ecogeográficas en playas arenosas

Las primeras investigaciones en playas arenosas se iniciaron a partir de estudios en taxonomía de especies macrobentónicas alrededor de 1900. No obstante, las investigaciones en estos ambientes permanecieron a la sombra de las investigaciones que se realizaban en las costas rocosas que se desarrollaron entre 1940 y 1950. Esto se explica en parte a que las playas arenosas presentaban una macrofauna semi-críptica, donde las especies se veían solamente cuando se movían en respuesta a cambios en las mareas (ver Brown y McLachlan 1990). A partir de estudios pioneros en ecología, taxonomía, y fisiología, junto al primer simposio internacional sobre playas arenosas realizado 1983 (McLachlan y Erasmus 1983), la ecología de las playas arenosas emergió por primera vez como un campo distinto de investigación en la costa (McLachlan y Defeo 2018).

Las playas arenosas son ecosistemas dominados físicamente donde la amplitud de las mareas, las condiciones de las olas y el tipo de sedimento juegan un papel central en la configuración de la distribución de la macrofauna bentónica (McLachlan y Defeo 2018). Las interacciones entre estas variables producen una serie de tipos morfodinámicos generando un gradiente que va desde las playas disipativas a reflectivas y una serie de estados intermedios. Las primeras son playas anchas con sedimentos finos y poca pendiente (planas), mientras que las playas reflectivas son estrechas, presentan sedimentos gruesos y pendientes pronunciadas (Short 1999). Desarrollando una teoría ecológica sobre las variaciones en las propiedades morfodinámicas, se han postulado dos hipótesis principales a nivel poblacional para explicar el papel de la morfodinámica en los rasgos de la historia de la vida de las especies (McLachlan y Defeo 2018). Una combinación de arena gruesa, alta frecuencia y velocidad de swash, y un aumento en la dinámica de la erosión-acreción, genera un ambiente hostil para las poblaciones que viven en la zona de acción de la ola. La hipótesis de la rigurosidad del hábitat (HHH por sus siglas en inglés) predice que el ambiente hostil en playas reflectivas obliga a los organismos que viven en esta zona a desviar más energía en mantenerse y alimentarse, por lo que tienen una menor abundancia, tamaños y pesos individuales, tasas de crecimiento, longevidad, fecundidad, producción reproductiva y sobrevivencia que en playas disipativas (Gómez y Defeo 1999, Defeo et al. 2001, 2003). Teniendo en cuenta que los ecosistemas de playas arenosas podrían dividirse en dos subsistemas (intermareal y supralitoral) con marcadas diferencias en la estructura y el funcionamiento, Defeo y Gómez (2005) propusieron la hipótesis de seguridad del hábitat (HSH por sus siglas en inglés). La misma predice que los ambientes reflectivos favorecen a las especies supralitorales que habitan en las playas de arena como *Excirolana braziliensis*. En este sentido, estas especies están menos influenciadas por el clima hostil de la zona de swash y, en general, tienen un movimiento activo autónomo y/o de enterramiento en los niveles superiores de la playa y presentarían mayores abundancias, tamaños y pesos individuales, tasas de crecimiento, longevidad, fecundidad, producción reproductiva y sobrevivencia que en playas disipativas. Short (1996, 1999) definió a las playas reflectivas como el tipo de playa más estable en relación a la poca movilidad de la zona de playa.

Los estudios en biogeografía ecológica en playas arenosas no son muy abundantes. Investigaciones realizadas a escala global y regional en estos ecosistemas mostraron tendencias consistentes en la biodiversidad, la abundancia y la organización de la comunidad, las cuales se encuentran estrechamente relacionadas con la morfodinámica de las playas y la latitud (Defeo y McLachlan 2011, 2013). La riqueza de especies aumenta de las regiones templadas a las tropicales para playas con morfodinámica similar. El tamaño corporal y la densidad muestran un patrón inverso, parcialmente explicado por las respuestas inversas al tipo de playa. Por lo tanto, las playas disipativas albergan comunidades con mayor abundancia y especies con menores tamaños corporales, un patrón que también puede afectar la escala tamaño corporal-densidad en comunidades de playas arenosas (Defeo y McLachlan 2013). En playas arenosas de ambas costas oceánicas de América del Sur, Defeo et al. (2017) mostraron que la riqueza de especies (macrofauna) disminuyó desde las playas tropicales a las templadas en el Pacífico y siguió una tendencia parabólica en el Atlántico, con la mayor biodiversidad encontrada en las zonas tropical y templada fría. La pendiente de la playa, la amplitud de las mareas y la clorofila resultaron las variables que más explicaron las tendencias latitudinales en la riqueza de macrofauna, seguidas por el tamaño del grano, la temperatura media superficial y el océano.

A nivel poblacional no hay muchos antecedentes en lo que refiere a reglas ecogeográficas. No obstante, se ha documentado evidencia del escalamiento tamaño corporal-densidad para el cangrejo anomuro *Emerita brasiliensis* (Defeo y Cardoso, 2004), sugiriendo que las formas más pequeñas que viven en la zona intermareal son más sensibles a las condiciones adversas de playas reflectivas (sedimentos gruesos, alta frecuencia de barrido y poca disponibilidad de comida) donde la densidad es menor. La correlación negativa entre el tamaño corporal y la temperatura (TSR) fue evaluada para este cangrejo anomuro donde solo se cumplió para las hembras (Defeo y Cardoso 2002). El patrón inverso de esta teoría fue encontrado para los machos, sugiriendo una competencia intraespecífica entre sexos. Por su parte, la hipótesis de abundancia central (ACH) fue evaluada para dos anfípodos con distribución en Namibia y Sudáfrica. *Talorchestia capensis* no mostró un patrón claro de distribución de la abundancia y *Africorchestia quadrispinosa* mostró un patrón en forma de rampa e inverso con el tamaño corporal (Baldanzi et al. 2013).

1.1.3 El isópodo *Excirolana braziliensis*

Los isópodos constituyen actualmente un Orden dentro del Subphylum Crustacea, Clase Malacostraca, Sub-clase Eumalacostraca, y el Superorden Peracarida. Los peracáridos se caracterizan por presentar desarrollo directo, donde los juveniles son transportados por la hembra en una bolsa de cría ventral hecha de osteguitos superpuestos (Johnson et al. 2001). Los isópodos (cuyo nombre significa "pie similar") se distribuyen desde el fondo del mar hasta los hábitats terrestres de montaña, así como en las profundidades subterráneas en cuevas o acuíferos donde existen 10339 especies (Poore y Bruce 2012, Boyko et al. 2008). *Excirolana braziliensis* Richardson 1912 (Fig. 1.1) pertenece a la familia Cirolanidae, de la Superfamilia Cymothoidea, del Sub-orden Cymothoida. Los isópodos cirolánidos son miembros conspicuos de las playas arenosas de todo el mundo, siendo dominantes en número o biomasa (Soares 2003). En América, además de *E. braziliensis*, existen 7 especies de este género que habitan en playas arenosas (Richardson 1912, Jaramillo 1982): *E. monodi*, *E. hirsuticauda*, *E. mayana*, *E. armata* y *E. chiltoni*. *E mayana* y *E. linguifrons.*

E. braziliensis se encuentra en playas arenosas, desde zonas tropicales a templadas, en ambos lados de América, desde Baja California (31°N) (Glynn et al. 1975) hasta el sur de Chile en el Pacífico (42°S) (Jaramillo et al. 2000) y desde el Golfo de México (21°N) (Dexter 1976) hasta Uruguay en el Atlántico (34°S) (Defeo et al. 1997). Esto representa 4 y 3 provincias biogeográficas (Spalding et al. 2007) para el Océano Atlántico y Océano Pacífico, respectivamente. Habitan las zonas supralitorales e intermareales de playas de arena fina y gruesa (Martínez et al. 2017). Este isópodo es un consumidor primario (Lercari et al. 2010) y nadador activo, aunque con menor capacidad de nado que especies congenéricas (*E. armata*) que viven principalmente en el intermareal (Yannicelli et al. 2002). Igualmente puede atacar presas vivas o alimentarse de restos orgánicos. A tales efectos, en zonas templadas realiza migraciones nocturnas desde la zona supralitoral a la zona de swash (Brazeiro y Defeo 1996, Yannicelli et al. 2002) o se desentierra cuando sube la marea en playas macromareales tropicales (Dexter 1977). Muestra óptimos de excavación para una amplia gama de tamaños de grano, dándole una amplia versatilidad ambiental en diferentes playas de arena (Yannicelli et al. 2002).

Los embriones de este isópodo reclutan a la población adulta como juveniles o "mancas" (Klapow 1970, Martínez y Defeo 2006). En playas arenosas de clima templado presenta un alto potencial reproductivo y por lo tanto, un esfuerzo reproductivo inusual dentro de los invertebrados que sucede en el período estival (ver Martínez y Defeo 2006). Esto lleva a la especie a asimilar energía como producción somática en el resto del año, retardando la madurez (Stearns 1976, Martínez y Defeo 2006). Teniendo en cuenta el gran esfuerzo reproductivo y la incubación interna de *E. braziliensis,* la misma puede considerarse semélpara en el sur de distribución geográfica (Martínez y Defeo 2006). En playas tropicales de Panamá las hembras también producirían solo una camada de embriones en su ciclo de vida (Dexter 1977). Vinculado a lo anterior, *E. braziliensis* muestra cambios latitudinales significativos para las tasas de crecimiento y mortalidad, la estrategia de reproducción, el tamaño corporal individual, la fecundidad, la longitud en la madurez y la longevidad (Cardoso y Defeo 2003, 2004). Estos resultados se relacionaron sistemáticamente con las tendencias en la temperatura local y la morfodinámica de las playas.

Figura 1.1. Individuos vivos de *Excirolana braziliensis* de Arachania, Rocha, Uruguay. Tamaño corporales: 6.8 mm (izquierda) y 7.5 mm (derecha).

Revisiones morfológicas anteriores concluyeron que *E. braziliensis* constituye una sola especie y que el complejo de especies constituye un grupo cercano de especies relacionadas morfológicamente (Glynn et al. 1975, Brusca et al. 1995). Hallazgos recientes sugieren que *E. braziliensis* constituiría un grupo de especies crípticas (Sponer y Lessios 2009, Varela y Haye 2012, Hurtado et al. 2016, Tourinho et al. 2016, Mattos et al. 2019). Se identificaron hasta 15 linajes divergentes y geográficamente restringidos a lo largo de las playas del Atlántico y del Pacífico, agrupados en tres clados monofiléticos (Hurtado et al. 2016).

Hasta el momento en playas arenosas y especialmente para *E. braziliensis* no se han evaluado explícitamente las reglas ecogeográficas mencionadas así como tampoco el análisis de las relaciones que involucran las mismas como latitud, tamaño corporal, historia de vida y abundancia. Tampoco se ha evaluado la vinculación de la ocurrencia y abundancia con la disponibilidad y características del hábitat, y la energía ambiental a lo largo de su distribución geográfica en ambos océanos. Esto es importante teniendo en cuenta la amplia distribución de este isópodo, y que el modo de desarrollo ovovivíparo limitaría su dispersión

(Weinberg y Starzcak 1988), lo cual puede haber llevado a la existencia de varios linajes.

1.2 Propósito del estudio

1.2.1 Planteamiento del problema

E. braziliensis muestra tendencias latitudinales tanto en aspectos de la dinámica poblacional como en patrones reproductivos a lo largo de su rango de distribución geográfica (Cardoso y Defeo 2003, 2004). Si bien estos trabajos realizan generalizaciones sobre los aspectos mencionados, a efectos de entender los patrones de distribución y la abundancia de este isópodo a lo largo de su gran distribución geográfica en América, las características de la especie brindan la oportunidad de analizar los patrones latitudinales de la ocurrencia, abundancia, tamaño corporal e historia de vida de este isópodo a través de tres reglas ecogeográficas: la ACH, la TSR y el escalamiento densidad-tamaño corporal. También se requiere analizar la vinculación de la distribución y la abundancia con la disponibilidad de hábitat (playas arenosas), y sus características (e.g. tamaño de grano, rango marea), así como también con las variables oceanográficas (e.g. temperatura superficial del agua, salinidad y producción primaria) a lo largo de su distribución geográfica en ambos océanos.

1.2.2 Hipótesis

La distribución y las variaciones en la abundancia de *E. braziliensis* en playas arenosas a lo largo de 4 provincias biogeográficas en el Océano Atlántico y 3 en el Océano Pacífico estarían asociadas a las reglas ecogeográficas, ACH, la TSR y el escalamiento densidad-tamaño corporal. Las variables oceanográficas junto a la disponibilidad y características del hábitat físico podrían explicar las tendencias geográficas de este isópodo.

1.2.3 Objetivo general

Evaluar los patrones latitudinales de la ocurrencia, abundancia, tamaño corporal e historia de vida de *E. braziliensis*, a través de la relación de variables que componen la ACH, la TSR y el escalamiento densidad-tamaño corporal y analizar su relación con la variables oceanográficas y con la disponibilidad y las características del hábitat físico.

1.2.4 Objetivos específicos

1) Evaluar los patrones latitudinales de la abundancia de *E. braziliensis* (ACH).
2) Evaluar los efectos relativos de la disponibilidad del hábitat (playas arenosas), idoneidad del hábitat o variables oceanográficas (temperatura superficial del mar, producción primaria y salinidad), y las características del hábitat físico (tamaño de grano, rango mareal) en la ocurrencia y la abundancia de este isópodo.
3) Evaluar los patrones latitudinales en el tamaño corporal y los parámetros de la historia de vida de *E. braziliensis* (TSR).
4) Evaluar los patrones del escalamiento tamaño corporal-densidad y su posible conexión con la TSR.

1.2.5 Organización de la Tesis

Los Capítulos 2 (Objetivos específicos 1 y 2) y 3 (Objetivos específicos 3 y 4) de esta tesis fueron elaborados como trabajos autocontenidos bajo el formato estándar de trabajo científico. El Capítulo 2 analiza los patrones de latitud de la abundancia de *E. braziliensis* (ACH), los roles de la disponibilidad del hábitat, las variables oceanográficas y las características del hábitat físico para determinar la ocurrencia y la abundancia de este isópodo. El Capítulo 3 evalúa los patrones latitudinales en el tamaño corporal y los parámetros de la historia de vida de *E. braziliensis* (TSR). Se evalúan también los patrones del escalamiento tamaño corporal-densidad y su posible conexión con la TSR. Finalmente se analiza el rol de las variables características del océano y las características del hábitat físico en el contexto de la conexión de ambas reglas.

CAPÍTULO 2

Distribución del isópodo *Excirolana braziliensis* en las playas de arena de los océanos Atlántico y Pacífico

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Distribution of the isopod *Excirolana braziliensis* on sandy beaches of the Atlantic and Pacific Oceans

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ABSTRACT: We assessed geographic patterns of abundance of the isopod *Excirolana braziliensis* across its whole distribution range in the context of the abundant centre hypothesis (ACH). We also evaluated auxiliary hypotheses to the ACH involving habitat availability and suitability. We compiled species abundance and occurrence information on 139 Pacific and Atlantic sandy beaches of the Americas. Abundance patterns were contrasted against 5 hypothetical distribution models. Habitat availability (sandy beach along the coast), and the role played by grain size on isopod abundance were analysed. Maximum entropy niche modelling based on primary production, salinity, water temperature and tidal range data was used to estimate trends in habitat suitability. *E. braziliensis* abundance peaked at the 2 edges of its range on the Atlantic coast and towards the centre of its range on the Pacific coast. Congruently, the niche model predicted very low habitat suitability at the centre of the species' range on the Atlantic coast. Primary production was the main contribution to the model (74.8%). The highest abundances were found in fine sediments (0.20 mm). Support for the ACH for *E. braziliensis* was found only for the Pacific coast, whereas habitat suitability and availability together with local in-beach morphodynamics accounted for deviations from ACH predictions in the Atlantic. The highest abundances registered in upwelling areas and on beaches with fine sands highlight the primary role played by regional and local conditions over geographic location.

KEY WORDS: Abundant-centre hypothesis · Habitat availability · Primary production · Salinity · Sandy beaches · Surface water temperature

INTRODUCTION

The abundant centre hypothesis (ACH) provides a mechanistic explanation for geographic trends in species abundance (Brown 1984). The ACH states that species abundance is highest in the centre of the range and decreases towards the limits in response to spatial trends in physiological (e.g. thermal) and ecological (e.g. biological interactions) performance (Brown 1984, Sagarin & Gaines 2002b). However, species exhibit variable distribution patterns across their geographic ranges (Sagarin & Gaines 2002a). Among 34 species studied in coastal ecosystems, only 8 showed normal or inverse quadratic models of abundance as predicted by the ACH (Sagarin & Gaines 2002b, Samis & Eckert 2007, Tuya et al. 2008, Rivadeneira et al. 2010, Fenberg & Rivadeneira 2011, Tam & Scrosati 2011, Baldanzi et al. 2013). This contradictory support for the ACH might reflect the occurrence of optimal conditions for peak abundance near species limits (ramped models, 13 species). However, for some species (13), no patterns were found, although some patterns may have been masked by a peak and tail pattern (McGill & Collins 2003). The failure of auxiliary hypotheses related to habitat availability (Samis & Eckert 2007) or life history traits (Rivadeneira et al. 2010) could also explain deviations from the predictions of the ACH (Brown 1984, Martínez-Meyer et al. 2013). Indeed, discontinuous distributions associated with environmental conditions and species interactions have been reported elsewhere (Sagarin et al. 2006).

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Sandy beaches present an ideal system for assessing geographical patterns in abundance because they are essentially 1-dimensional (i.e. <0.1 km wide at all points) (Sagarin et al. 2006). The morphodynamic environment of benthic macrofauna is characterized by interactions among tidal regimes, wave conditions and sediment types (Defeo & McLachlan 2005), which typically account for the spatial variation in abundance of sandy beach species at different scales (Baldanzi et al. 2013). However, identification of large-scale distribution patterns is often limited by the restricted spatial coverage of most studies, partial samplings and use of different methods (Defeo & McLachlan 2005).

The cirolanid isopod *Excirolana braziliensis* is an excellent candidate for addressing biogeographic distribution patterns. In America, there are 8 species of the genus *Excirolana* that range from Canada to Chile in the Pacific and from the USA to Argentina in the Atlantic. Among them, *E. braziliensis* has the widest distribution on both sides of tropical and subtropical America, inhabiting micro- and macro-tidal beaches with fine and coarse sands from the Gulf of California to southern Chile in the Pacific and from the Gulf of Mexico to Uruguay in the Atlantic. Populations are largely isolated because the species' ovoviviparous mode of development limits its dispersal (Weinberg & Starczak 1988). In addition, *E. braziliensis* has been sampled with similar methodologies in several studies over most of its distribution in the 2 oceans.

Sandy beach ecosystems are facing escalating anthropogenic pressures, and this isopod has been used as bioindicator regarding ecosystem health (Betz et al. 1982, Veloso et al. 2011, Vieira et al. 2012), and also to assess the role played by natural impacts (e.g. tsunamis; Jaramillo et al. 2012). Lastly, *E. braziliensis* plays an important role in sandy beach food webs as a primary consumer (Lercari et al. 2010).

We investigated variation in *E. braziliensis* abundance across its geographic range on Atlantic and Pacific sandy beaches of the Americas, encompassing 4 and 3 biogeographic provinces, respectively. Our goals were to assess latitudinal patterns in abundance and to evaluate the roles of habitat suitability, habitat availability and beach morphodynamics in shaping the species' occurrence and abundance.

MATERIALS AND METHODS

The methodological approach can be summarized as follows: we first analysed abundance data of *Excirolana braziliensis* and tested the ACH. Then, a predictive species distribution model (PSDM) was developed for each ocean, considering the role of habitat suitability on distribution patterns. The PSDM took into account the roles of primary production, tidal range, salinity and water temperature as predictors of isopod distribution. The role played by habitat availability in geographic trends of abundance was analysed by assessing the proportion of sandy beach habitat throughout the geographic range of the species. Finally, we analysed the role played by grain size, a widely used proxy for beach morphodynamics (Defeo & McLachlan 2005).

Species

Cirolanid isopods are conspicuous members of sandy beaches around the world and are dominant in terms of numbers or biomass (Soares 2003). *Excirolana braziliensis* is a dioecious species: embryos recruit to the adult population as juveniles or 'mancas' (Martínez & Defeo 2006). It is an active swimmer and shows burrowing optima in a wide range of grain sizes (Yannicelli et al. 2002).

Data

Our database included information on the occurrence and abundance of *E. braziliensis* and grain sizes from Atlantic (n = 105) and Pacific (n = 77) sandy beaches. Using Scopus, JSTOR and Google Scholar search engines, we compiled information on species abundance and occurrence along with environmental variables. Unpublished data from Uruguayan sandy beaches were also integrated into the database. The data covered the period from 1972 to date (see Table S2 in the Supplement at www.int-res.com/articles/suppl/m583p137_supp.pdf). We approximated abundance data from graphics (Nava & Severyn 2010) only in 2 cases. When monthly or seasonal surveys were present in the data sources, the species pool collected across all samples reported was used to provide only 1 estimate for each beach.

Testing the ACH

We analysed the geographic patterns of abundance of *E. braziliensis* separately for Atlantic (n = 77) and Pacific (n = 62) beaches. Large-scale variations in abundance were assessed in terms of density (ind. m^{-2}) because most data in the literature were expressed in this unit. When more than one estimate was available for the same beach, a mean value was computed. Relative densities (RDs) were estimated by dividing the densities by the maximum value observed in the geographic range. Geographical positions were standardised by the expression $RI = 2 \times (L - S) \times R^{-1}$, where RI is the range index, L is the latitude, S is the latitudinal midpoint, and R is the total range of the species (Sagarin & Gaines 2002a). RI ranges from −1 to 1, with values close to zero indicating that the site is located near the centre of the range and values close to −1 and 1 indicating that the site is near the southern and northern range limits, respectively.

The distribution of abundance along the species' geographic range was contrasted with 5 biogeographical models that encompass theoretical expectations and previously reported patterns (Sagarin & Gaines 2002b, Fenberg & Rivadeneira 2011). These models were (1) a normal distribution; (2) an inverse quadratic distribution, which assumes that the maximum abundance is reached symmetrically at the centre of the distribution and that abundance decline gradually towards the edges; (3) the abundant edge distribution, which predicts maximum abundances at the 2 edges of the range and minimum densities at the centre; and (4 & 5) ramped northern and southern distributions, which assume that abundance declines from one range limit to the other, with intermediate abundance at the centre of the range. We also considered (6) a null model of constant abundance across the geographical distribution of the species.

The goodness of fit of each model to the observed data was evaluated by calculating the residual sum of squared deviations (RSS) for sites exceeding the constraint boundary generated by each model (Sagarin & Gaines 2002b). Small values of RSS indicate a good fit between the model and the observed data. The significance of the observed RSS values was evaluated by generating 1000 randomized values of RI and relative abundance. The fit of the model was considered significant when the observed RSS value was lower than the 5th percentile of the randomised distribution. The degree of support for each model was evaluated by calculating Akaike's information criterion (AIC), and all models with Akaike weights (AIC_w) > 0.25 were selected. Analyses were carried out using a script in R v.2.11 (R Development Core Team 2007) written by Fenberg & Rivadeneira (2011).

Predictive species distribution modelling

A PSDM was built using Maxent v.3.4.1 software (Phillips et al. 2017; https://biodiversityinformatics.amnh.org/open_source/maxent/). The environmental layers used for modelling were mean annual estimates of primary production (mg C m^{-2} d^{-1}), salinity, sea surface temperature (°C), its SD and tidal range. All variables were obtained from the AquaMaps environmental dataset with a 0.5° grid cell resolution (Kaschner et al. 2008), except for tidal range, which was obtained from OSU Tidal Data Inversion with a 0.25° grid cell resolution (Egbert & Erofeeva 2002). The AquaMaps dataset was also used to analyse other invertebrate coastal species' distributions, including sandy beach ecosystems (Hermosilla et al. 2011, Lee & Riberos 2011, Barboza & Defeo 2015). The distribution model was built using presence data of *E. braziliensis* along its geographical distribution and 10 005 background points, using 50% of the localities for training, and the remaining 50% for model testing. Presence records from beaches <0.5° distant in latitude or longitude were considered redundant and removed from the analysis. The final screening reduced our dataset from 182 to 70 sandy beach locations; 36 from the Pacific Ocean and 34 from the Atlantic Ocean. The 10th percentile training presence logistic threshold was used, which provided the minimum requirements for the species' climate preferences. The output format is Cloglog, and model performance was measured by the average area under the curve (AUC) ± SD; AUC ranges between 0 and 1 (maximum) (Phillips et al. 2017). Spatial autocorrelation was examined considering all environmental variables for each sampling point based on Moran's I index and using the distance criterion included in the Spatial Analysis in Macroecology v.1.1 (SAM) software (Rangel et al. 2006). The percentage contribution of each variable to the final model was retained. Auxiliary estimates of the contributions of each variable to the final model were provided by jackknife tests (Phillips et al. 2006).

Habitat availability

We measured the amount of sandy beach habitat present throughout (and beyond) the geographic range of *E. braziliensis* using Google Earth v.6.0.3.2197, following Fenberg & Rivadeneira (2011). We traced the contours of the Atlantic coast from 42° 00′ S (Peninsula Valdez, Argentina) to 36° 27′ N (North Carolina, USA) and the Pacific coast from 48° 37′ S (Isla Campana, Chile) to 34° 46′ N (California, USA) in cumulative, 400 km sections at a constant elevation of 500 m. Within each section, we measured the amount of coastline that consisted of sandy beach habitat by summing each stretch and calculating the percentage of suitable habitat per section. Natural gaps of sandy beaches were also measured in each section as rocky shores, estuaries, mangroves/swamps/marshes/forest patches and anthropogenic infrastructure.

Grain size

Data on sand grain size for each beach was obtained (see references in Table S2) and standardised to mm. We estimated the frequency of occurrence for each grain size class as defined by Wentworth (1922) as follows: very fine (0.063–0.125 mm), fine (0.125–0.250 mm), medium (0.250–0.500 mm) and coarse (0.500–1 mm). We also analysed geographic variation in grain size across the distributional range of *E. braziliensis*. To analyse the abundance–grain size relationship for each ocean, we modelled the upper boundaries of abundance for each grain size class, determining a constraint envelope pattern (CEP; sensu Caddy & Defeo 2003). This procedure involves dividing grain size into intervals of equal length (0.1 mm) and recording the maximum value of the response variable (abundance) for each interval. Then, the relationship defined by the points of the upper boundary is visualised through a simple scatter plot, and the appropriate model is fitted. The upper limit corresponds to optimal combinations of grain size and abundance, whereas values within this 'envelope' represent a wide range of suboptimal conditions.

RESULTS

In the Atlantic Ocean, *Excirolana braziliensis* showed an asymmetric geographic distribution covering 56° in latitude (Fig. 1). The northernmost site was Progreso (Yucatan, Mexico: 21° 16′ N, 89° 49′ W), the southernmost site was Manantiales (Maldonado, Uruguay: 34° 50′ S, 54° 50′ W), and the centre of the range was at Lucena, Paraíba, Brazil (6° 52′ S, 34° 54′ W) (Fig. 1). In the Pacific Ocean, there was also an asymmetric distribution covering ca. 73° in latitude and 3 biogeographic provinces (Fig. 1). The northernmost site was Puerto Peñasco, México (31° 18′ N, 113° 37′ W) in the Gulf of California, and the southernmost site was at Chiloe Island, Chile (41° 53′ S, 74° 00′ W). The centre of the range was at Tortuga Beach, Piura, Peru (5° 16′ S, 81° 18′ W) (Fig. 1).

Geographic patterns of abundance and distribution models

Abundance patterns in the Atlantic Ocean followed the abundance edge model, which showed the lowest RSS value and the best fit, denoted by an AIC_w value close to 1 (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m583p137_supp.pdf). The highest abundance in the Southern Atlantic was registered at Praia do Pontal Beach in Rio de Janeiro (Brazil) (350 ind. m^{-2}) and in the northern Atlantic, at La Mancha Beach in Veracruz (Mexico) (210 ind. m^{-2}) (Fig. 1). Towards the centre of the range, the lowest abundance occurred at Ilhéus Beach, Bahía, Brazil (34 ind. m^{-2}; Fig. 1) and Castilletes, Zulia, Venezuela (11° 48′ N, 71° 30′ W) (11 ind. m^{-2}). From 1° S to 10° N (ca. 2800 km of coastline), no information on isopod occurrence was found.

The Maxent model for *E. braziliensis* showed an AUC ± SD of 0.922 ± 0.019. Primary production presented the largest contribution to the model (73.4 %), followed by sea surface temperature (20.7 %). Tidal range, the SD of temperature and salinity contributed 4.5, 1.3 and 0.1 %, respectively. The contribution of all predictors based on jackknife procedures was congruent with previous values (see Fig. S1 in the Supplement). The predicted occurrence of *E. braziliensis* for the Atlantic Ocean was consistent with literature reports (Fig. 1). The model predicted very low suitability in the following 3 zones: the southern limit in Uruguay and the Rio de la Plata estuary (35° S); from 12° S up to São Luis River (ca. 2° S, Fig. 1), which included the centre of the range, 7° S; and from 19 to 26° N in the Gulf of Mexico (Fig. 1).

The inverse quadratic model best explained large-scale isopod patterns in the Pacific Ocean (Fig. 2, Table S1 in the Supplement). The highest abundance was registered in Naos Island, Panama (8° 55′ N, 79° 32′ W), with 2147 ind. m^{-2}, followed by Trujillo, Peru (8° 09′ S, 79° 03′ W) near the centre of the range, with 1205 ind. m^{-2}. At the edges, the highest abundances were registered in Mehuín, Chile (140 ind. m^{-2}) and Bahía La Paz, Mexico (24° 20′ N, 110° 20′ W) (238 ind. m^{-2}; Fig. 2). Following the same trend as in Atlantic beaches, Pacific beaches showed large variation in local abundance at the same latitude, especially towards the centre of the range.

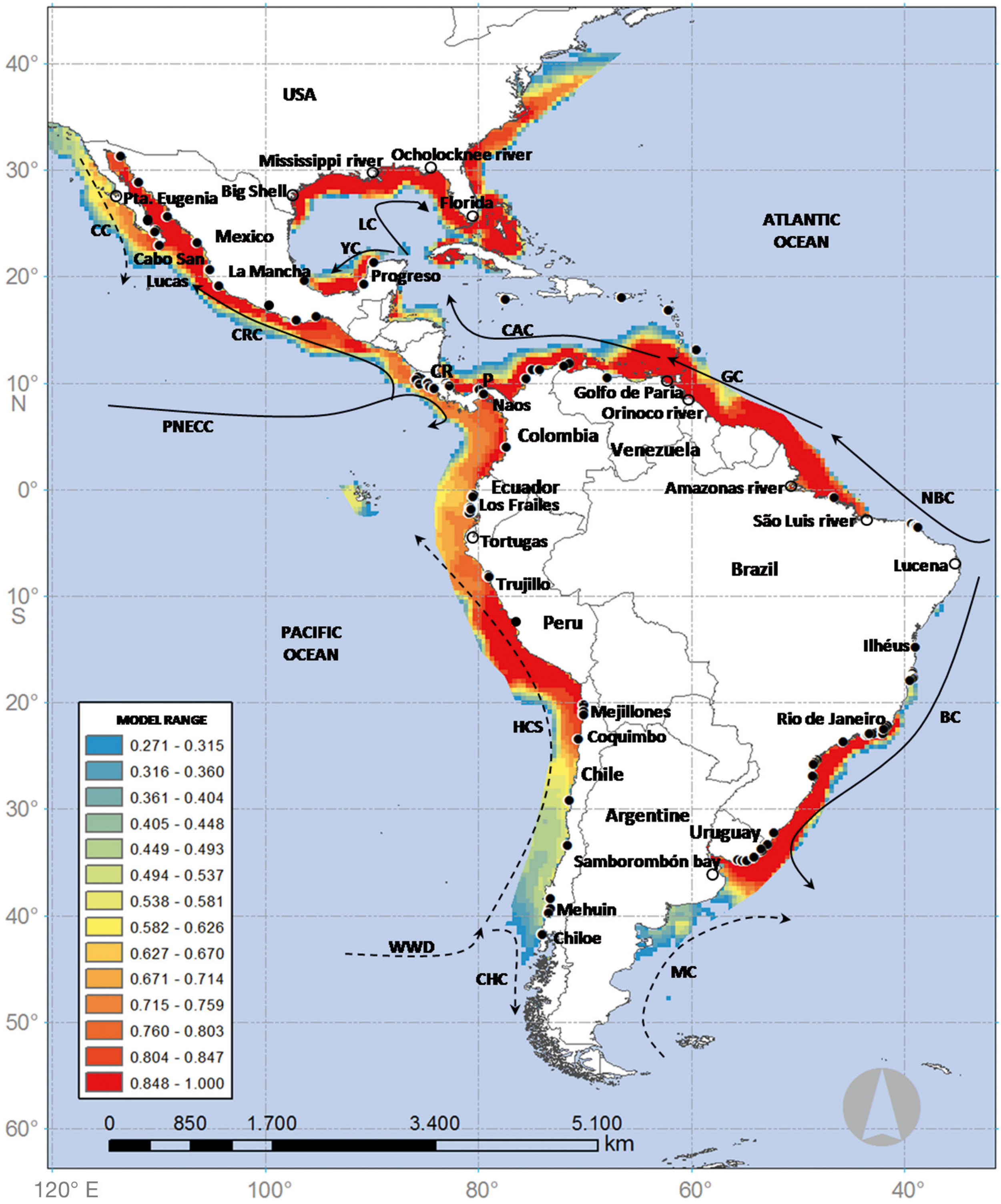

Fig. 1. Observed and predicted distribution of *Excirolana braziliensis* along the Atlantic and Pacific coasts of America. The colour gradient provides the predicted isopod distribution using a maximum entropy (Maxent) model. A suitability of 0.271 was used as baseline for the possible areas of distribution. Filled circles: occurrence sites; open circles: other locations mentioned in the text. CR: Costa Rica; P: Panama. Cold (dashed lines) and warm (solid lines) currents are indicated: WWD: west wind driven; CHC: Cabo de Hornos (Cape Horn); HCS: Humboldt System; ECC: Equatorial Counter; CRC: Costa Rica; CC: California; MC: Malvinas (Falklands); BC: Brazil; NBC: North Brazil; GC: Guyana; CAC: Caribbean; YC: Yucatan; LC: Loop

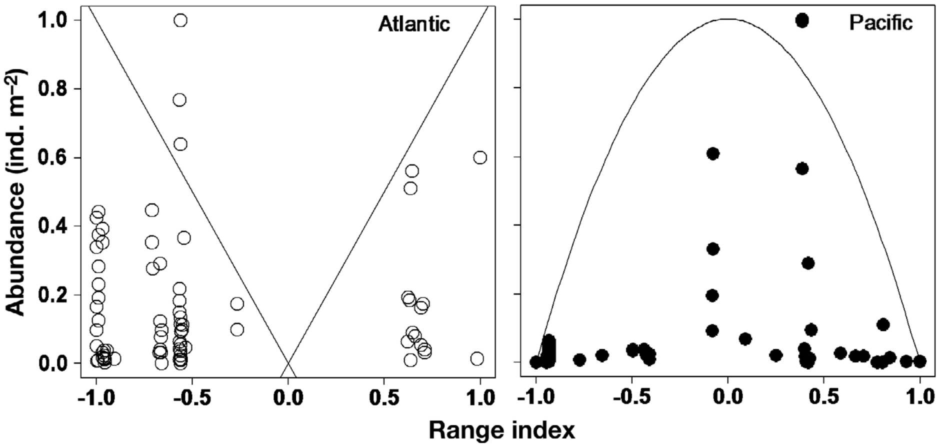

Fig. 2. Geographic variation in *Excirolana braziliensis* abundance. Geographic position (*x*-axis) and abundance (*y*-axis) are standardised. Best fit models (Akaike's information criterion weights, AIC_w, close to 1) are shown

The PSDM model for Pacific beaches showed a continuous distribution from 20° S to Punta Eugenia, Mexico (27° 51′ N, 115° 04′ W) (see Fig. 1). The highest suitability values (0.7 and 1) were predicted from Los Frailes, Ecuador (1° 30′ N) to Topolobampo Bay in the Gulf of California, Mexico (25° 34′ N, 109° 10′ W). A gradual decrease was predicted southwards from 20° S, suggesting that the southernmost limit of *E. braziliensis* in the Pacific Ocean occurs at Chiloe Island, Chile (41° 53′ S, 74° 00′ W).

Habitat availability

The Atlantic coastline covers 21 600 km and spans 4 biogeographic provinces according to Spalding et al. (2007), and it included 13 900 km of *E. braziliensis* distribution. Sandy beaches represented 56 % (12 300 km) of the coastline. Mangroves, swamps, marshes and forest patches together made up 21 % of the coastline, and estuaries, rocky shores and reefs represented 12, 7 and 1.6 % of the coastline, respectively. Anthropogenic infrastructure represented 2 % of the total. The analysis of habitat availability for *E. braziliensis* showed that marshes (100 km) at Samborombon Bay and the Rio de la Plata estuary constitute a physical barrier of 195 km (Fig. 3). In the range between 0 and 10° N (Amazon River to southern Venezuela) (7 bins = 2800 km), oceanic beaches composed only 7 % of the total coastline (Fig. 3). In the Gulf of Mexico, swamps and marsh stretches began to prevail north of 30° N (Galveston Bay, USA) along the coastline, interspersed with sandy barrier islands. Three physical barriers to isopod dispersal were apparent along the US coastline: the longshore currents convergence zone in Big Shell beach on Padre Island (27° N; McGowen et al. 1977), the Mississippi and Atchafalaya River System (>200 km of coastline), and salt marshes and mangroves (600 km) from the Ochologknee River mouth to Key Biscayne, Florida (Fig. 1). Northwards, sandy beaches prevailed (>85 %) through 3200 km of coastline.

The Pacific coastline traced 21 462 km along 5 biogeographic provinces and included 18 017 km of *E. braziliensis* distribution. Sandy beaches (45 %) and rocky shores (44 %) were the most prevalent habitats. Mangroves, swamps, marshes and forest patches composed 5 % of the coastline, and estuaries and anthropogenic infrastructure composed 5 and 1 % of coastline, respectively. The Pacific coast consists of an interspersed mosaic of sandy beaches and rocky shores. Literature reports and the present analysis predicted that Chiloe Island (see Fig. 1) might be the species' southernmost border. Southwards, fjords with rocky intertidal habitats and estuaries became prevalent along 500 km (Fig. 3). From 30 to 24° S, sandy beaches sporadically occurred (Mejillones-Coquimbo, 12.3 %; Figs. 1 & 3). From 24° S to the northern limit registered for *E. braziliensis* in the Pacific Ocean (Cabo San Lucas, Mexico; Fig. 1) and northwards to California (35° N), sandy shores were well represented (Fig. 3). This result suggests that habitat availability did not play a role in determining the northernmost limit of the species' distribution in the Pacific Ocean.

Relationship between *E. braziliensis* and sediment

E. braziliensis inhabited the supralittoral and upper mesolittoral zones of protected and exposed sandy

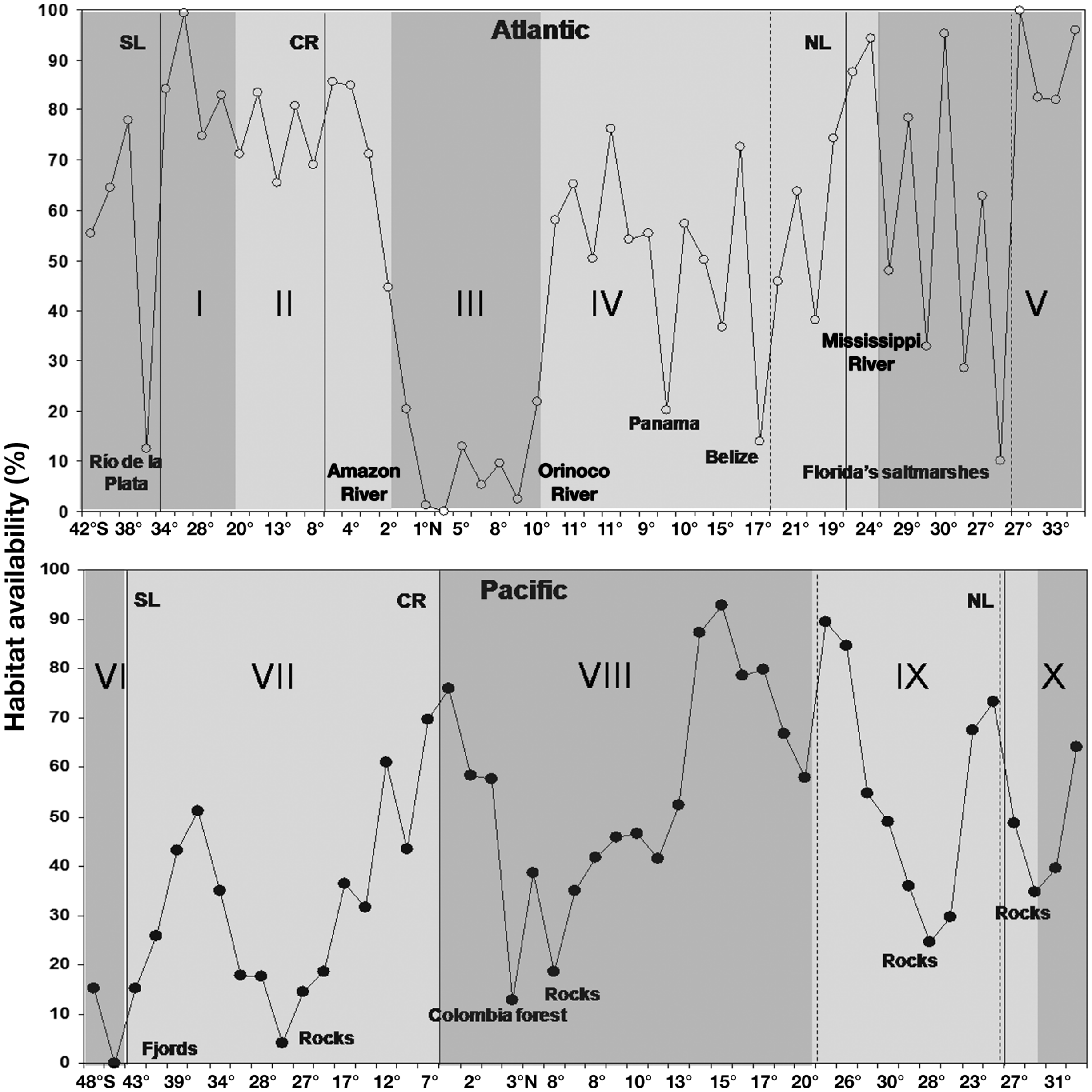

Fig. 3. Available sandy beach habitat (dots) within successive 400 km bins (dots, tic marks) across the range of *Excirolana braziliensis* and beyond; latitudes added for orientation. Repeated latitudes are due to variations in longitude. A value of 100 (zero) means that the entire (none of the) shoreline in a bin consisted of sandy beach. Solid vertical lines: published southern (SL) and northern (NL) range limits, and central range (CR). Dashed vertical lines: Gulf of Mexico limits in the Atlantic Ocean and Gulf of California limits in the Pacific Ocean. Dark and light grey zones: biogeographic provinces after Spalding et al. (2007): I: Warm Temperate SW Atlantic; II: Tropical SW Atlantic; III: North Brazil Shelf; IV: Tropical NW Atlantic; V: Warm Temperate NW Atlantic; VI: Magellanic; VII: Warm Temperate SE Pacific; VIII: Tropical Pacific; IX: Warm Temperate NE Pacific; X: Cold Temperate NE Pacific

beaches. It occurred in 4 of the 5 grain-size classes of the Wentworth (1922) grade scale, from very fine (0.14 mm) to coarse (0.91 mm) sand. Different patterns were found in the Atlantic and Pacific oceans (Table 1). In the Pacific Ocean, the species mainly occurred in beaches with fine sand (67 %; Table 1). The highest occurrence of *E. braziliensis* in the Atlantic Ocean was found on beaches with medium grain size (40 %), followed by fine- and coarse-sand beaches. All of the grain sizes of beaches in which *E. braziliensis* was present were well represented with the species' widespread distribution among Atlantic and Pacific beaches (see Fig. S2 in the Supplement).

Table 1. Relative frequency of sand classes of beaches where *Excirolana braziliensis* was present. See 'Materials and methods: Grain size' for size-class ranges

Grain size	Relative frequency (%) Atlantic Ocean	 Pacific Ocean
Very fine	0	1.5
Fine	32.2	67.0
Medium	40.2	30.0
Coarse	27.6	1.5

In the Atlantic Ocean, the CEP that joined the highest abundances at each grain size (i.e. optimal environmental conditions) was fitted with a negative linear function (abundance = 451.3 − 425.4 × grain size; $R^2 = 0.86$, $p < 0.01$). This relationship indicated that isopod abundance was highest for fine grains close to 0.20 mm in size and lowest for coarse sediments; in the latter, the differences between optimal and suboptimal conditions were reduced (Fig. 4a). In

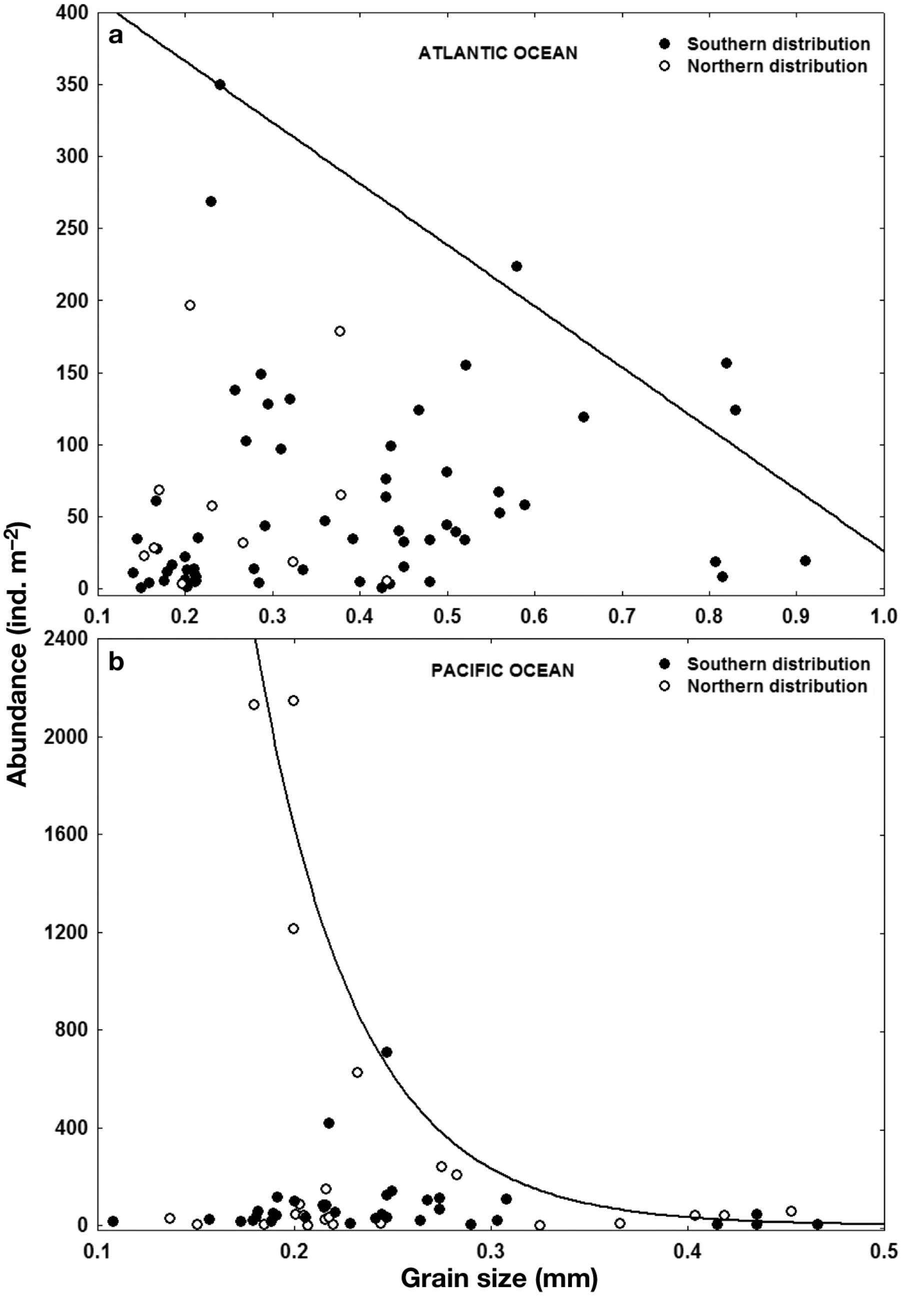

Fig. 4. Abundance of *Excirolana braziliensis* versus sand grain size, discriminated by centre range latitude (southern and northern distributions) in the (a) Atlantic and (b) Pacific oceans. Constraint envelope patterns for the Atlantic and Pacific oceans were fitted, respectively, by a linear and exponential function. Note different *x*- and *y*-axis scales

the Pacific Ocean, the CEP fit a decreasing exponential function (abundance = $79152.5 \times \exp[-19.4 \times$ grain size], $R^2 = 0.87$, $p < 0.01$), with the highest densities found in fine sediments between 0.18 and 0.24 mm (Fig. 4b). Large differences between optimal and suboptimal conditions were found at this range size, whereas small differences were found in sediments of very fine and medium grain sizes.

DISCUSSION

Abundance patterns of *Excirolana braziliensis* across its whole geographic range on Atlantic and Pacific sandy beaches of the Americas provided partial support for the ACH. In the Pacific Ocean, the highest abundances were observed at the range centre, but the opposite pattern was found in the Atlantic Ocean. These contrasting patterns might be explained by the different geological histories that determine the very dissimilar configuration of Atlantic and Pacific coastlines of the Americas (Kellogg & Mohriak 2001, Mann et al. 2007), which in turn defines marked between-ocean differences in habitat availability. Indeed, abundance in the Atlantic closely followed trends in habitat availability and suitability and thereby deviated from the pattern predicted by the ACH. However, habitat suitability in the Pacific peaked at intermediate locations of the species' range, and the ACH holds. Therefore, local conditions of habitat quality and morphodynamics significantly contribute to the geographic pattern. In the Atlantic Ocean, the highest abundance and predicted habitat suitability were located in 2 zones with high primary production due to coastal upwelling in the summer (see Fig. 1): (1) between 22 and 24° S (Rio de Janeiro; Paes & Moraes 2007); and (2) in the Campeche Bank (20° N, Gulf of Mexico; Zavala-Hidalgo et al. 2006). Both zones also have high water temperature (24.71 and 26.44°C, respectively). In the Pacific Ocean, the highest isopod abundances also occurred in 2 areas with high primary production and upwelling towards the centre of the range (Fig. 2b): Peru (Llanillo et al. 2012) and Panama (D'Croz & O'Dea 2007), which also have high sea surface temperatures (20.46 and 27.77°C, respectively). Considering that similar suitability conditions can be found from the Gulf of Tehuantepec, Papagayo and Nicoya in Pacific Central America (Gocke et al. 2001, López-Calderón et al. 2006, Tapia-Garcia et al. 2007), these zones could also hold high abundances of this species.

The predicted occurrence of *E. braziliensis* was consistent with literature reports, except for the Caribbean islands, where Maxent seemed not to include them in the analysis. The highest probabilities of occurrence concurred with areas of high abundance. Overestimated areas (e.g. Atlantic coast of the USA) could be interpreted as potential areas that are not occupied by the species due to dispersal limitations (Guisan & Zimmermann 2000, Valle et al. 2014). Refinement models for intertidal species could be obtained including habitat availability and variations in local habitat (e.g. morphodynamics in sandy beaches or protected or exposed habitats in rocky shores).

Sandy beaches are physically (tidal and/or wave) dominated systems where swash conditions play a central role in determining species richness and abundance (Defeo & McLachlan 2005). The hard swash (waves break directly on the beach surface) excludes many intertidal species from reflective beaches, which are characterized by a low number of species, particularly in the supralittoral zone (McLachlan et al. 1995). The highest abundances of *E. braziliensis* occurred in beaches with fine sediments (<0.25 mm) and different tidal regimes: macrotidal (Panama), mesotidal (Peru) and microtidal (Rio de Janeiro, Brazil). However, southwards from Rio de Janeiro, high isopod densities were found at intermediate and reflective beaches (i.e. beaches with minimal wave-energy dissipation) with coarse sediments (Defeo et al. 1997, this study) and low local net primary production (Lercari et al. 2010). Therefore, other mechanisms are likely contributing to the geographic trends in *E. braziliensis* abundance. One possible influence is the lack of a 'safety zone' in microtidal dissipative beaches. These beaches lie very close to the South Atlantic storm belt (Vera et al. 2001) and are thus fully exposed to storm surges (Guimaraes et al. 2014), barometric tides and wind-driven surf (Parise et al. 2009, Calliari et al. 2010, Ortega et al. 2013). This exposure makes the supralitoral fringe an unpredictable and harsh environment, which precludes the existence of *E. braziliensis* populations (Defeo & Martínez 2003). This detrimental environmental effect in beaches with fine sand might be magnified by competition with *Excirolana armata*, which is a better swimmer than *E. braziliensis* and shows high substrate specificity for fine-grain sand (Defeo et al. 1997, Yannicelli et al. 2002).

Range limits in both oceans were congruent with biogeographic province boundaries (vanishing at definite points in space) due to the combined effects of habitat availability, surface currents and physiological constraints defined by temperature. The low abundance of the species at the central part of its range in the Atlantic Ocean might also reflect such effects. In the Gulf of Mexico, with northward currents (Expósito-Díaz et al. 2009) up to Mexico and high habitat availability (Fig. 3), the alongshore currents convergence zone located in Big Shell beach on Padre Island, Texas, USA (McGowen et al. 1977) sets the northern limit of the species (Fig. 1) (Tropical NW Atlantic province limit). Shelton & Robertson (1981) indicated that cirolanid isopods were replaced by haustoriid amphipods in the Warm Temperate NW Atlantic province and above. In the Atlantic centre range, the sediment discharge of the Amazon and Orinoco Rivers (North Brazil Shelf province; Spalding et al. 2007) largely eliminates sandy beaches and forms the longest muddy coast in the world (Warne et al. 2002, Anthony et al. 2010). Between 2 and 22° S, low abundances of *E. braziliensis* might be due to low primary production (North Brazil current) and the scarcity of dissipative beaches (Soares 2003). The southern edge of the range lies where the Río de la Plata estuary joins the marshes of Samborombon Bay, which constitute a physical barrier to dispersal. Moreover, the Uruguayan shelf is characterized by the strong influence of the diluted waters of the Río de la Plata and the convergence of shelf water masses advected by the Brazil and Malvinas Currents (Lima et al. 1996, Ortega & Martínez 2007), constituting a 2-way flow-mediated range boundary (Gaylord & Gaines 2000) for *E. braziliensis*.

In the Pacific Ocean, sandy beaches are well represented northwards from Cabo San Lucas up to 30° N (see Fig. 1). Considering that the cold temperate water of the California Current occurs north of Punta Eugenia (28° N, Fig. 1) (Durazo et al. 2010), the zone between this point and Cabo San Lucas likely represents the northern limit of *E. braziliensis* in the Pacific Ocean. This current constitutes a 1-way (alongshore) flow-mediated boundary (Gaylord & Gaines 2000). Moreover, Hayden & Dolan (1976) reported the beginning of a transition zone of fauna at 30° N by analysing geographic ranges of 968 marine species. The following 3 concurrent effects might explain the southern limit of the species in Chiloe Island, Chile (Warm Temperate SE Pacific province limit): (1) a diverging 2-way boundary limiting dispersal (Gaylord & Gaines 2000) between the Peru–Chile Coastal Current and the Cabo de Hornos Current (Fig. 1); (2) a lack of habitat availability, with a decline in sandy beaches to 0 % due to Golfo de Corcovados and fjords (Fig. 2b); and (3) physiological stress, with the coldest mean annual temperature within the species' distribution in both oceans being registered at this location (mean ± SD = 12.15 ± 1.75°C).

An alternative interpretation of the discontinuous distribution in the Atlantic is the existence of cryptic species. Recent findings in Chile (Varela 2008), Panama (Spooner & Lessios 2009) and Uruguay (Tourinho et al. 2016) suggest that *E. braziliensis* might be a complex of species. Furthermore, Varela (2008) showed that the congeneric *E. hirsuticauda* in Chile is also in the process of incipient speciation. These findings highlight the need for phylogeographic studies of the Genus *Excirolana* in the Americas (8 species). The direct development mode of the genus might significantly reduce gene flow among populations (particularly distant ones), promoting speciation even with low ecological divergence. If *E. braziliensis* actually represents multiple species, the biogeographical considerations presented above are equally valid at this aggregated level. However, the relationship between trends in abundances and geographic limits, with species turnover and interactions, can only be elucidated once the taxonomy of the genus is fully resolved.

In summary, abundance patterns of *E. braziliensis* showed opposite trends between oceans. Deviations or congruence with ACH expectations might be accounted for by the trends in the mechanisms that support the ACH, e.g. habitat suitability, habitat availability and local beach morphodynamics. Both local and global trends in abundance were identified as interrelated phenomena, with main drivers operating at each scale but with a mutual influence that could not be determined from local or regional analyses. Our findings suggest that the abundance patterns of *E. braziliensis* appear to be more related to an environmental niche centre than to a geographic range centre. The highest abundances, which were registered in upwelling areas, high water temperatures and in dissipative beaches (fine grains, flat slopes and high local primary production), indicate the combined effects of regional and local conditions over geographic location. These findings are in agreement with a recent continental-scale analysis of aggregate patterns of macrofaunal diversity for sandy beaches in both South American ocean coasts (Defeo et al. 2017). Therefore, our results reinforce the importance of conducting a systematic analysis of main theoretical predictions and associated auxiliary hypotheses as a mandatory step for the construction of a robust biogeographic theory.

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The following supplement accompanies the article

Distribution of the isopod *Excirolana braziliensis* on sandy beaches of the Atlantic and Pacific Oceans

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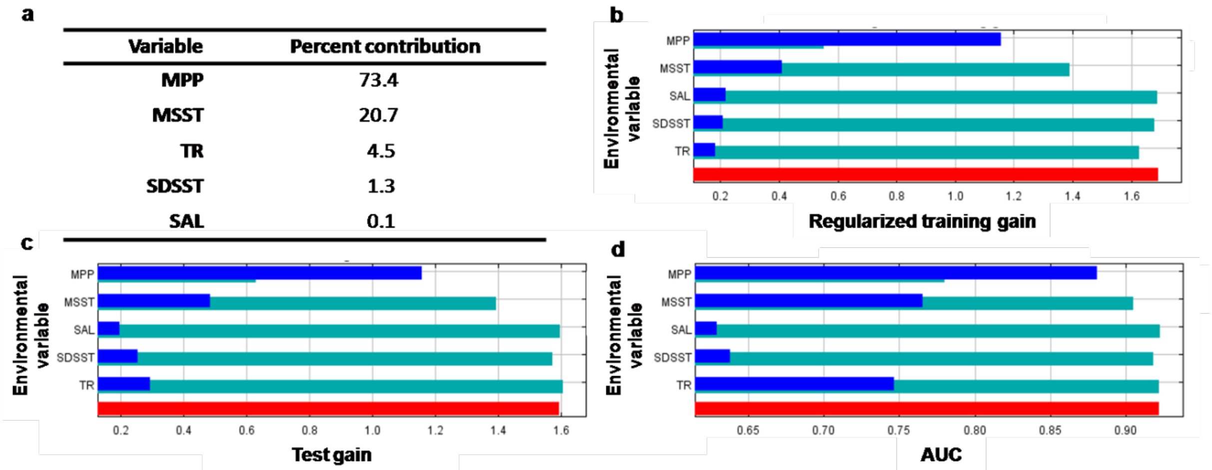

Variable	Percent contribution
MPP	73.4
MSST	20.7
TR	4.5
SDSST	1.3
SAL	0.1

Figure S1. Outputs of the analysis of variable contributions by Maxent model. a) Relative contributions of the environmental variables to model. Results of the jackknife test of variable importance through b) increase in regularized training gain, c) test gain and d) AUC. See text for details. Turquoise, blue and red bars indicate without variable, with only variable and with all variables models respectively.

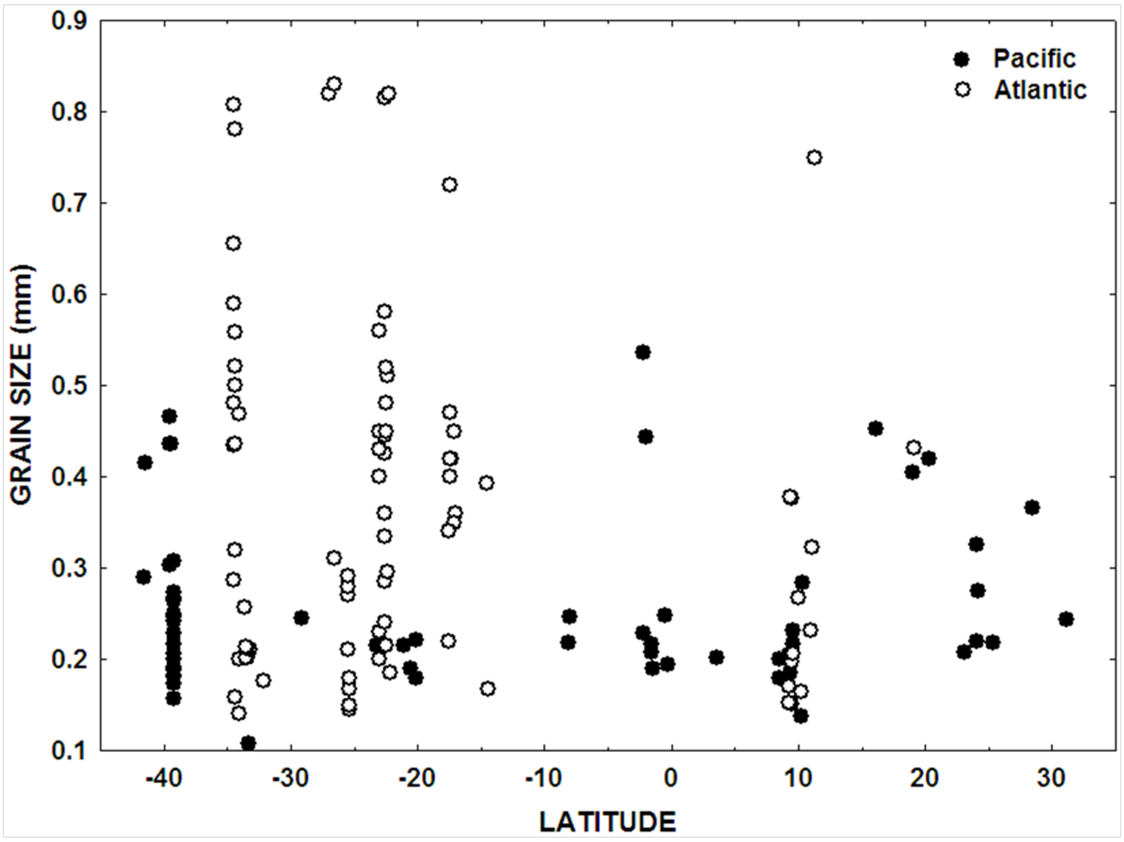

Figure S2. Geographic variation of grain size across Atlantic and Pacific distributional ranges of *E. braziliensis*.

Table S1. Degree of fit of six hypothetical models to the observed abundance of *E. braziliensis* (ind·m^{-2}) in the Pacific (N=77) and Atlantic (N=62) coasts of America. Significant values are in bold.

		Atlantic			**Pacific**		
Models	**P**	**RSS**	**AICs**	**Akaike w**	**RSS**	**AICs**	**Akaike w**
Normal	2	2.933	-49.57	0.000	**0.913**	-78.75	0.000
Inverse quadratic	2	1.439	-67.38	0.000	**0.066**	**-144.45**	**0.999**
Abundance edge	4	**0.238**	**-108.36**	**0.999**	1.503	-62.29	0.000
Ramped north	2	2.365	-54.95	0.000	**0.300**	-106.53	0.000
Ramped south	2	**0.441**	-86.71	0.000	1.507	-66.22	0.000
Null	1	2.222	-56.50	0.000	2.967	-49.28	0.000

Table S2. Bibliography where information on the occurrence and abundance of the isopod *Excirolana braziliensis* was taken.

Biogeographic province	Occurrence	Abundance	References
Atlantic Ocean			
Warm Temperate SW	63	58	5-7 11 16-18 23 24 32 35 38 39 43 44
Tropical SW	18	2	34 38 45
North Brazil Shelf	1	0	37
Tropical NW	23	17	2 19-22 31 33
Pacific Ocean			
Warm Temperate SE	43	38	3 4 8 13 14 16 26-30 40 47
Tropical East	26	17	1 9 10 12 15 19 25 36 38 42 46
Warm Temperate NE	8	7	10 15 36 41

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REPLY COMMENT

Genetics, taxonomy and species complex in sandy beach macrofauna: Reply to Mattos et al. (2018)

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ABSTRACT: Mattos et al. (2018; Mar Ecol Prog Ser 601:269–271) commented on our evaluation of the abundant-centre hypothesis (ACH) for the distribution of the isopod *Excirolana braziliensis* (Martínez et al. 2017; Mar Ecol Prog Ser 583:137–148). They stated that our treatment of *E. braziliensis* as a single species (i.e. ignoring cryptic diversity) invalidates the connection between reported distribution patterns and the ACH. However, from the introduction of the ACH, the set of mechanisms determining distribution patterns has been considered equally important for a single species and for a set of species with similar functional traits, as is the case for the *E. braziliensis* complex.

KEY WORDS: Morphologically related species · Cryptic diversity · *Excirolana*

Mattos et al. (2018) commented on our article about the distribution of the isopod *Excirolana braziliensis* on sandy beaches of the Atlantic and Pacific Oceans, and the evaluation of the abundant-centre hypothesis (ACH) for this species (Martínez et al. 2017). They call attention to recent genetic results that identified 13 divergent and geographically restricted lineages along Atlantic and Pacific beaches (Hurtado et al. 2016), where *E. braziliensis* was formerly considered as a single species (Glynn et al. 1975, Brusca et al. 1995). In this context, Mattos et al. (2018) stated that ignoring this cryptic diversity results in our study not contributing to the general understanding of the ACH. However, unless there is a population rescue effect (Holt & Keitt 2000), the mechanisms that we considered as determinants of the ACH are valid for the distribution trend of ecologically closely related species: sister species (Péron & Altwegg 2015) and species assemblages (Enquist et al. 1995, Ren et al. 2013, Dallas et al. 2017) throughout their geographic range. This is particularly important for the species that comprise the complex grouped as *E. braziliensis*, which occupy the supralittoral and upper-littoral zones on sandy beaches and have similar biology, life-history traits, and relationships with environmental variables (e.g. Cardoso & Defeo 2003, 2004, Martínez & Defeo 2006). As mentioned by Mattos et al. (2018), morphological revisions concluded that *E. braziliensis* constitutes a single species (Glynn et al. 1975, Brusca et al. 1995) and, therefore, most of the results and interpretations in our article (Martínez et al. 2017) are valid. This is also true if the analysis reflects the geographic trend in a group of very closely morphologically related species, as detailed in Brown (1984), where the theoretical basis of the ACH was developed.

Unfortunately, we were not aware of the results that identified 13 divergent and geographically restricted lineages along Atlantic and Pacific beaches (Hurtado et al. 2016) that had formerly been considered as a single species, i.e. *E. braziliensis*. However, we explicitly discussed the potential existence of cryptic species in our paper. We are aware that the direct development mode in these ovoviviparous

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species tends to isolate populations with low gene flow and connectivity, thus increasing the probability of genetic differentiation between scattered populations over their extensive range (McLachlan & Defeo 2018). In this context, Sponer & Lessios (2009), Varela & Haye (2012), Tourinho et al. (2016) and Hurtado et al. (2016, 2017) have also provided critical insight into the genetic diversity and evolutionary history of *E. braziliensis* and other congeneric species, which could set the basis for a deeper understanding of macroecological distribution patterns in sandy beach macrofauna.

The identification of the existence of cryptic species by Hurtado et al. (2016, 2017) represents a significant advance in our understanding of evolutionary processes and macroecological patterns in *E. braziliensis*, which has been one of the main model species in sandy beach macrofauna. However, morphologically cryptic species could likely respond similarly to environmental conditions when living in sympatry at similar latitudes (Struck et al. 2017). These responses are mostly driven by selection pressures towards very similar morphological forms regardless of the reproductive isolation between them. Therefore, in this context also, our approach is valid to test the ACH. A separate test for the ACH taking into account divergent lineages, as suggested by Mattos et al. (2018), would represent a valuable evaluation of the sensitivity of macroecological distribution patterns to the existence of cryptic species. However, we think that phylogeographic studies and taxonomic revision of the genus *Excirolana* need to be completed (see also Hurtado et al. 2016). Even though cryptic species could represent a substantial fraction of biodiversity (including those inhabiting sandy beaches), Struck et al. (2017) recently highlighted that an effort should be made to clearly differentiate taxonomical errors from true cryptic biodiversity. This topic is under debate (Heethoff 2018). In the specific case of *E. braziliensis*, taxonomic uncertainties still remain. We think that a useful approach to fill these gaps should be to follow an integrative taxonomy framework, combining information from different approaches and disciplines (e.g. geometric morphometrics methods, DNA barcodes, nuclear gene sequences, full mitochondrial genome data) to provide a comprehensive description of species (Zúñiga-Reinoso & Benítez 2015, Beermann et al. 2018, Eme et al. 2018, Struck et al. 2018). These different approaches, combined with morphological, ecological, and geographical information, will facilitate a rigorous identification of entities within species complexes and therefore a deeper understanding of macroscale patterns in sandy beach populations.

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CAPÍTULO 3

Conexiones causales entre la regla de temperatura-tamaño corporal, y el escalamiento densidad-tamaño corporal en el isópodo de playa de arena *Excirolana braziliensis*

(Para ser enviado a Estuarine, Coastal and Shelf Science)

Causal connections between the temperature-size rule and the density-body size scaling on the sandy beach isopod *Excirolana braziliensis*

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Abstract

We tested the temperature size rule (TSR) and the density-body size scaling on the isopod *Excirolana braziliensis* on Atlantic and Pacific sandy beaches of the America, throughout its whole distribution range. We assessed latitudinal patterns of surface water temperature, body size and life history parameters, and evaluated the role of oceanographic variables and characteristics of the physical habitat on the density-body size scaling relationship. We also assessed the density-body size scaling, explicitly. The information of three clades was included. Path analysis models were developed to analyze the connection between both rules and between latitude, oceanographic variables and characteristics of the physical habitat. The isopod *Excirolana braziliensis* followed the TSR with the same relationship in the two oceans and among clades. At low latitudes and higher SST it showed lower growth acceleration (K), and higher size at maturity, lifespan and maximum fecundity. The density-body size scaling also holds. The connection of both rules mediated by SST and its geographical life history responses, allowed to have a better understanding of the distribution of *E. braziliensis* along a wide geographical range in both oceans. Environmental variables of the ocean and of the local showed low causal link connection with density.

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KEYWORDS: ecogeographical rules, surface water temperature, life history parameters, mophodynamic

1. Introduction

Ecogeographical rules describe general trends in biological traits (Gaston et al., 2008). These rules were developed under different theoretical frameworks (Gaston and Blackburn 1999) and their unification has become a central aim in Ecology (Lomolino et al. 2006, Gaston et al. 2008). Two of the most familiar rules with an intraspecific approach are the Bergmann’s or more generally the temperature-size rule (TSR), from which individuals are bigger at lower temperatures, and the negative density-body size scaling.

Bergmann’s rule is the tendency of organisms to be smaller at high temperatures and consequently at low latitudes (Bergman 1847, Rensch 1938, Mayr 1942, 1956, Meiri 2011). Originally intended for endotherms, this rule has been also applied to ectotherms (Rensch 1938, Mayr 1942) and to explain intraspecific variations in body size (James 1970, Stelzer 2002, Virgos et al. 2011, Forster et al. 2012). Reviews reported that 84% and 61% of ectotherm species conform this pattern (Atkinson 1994, Watt et al. 2010, respectively). The TSR describes the effects of temperature on growth rate and age at maturity (Atkinson and Sibly 1997), and states that individuals from cooler latitudes reach maturity at a larger size (Atkinson 1994). Several mechanisms were proposed to be important determinants of geographic variations in body size (Anguilletta et al. 2004b). The effects of temperature, via its effect on metabolism, in cell size or number (James et al. 1995, Van Voorghies 1996), enzyme kinetics adult size dependance on activation of growth or development rate (Van der Have and de Jong 1996) and constraints on growth during ontogeny (Anguilletta and Dunham 2003). Cell size is also invoked to the converse TSR in insects, and for marine crustaceans counter examples were also reported (Lonsdale and Levinto 1985, Orensanz et al. 2007). All the associations between latitude and body size are mediated by geographic trends in temperature, and therefore the Bergmann's rule and the TSR could be unified (Horne et al. 2015). The negative correlation between body size and temperature also determines trends in life-history parameters (Enquist et al. 1998, Brown et al. 2004). Consequently, the association between temperature and body size may also be related to life history strategies and variations in population density (Brown et al. 2004, White et al. 2007).

The relationship between body size and density has been analysed by several complementary approaches (reviewed in White et al. 2007 and Arim et al. 2011). A decrease in density with body size, balancing the rise in metabolic demand ($D \alpha BS^{-0.75}$), is congruent with a main role of energetic demand on population density (Cyr et al. 1997). However, the implicit assumption of a constant amount of resources for all body sizes is difficult to support (Isaac et al. 2010, Arim et al. 2011). Indeed, the density-size relationship presents an important variability among species, suggesting that further mechanisms may be considered (Isaac et al. 2010). Temperature may affect the density-body size scaling by the TSR, but also determines individual metabolism and consequently affects population density (Allen et al. 2002, Brown et al. 2004). In this context, a joint analysis of the temperature-body size and life history parameters, and the density-body size scaling is required. The interplay among body size, density, temperature and latitude has been studied through empirical studies at the interspecific (Enquist and Nicklaus 2001, Lindersfor et al. 2007) and intraspecific (Berven and Hill 1983, Reading and Clarcke 1995, Crozier et al. 2010, Parra et al. 2012) levels. Considering that metabolic scaling (Guinzburg and Damuth 2008), temperature dependence (McNab 2002; Angilletta 2009) and the density-size relationship (Ziegler et al. 2013) could present different patterns at the intraspecific versus interspecific levels, evidence must be accumulated on both scales (Meiri 2011).

Sandy beaches are physically-dominated ecosystems where tidal range, wave conditions and sediment type play a central role shaping benthic macrofauna distribution (Defeo and McLachlan 2005). Previous macroecological studies in these ecosystems reported consistent trends in biodiversity, abundance, and community organization, which have been closely linked to beach morphodynamics and latitude (reviewed in McLachlan and Defeo 2018). Species richness increases from temperate to tropical regions for beaches with similar morphodynamic type. Body size and density showed an inverse pattern, partially explained by inverse responses to beach type. Therefore, dissipative beaches harbour communities with highest abundance and species with the smallest body sizes, a pattern that may also affect the abundance-body size scaling in sandy beach communities (McLachlan and

Defeo 2018). Evidence of scaling of density to body size has been documented for the mole crab *Emerita brasiliensis* (Defeo and Cardoso 2004), suggesting that smaller forms are more sensitive to harsh conditions in reflective beaches (coarse sediments, high swash frequency, and low food availability) where density is lower. However, the integrated analysis of the relationships between latitude, water temperature, body size, life history and density has not been documented in these ecosystems.

In this paper we focus on the connection among latitude, surface water temperature (SST), body size, life history parameters and density among local populations of *Excirolana braziliensis*, Richardson 1912 (Isopoda: Cirolanidae). We stand on an exceptional database that covers a large geographic gradient among 73 degrees of latitude in the Pacific and Atlantic coasts of the America. This isopod is a primary consumer found on sandy beaches on both sides of tropical to temperate America, from Baja California (Glynn et al. 1975) to southern Chile in the Pacific (Jaramillo et al. 2000) and from Gulf of Mexico (Dexter 1976) to Uruguay in the Atlantic (Defeo et al. 1997), inhabiting the supralittoral and intertidal zones of sandy beaches with fine and coarse sand (Martínez et al. 2017). Significant latitudinal changes were reported for *E. braziliensis's* growth and mortality rates, reproduction strategy, individual body size, fecundity, length at maturity, and longevity (Cardoso and Defeo 2003, 2004). These results were consistently related with trends in local temperature and beach morphodynamics. Recent findings suggest that *E. braziliensis* might be a group of cryptic species (Sponer and Lessios 2009, Varela and Haye 2012, Hurtado et al. 2016, Tourinho et al. 2016, Mattos et al. 2019). Fifteen divergent and geographically restricted lineages were identified along Atlantic and Pacific beaches, grouped in three monophyletic clades (Hurtado et al. 2016). However, this species complex constitutes a close group of morphologically-related species, and previous morphological revisions concluded that *E. braziliensis* constitutes a single species (Glynn et al. 1975, Brusca et al. 1995). This brings the opportunity to include clades in the analysis of the relationships contained in these macroecological rules. Specifically, our goals were to assess: 1) latitudinal patterns in *E. braziliensis* body size and life history parameters, advancing in the putative role of surface water temperature on geographic trends; 2) the density-body size scaling, explicitly evaluating the role of oceanopraphic variables (surface water temperature, salinity and primary production) and characteristics of the physical habitat (grain size, tidal range) on this relationship; and 3) the connection between the TSR and density-body size scaling at the intraspecific level.

2. Material and methods

The methodological approach was as follows: firstly, we analysed the connection among latitude, temperature, body size and life history parameters (growth, size at maturity, lifespan and maximum fecundity), testing the TSR. Then we analysed the connection between body size and density, testing their scaling. The information of three clades (A, B and C) was included in this analysis. Secondly, a path analysis model was developed, considering a join analysis of latitude, surface water temperature, body size and density of *E. braziliensis* throughout the geographic range of the species. Finally, we assessed the connection between latitude, the oceanographic variables (sea surface temperature, salinity and primary production) and characteristics of the physical habitat (grain size, tidal range) of *E. braziliensis*.

2.1. Data

Our database included sandy beaches from Atlantic and Pacific sandy beaches that contained information on density and body size of *E. braziliensis* (N=45) (Appendix A). Abundance was assessed in terms of density (ind·m^{-2}) because most data in the literature were expressed in this unit. When more than one estimate was available for the same beach, a mean value was computed. Unpublished data from Uruguayan and Brazilian sandy beaches were also integrated into the database. The data covered the period from 1972 to date. For life history information, data from 16 sandy beaches along its distribution was extracted.

Two types of environmental variables were included in the analysis (Defeo et al. 2017): a) oceanographic variables (sea surface temperature, salinity and primary production) and b) characteristics of the physical habitat (grain size, tidal range). Mean annual estimates of SST and its standard deviation (SD) were obtained from IRI/ LDEO Climate Data Library (Reynolds et al. 2002) and AquaMaps (Kaschner et al. 2008), following the coastline in the range 20ºN - 35ºS in the Atlantic Ocean and the range 29°N - 42ºS in the Pacific Ocean, covering the entire distribution of *E. braziliensis*. Salinity and primary production ($mgC \cdot m^{-2} \cdot day^{-1}$) were obtained from the AquaMaps environmental dataset (Kaschner et al. 2008) and tidal range from OSU Tidal Data Inversion (Egbert and Erofeeva 2002). Grain size (standardised to mm) for each beach was gathered from all the articles used to build the dataset.

Clades A, B and C of *E. braziliensis* were obtained by the information included in Hurtado et al. (2016) and Mattos et al. (2018), and information of species distribution by Martínez et al. (2017). Clade A ranged from Yucatán Mexico (ca 21°N) to Cabo Frío, Brazil (23°S) in the Atlantic Ocean and from Arica (28°29'S) up to Chiloe island (Chile) (ca. 42°S) in the Pacific Ocean. One data from northern Yucatan was included in this clade. One data from Naos, Panama in the Pacific Ocean was included as clade A (Sponer and Lessios, 2009). Atlantic and Pacific populations from this clade were analysed separately whenever possible. Clade B ranged from Cabo Frío (23°S) to Uruguay (35°S), and clade C from Cabo San Lucas (ca. 23°N), Gulf of California (USA) to Arica (Chile). Data from Peru was included in this clade.

2.2. Testing the TSR

To test the TSR, we first analysed the relationship between latitude, SST and mean and maximum length, measured to the nearest 0.1 mm (except for two data) from the tip of the cephalon to the end of the telson. Geographical positions were expressed as latitude and by the expression Range Index = 2 × (L − S) × R−1, where L is the latitude, S is the latitudinal midpoint, and R is the total range of the species (Martínez et al. 2017). Range Index ranges from −1 to 1, with values close to zero indicating that the site is located near the centre of the range and values close to −1 and 1 indicating that the site is near the southern and northern range limits, respectively.

To analyse the connection between latitude, SST and body size, the following relationships were separately considered for Atlantic and Pacific Oceans: a) SST – Latitude; b) the Atlantic-Pacific Index (API) for SST and its standard deviation (SD)-Latitude; c) mean length (ML) – SST; and d) maximum length - SST. a) and b) were developed in order to explain differences in body size between oceans. For b) the API for SST and SD resulted from the subtraction of these variables in both oceans at the same latitude. Positive values indicate higher values for the Atlantic Ocean and negative for the Pacific Ocean. For c) and d) an analysis of covariance (ANCOVA) was used to analyse differences in body size between oceans, with SST as main factor, and mean length and maximum length as covariates.

Two analyses were performed to compare clades: a) an ANOVA of SST, where clade A localities per ocean were included in the analysis as follows: Atlantic (AT), Pacific (AP), and b) a non parametric analyses of mean length.

Four life history parameters were chosen to analyse the connection with range Index and SST: a) K (year^{-1}), the curvature parameter of the von Bertalanffy growth function (Gayanilo and Pauly 1997); b) $L_{50\%}$, average size at maturity (Restrepo and Wilson 1991); c) lifespan (months); and d) maximum fecundity (number of ova/embryos·female^{-1}).

A general procedure was followed to analyse univariate relationships, where a linear model and 4 non-linear models were analysed: 1) Linear ($y=a+b\cdot x$), 2) Quadratic ($y=a+b\cdot x+ b\cdot x^2$), 3) Exponential ($y=a\cdot \exp^{(b\cdot x)}$), 4) Potential ($y=a\cdot b^x$) and 5) Third-degree polynomials ($y=a+b\cdot x+ b\cdot x^2+c\cdot x^3$). The convergent models with significant parameters were selected by the corrected Akaike 's information criterion (AICc), and its weight of evidence AICw (Brewer et al., 2016). Differences in AICc values greater than 2.0 were deemed significant (Hilborn and Mangel, 1997). AICw could be interpreted as the probability that a given model is the best when compared with the set of models evaluated (Burnham and Anderson 2004).

2.3. Density-body size scaling

The $\log_{(10)}$ transformed relationship between density and body size (ML) was estimated by an ordinary least square regression (OLS). As the scaling has been originally estimated using body mass (Glazier 2005), theoretical coefficients were transformed to length in order to be compared with those estimated for *E. braziliensis*, with the following procedure. Density (D) and body mass (BM) show a power relationship of the form:

$$D \ \alpha \ BM^{-0.75} \qquad \text{(Eq. 1)}$$

Assuming isometric growth, body mass (BM) could be transformed to body length (BL) by:

$$BM \ \alpha \ BL^{3}$$

Replacing in Eq. 1,

$$D \ \alpha \ (BL^{3})^{-0.75}$$

$$D \ \alpha \ BL^{-2.25} \qquad \text{(Eq. 2)}$$

Ginzburg and Damuth (2008) predicted that at the intraspecific level:

$$D \ \alpha \ BM^{-0.66}$$

$$D \ \alpha \ (BS^{3})^{-0.66}$$

$$D \ \alpha \ BS^{-1.98} \qquad \text{(Eq. 3)}$$

Finally, to analyse differences between our estimates and those expected by theory (Eq. 2 and 3), -b ± confidence interval was used (Glazier 2005). If the range of the confidence intervals estimated here covers the theoretical exponents, it would be considered that the theoretical density-body size scaling fulfils.

2.4. Integrated rules analysis and the environment

A path analysis was performed to evaluate the putative role of SST and its causal connection with range Index, body size and density. SST was expressed as 1/K·SST, where K is the Boltzmann constant. Density was $\log_{10}$ transformed. We used structural equation modelling (SEM) to test the overall path diagram and the significance of each single connection between variables. The path analysis was used with maximum likelihood methods, working with standardised coefficients and estimating the explained variance (R^2) for each endogenous variable as one minus the path coefficient between its associated error variable (Shipley 2000). To assess the significance of the overall path model, we used a χ^2 statistic computed by assessing the difference between the observed and expected covariance matrix derived from the proposed model. A significant value ($P < 0.05$) indicates that the data do not support the model.

Selection of the models, with significant standardised coefficients and regression parameters ($p<0.05$), was done with AICc and AICw (Burnham and Anderson 2004, Brewer et al. 2016) for SEM models with AICcmodavg package in R (Mazerolle 2017). The standardized root mean square residual (SRMR) Index was fitted for the selected model, where values < 0.08 were considered a good model fit (Hu and Bentler 1999). Our data matrix satisfied the assumption of multivariate normality, where analysis based on kurtosis was performed using the mvnorm.kur.test function (W = 8.345, w1 = 0.889, df1 = 9.000, w2 = 1.333, df2 = 1.000, p = 0.535) and skewness using mvnorm.skew.test function (U = 0.13394, df = 4, p-value = 0.998) of the ICS package in R ver. 2.15.2 (Canavero et al. 2017). SEM models were fitted using the R-package lavaan (Rosseel 2012). We also performed a SEM to relate latitude, environmental variables and density of *E. braziliensis*. Primary production and density were $\log_{10}$ transformed. To evaluate the putative role of the environment on isopod abundance, two latent variables were considered: 1) oceanographic variables, including SST, salinity and primary production, and 2) characteristics of the physical habitat that included grain size and tidal range. Therefore, two path analyses were done: 1) one latent variable including all environmental variables together and 2) oceanographic variables and the physical habitat analysed separately.

3. Results

3.1. *Temperature size rule*

a) Latitude and SST

Considering the geographic range of distribution of *E. braziliensis*, the best relationship between latitude (L) and SST (both oceans), was third-degree polynomials (Fig. 2a, Table 1). In the Atlantic Ocean, SST showed a stable pattern above 26°C from southern Gulf of Mexico (ca. 21°N) to Espiritu Santo (19° 30'S) (Fig. 1), the maximum being registered in Costa Rica (ca. 9°30'N) (28.53 ± 0.44°C) (Fig. 1, 2a). Southwards from 20°S, SST decreased until reaching the lowest SST and its highest SD (17.40 ± 5.56°C) in Atlantic waters of Uruguay (Fig. 2a). Moreover, the highest SST change rate by latitude (0.6°C) for the Atlantic Ocean was registered between 22° and 34°S. In the Pacific

Ocean, highest SST values occurred from 19°N (Mexico) to 2°N (Ecuador), peaking in El Salvador (ca.13°30'N) (29.36 ± 1.31°C: Fig. 1, 2a), decreasing towards the Gulf of California (range=21-25°C). Southwards from Ecuador, SST markedly decreased towards the southern limit of the isopod distribution in Chile (ca. 42°S) where the lowest SST was registered (12.83 ± 1.76°C). In this sense, two high SST change by latitude were registered in this stretch: a) 0.7°C from 5°N to 5°S (Fig. 2a) and b) 0.5°C from 20° to 43°S.

Despite the similar latitudinal patterns found for the Atlantic and Pacific Oceans, the API for SST showed higher values in the Atlantic Ocean northwards from 20°N but specially southwards from 0° (Fig. 2b). The higher SST differences were found in the range 5°- 17°S, peaking in 12°S (7.78°C) between Cacimba, Bahia (Brazil) and Lima (Peru) (Fig. 1). The API for SD (SST) showed higher values for the Pacific Ocean northwards from 20°N and southwards for the range between 2°30'- 23°S. In the range 24°-35°S, the Atlantic Ocean show higherer SD (SST), where maximum differences (API for SD = 4°C) were registered between Uruguay and Maule (Chile) (35°S, Fig. 1).

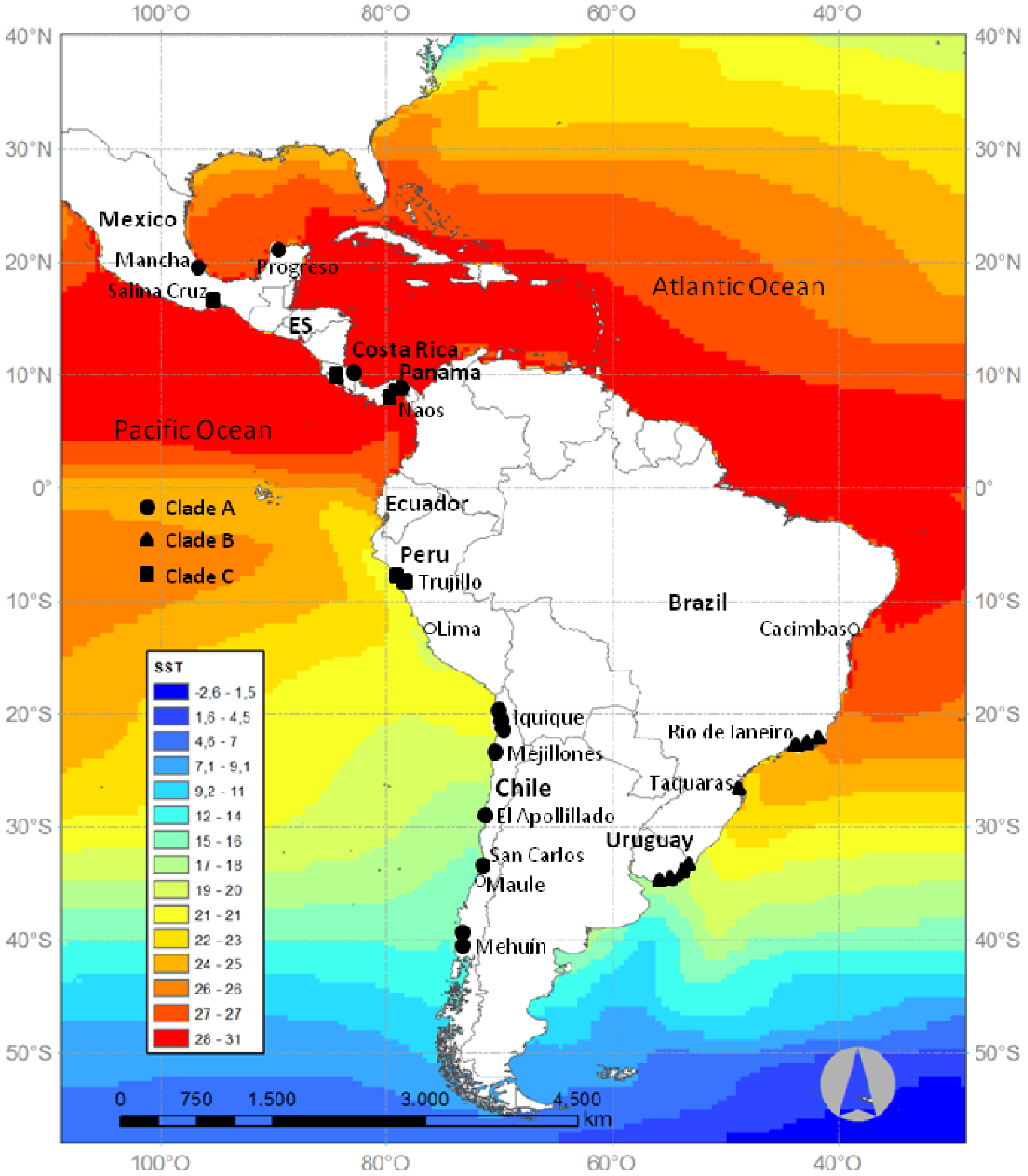

Figure 1. Geographic location of the sandy beaches considered in the analysis of the isopod *Excirolana braziliensis* along Atlantic and Pacific shorelines of America. Information about clades was included for each location. The colour gradient is mean sea surface temperature (in °C). Open circles indicate other locations mentioned in the text. ES: El Salvador.

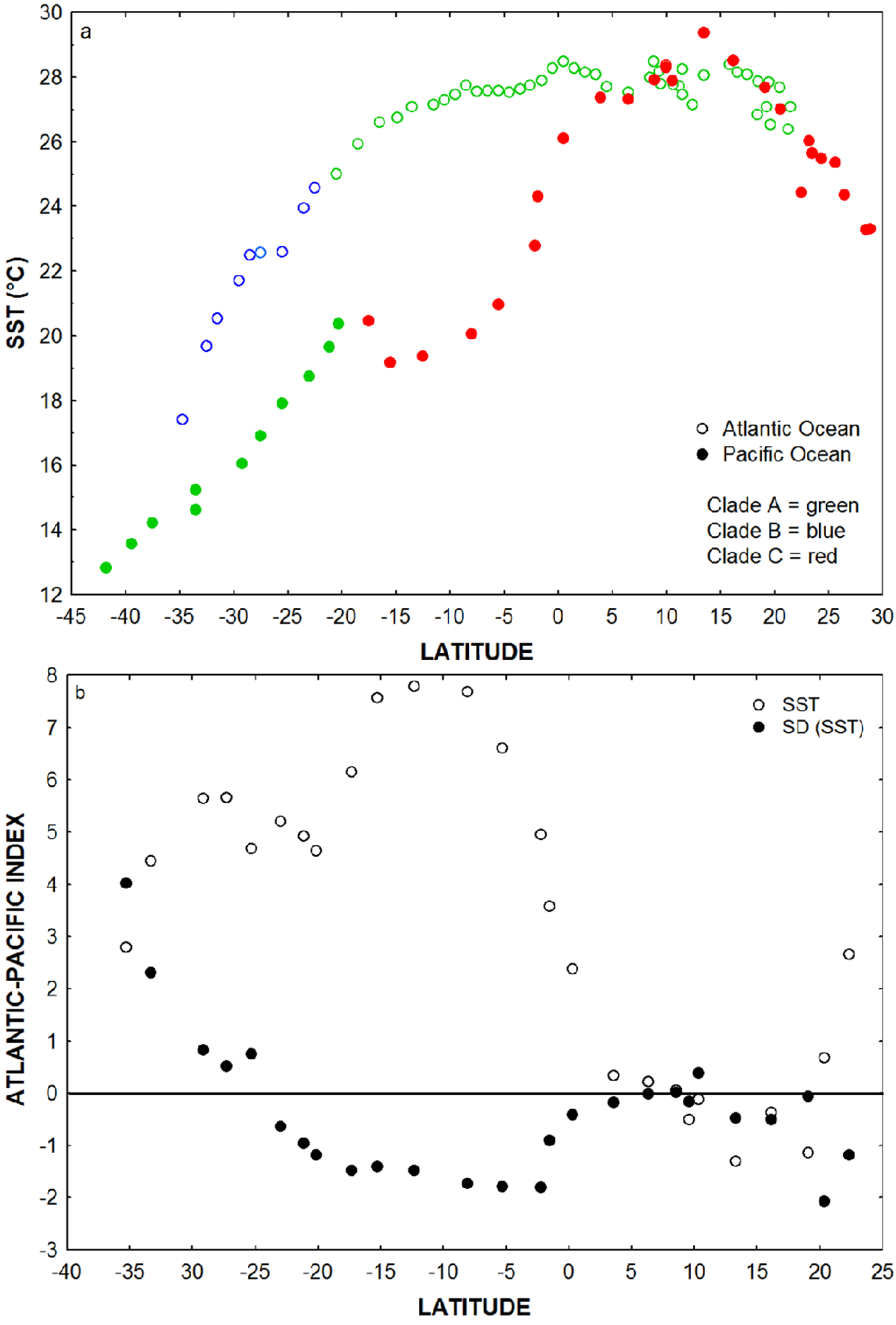

Figure 2. a) Latitudinal variation in sea surface temperature (SST) in Atlantic (empty circles) and Pacific (filled circles) oceans of the Americas. Clades are also included. b) Atlantic-Pacific Index for variation in SST and its standard deviation (SD) discriminated by latitude.

b) Body size and SST

The isopod *Excirolana braziliensis* followed the TSR with the same relationship in the two oceans and among clades. A linear decreasing function best explained the relationship between mean length and SST in the Atlantic Ocean (Table 1). The highest mean length (12.5 mm) and the lowest SST (mean ± SD, 17.40 ± 5.56 °C) were registered in Uruguay (ca. 35°S) at the southernmost edge of the species distribution in the Atlantic. Towards the northern limit of the isopod (ca. 19°N, Progreso, Gulf of Mexico, Fig. 1), the lowest mean length (3.76 mm) and the highest SST (26.38 ± 1.97°C) (Fig. 2b) were registered. The relationship between mean length and SST in the Pacific Ocean was explained by a non-monotonic inverse quadratic function (Fig. 2b, Table 1), where the highest mean length were registered in Chile (ML=7.52 mm, Mehuin and ML=8.3 mm, Iquique, Fig. 1) at SST values of 13.57 ± 1.75°C and 20.37 ± 2.56°C, respectively. The lowest mean length in the Pacific was found in Panama (ca. 9°N, Naos Island, ML=2.96 mm) (Fig. 2b). The mean length – SST relationship did not differ between oceans (ANCOVA $F_{1, 27}=0.016$; $P=0.90$). The analysis of SST by clade (AT, AP, B, C) revealed significant differences (ANOVA, $F_{(3,86)}=99.217$, $P<0.01$), where AT>C>B>AP. The highest differences were found within clade A, where mean SST differences were 11.18°C. However, no significant differences were found in mean length between clades ($X^2_{2,31}=4.43$, $P=0.11$).

Monotonic linear models best explained the relationship between maximum length and SST in both oceans (Fig. 3b, Table 1). The highest maximum length in the Atlantic Ocean was registered in the Uruguayan coast (12.50 mm), whereas the lowest one (4.80 mm) was registered in 19°N, Mancha, Gulf of Mexico (Fig. 1), concurrently with almost the highest SST (26.52 ± 2.28°C) (Fig. 3b). The highest maximum length in the Pacific Ocean was registered close to the southernmost geographical distribution limit of the species (ca. 40°S, Calfuco, Chile: 13 mm), being 9 times larger than the lowest (3.8 mm) registered in Naos Island, Panama (ca. 9°N, Fig. 1). The SST in the latter was almost 14°C higher than in Chile (Fig. 3b). Contrary to what was expected in accordance to the TSR, Atlantic populations showed higher maximum length-SST relationships than their counterparts in the Pacific Ocean

(ANCOVA $F_{1, 41}$ =13.83; P <0.01). These differences were more pronounced when lines bifurcate (SST < 28°C) towards southern and colder coastal waters of both oceans (Fig 3b). Clade B showed higher maximum length-SST relationships than clade A and C (ANCOVA $F_{2, 42}$ =12.99; P <0.01).

c) Life history and SST

E. braziliensis showed statistically significant geographic patterns, with lower growth acceleration K and higher size at maturity, lifespan and maximum fecundity found at low latitudes and higher SST (Fig. 4, Table 1). The curvature parameter K significantly increased with SST through an inverse quadratic function (Fig. 4a, Table 1). K was almost two times higher in the subtropical Atlantic (ca. 23°S, Rio de Janeiro, Fig. 1) than in the temperate Chile (ca. 39°S, Fig. 1) (0.66 year^{-1}) (Fig. 4a). A quadratic model (including data from all clades) best explained the relationship between L_{50} and Range Index (Fig. 3b, Table 1). The highest $L_{50\%}$ was registered in southern Chile, which resulted 2.18 times higher than the lowest one registered in Panama (Fig. 1, 3b). A quadratic model (including data from clades A and B) best explained the relationship between lifespan and SST (Fig. 3c, Table 1). Lifespan was 2.19 times higher in southern Chile (see SST above) than in Rio de Janeiro, Brazil (Fig. 1, 3c). Maximum fecundity decreased linearly (including data from all clades) with SST (Fig. 4d, Table 1), being 2.47 times higher in Uruguay than the lowest value registered in Panama (Fig. 1).

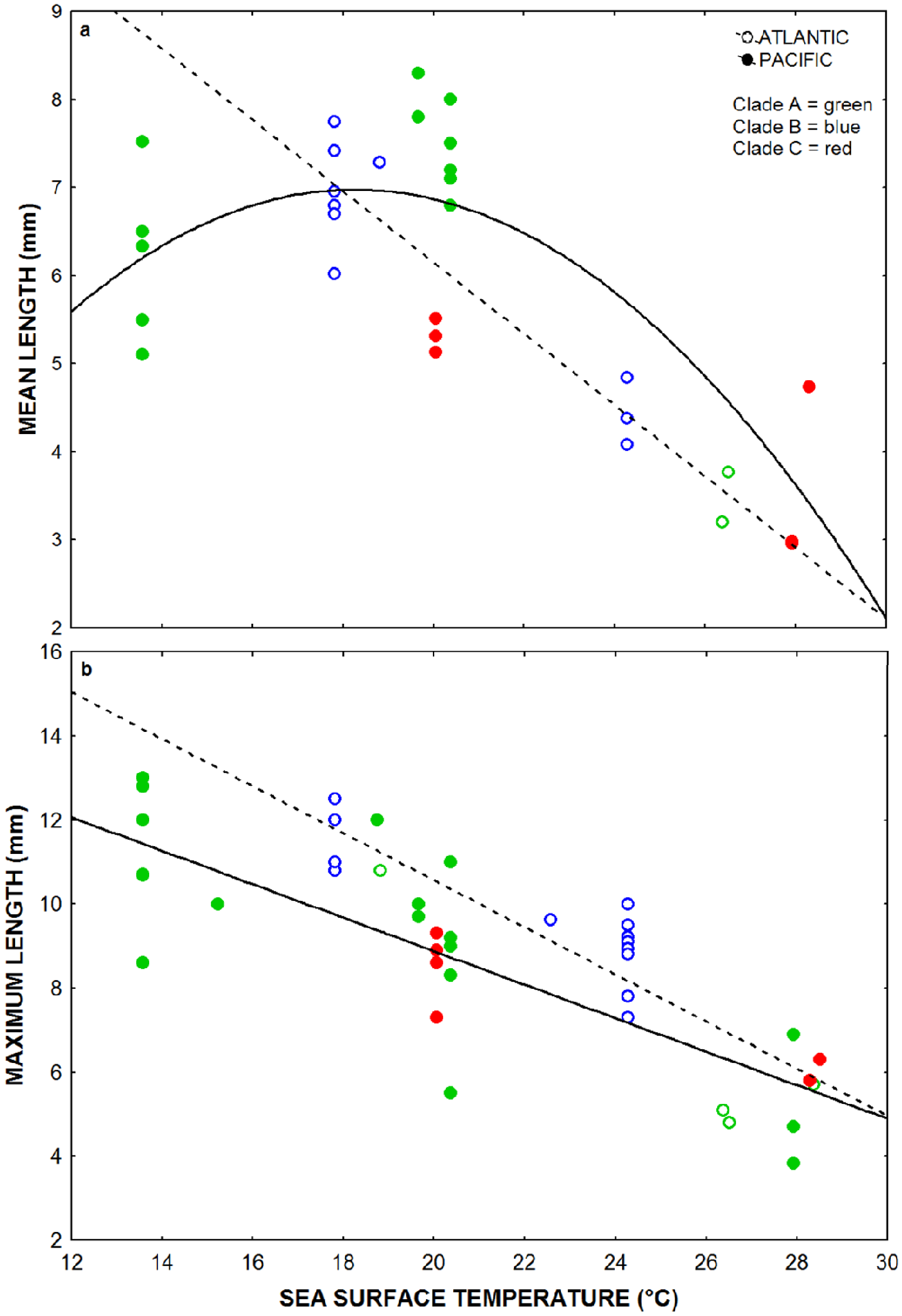

Figure 3. a) Geographic variation in mean length and sea surface temperature across Atlantic (dotted line) and Pacific (solid line) Oceans. b) Scatter plot and linear functions relating maximum length of *E. braziliensis* and SST discriminated by ocean. Clade information was included in both scatterplots.

Table 1. Results of model selection for univariate relationships: Linear ($y=a+b\cdot x$), Quadratic ($y=a+b\cdot x+b\cdot x^2$), Exponential ($y=a\cdot \exp^{(b\cdot x)}$), Potential ($y=a\cdot b^x$), Third-degree polynomials ($y=a+b\cdot x+ b\cdot x^2+c\cdot x^3$). AICc (corrected Akaike 's information criterion) and AICw (weight of evidence) are indicated only for models that converged and with significant parameters.

Model	df	AICc	AICw
Mean Length (ML) and SST (Atlantic Ocean)			
Linear	**3**	**22.94966**	**0.62**
Exponencial	3	23.93619	0.38
$ML=14.25-0.4\cdot SST$, $R^2=0.89$, $p<0.01$, $n=12$			
Mean Length (ML) - SST (Pacific Ocean)			
Linear	3	68.82293	0.02
Quadratic	**4**	**61.25809**	**0.98**
$ML=-4.80+1.29\cdot SST-0.035\cdot SST^2$, $R^2=0.52$, $p<0.001$, $n=18$			
Maximum length - SST (Atlantic Ocean)			
Linear	**3**	**63.83655**	**0.79**
Potential	3	66,50954	0.21
$MXL=21.76-0.57\cdot SST$, $R^2=0.79$, $p<0.01$, $n=20$			
Maximum length - Sea surface temperature (SST) (Pacific Ocean)			
Linear	**3**	**80.29112**	**0.71**
Exponential	3	82.48196	0.24
Potential	3	85.77269	0.05
$MXL=16.70-0.39\cdot SST$, $R^2=0.73$, $p<0.01$, $n=23$			
Sea surface temperature (SST) - Latitude (L) (Atlantic Ocean)			
Linear	3	193.7915	0.00
Quadratic	**4**	**93.8965**	**1.00**
Exponential	3	197.5301	0.00
$SST=28.3665+0.0458\cdot L-0.0062\cdot L^2$, $R^2=0.95$, $p<0.001$, $n=49$			
Sea surface temperature (SST) - Latitude (L) (Pacific Ocean)			
Linear	3	251.7037	0.00
Quadratic	4	221.3761	0.00
Exponential	3	255.0166	0.00
Polinomial	**5**	**192.9454**	**1.00**
$SST=25.47+0.28\cdot L-0.008\cdot L^2 +0.0002\cdot L^3$, $R^2=0.85$, $p<0.001$, $n=47$			
k - Sea surface temperature (SST)			
Linear	3	-0.5843	0.01

Quadratic	**4**	**-12.6103**	**0.99**
$k=-3.48+0.44\cdot SST-0.01\cdot SST^2$, $R^2=0.90$, $p<0.01$, $n=9$			
Size at maturity ($L_{50\%)}$) - Range Index (RI)			
Linear	3	20.9591	0.00
Quadratic	**4**	**6.0927**	**0.89**
Exponential	3	10.2165	0.11
Lifespan (LS) - Sea surface temperature (SST)			
Linear	3	58.2401	0.03
Quadratic	**4**	**51.5011**	**0.93**
Exponential	3	57.9639	0.04
$LS=138.08-11.41\cdot SST+0.26\cdot SST^2$, $R^2=0.81$, $p<0.001$, $n=9$			
Maximum fecundity (MF) - Sea surface temperature (SST)			
Linear	3	-	-
$MF=78.85-2.26\cdot SST$, $R^2=0.66$, $p< 0.01$, $n=11$			
Log Density (D) - Log Mean length (ML)			
Linear	**3**	**33.5330**	**0.25**
Exponential	**3**	**32.8876**	**0.34**
Potential	**3**	**32.5537**	**0.41**
$\text{Log } D=5.05-4.37\cdot \text{Log } ML$, $R^2=0.48$, $p<0.01$, $n=17$			
$\text{Log } D=8.60\cdot \exp^{(-2.14\cdot \text{Log } ML)}$, $R^2=0.50$, $p<0.01$, $n=17$			
$\text{Log } D=1.17\cdot \text{Log } ML^{-1.35}$, $R^2=0.51$, $p<0.01$, $n=17$			

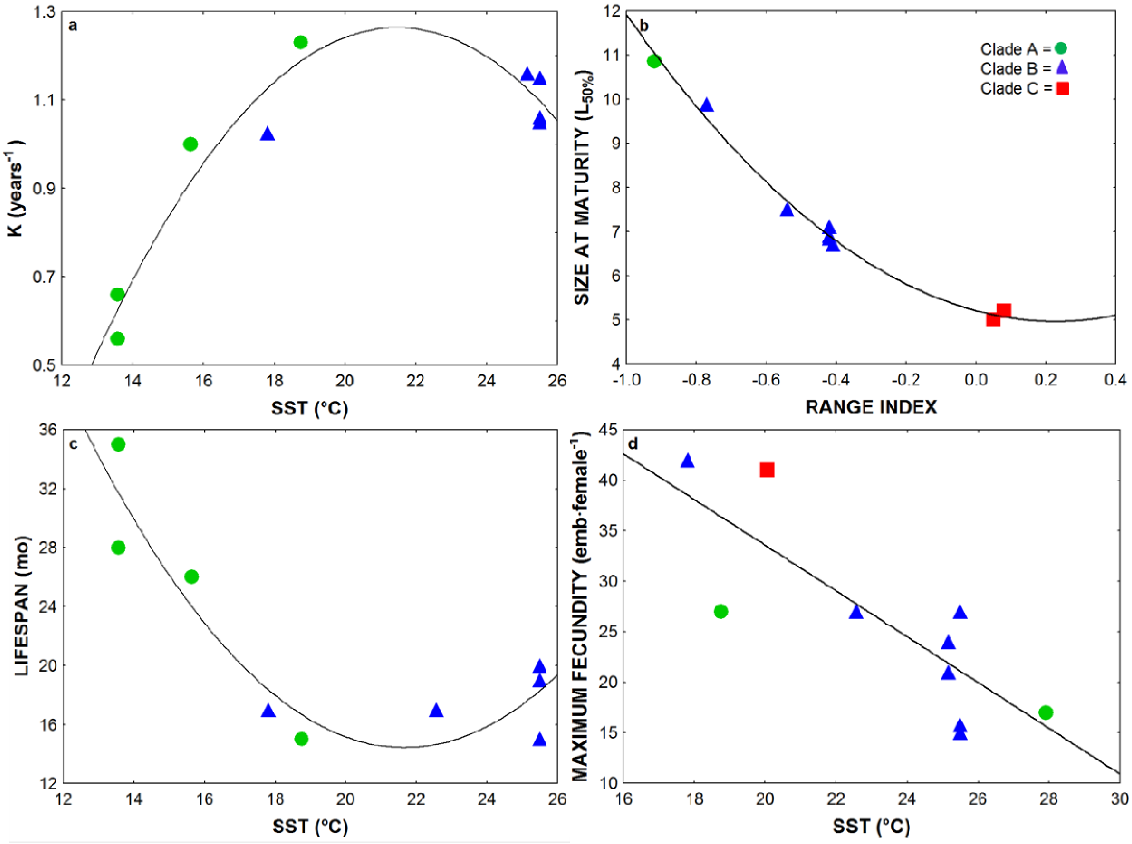

Figure 4**.** Scatterplots relating (a) growth, (c) lifespan and (d) maximum fecundity of *E. braziliensis* with SST. (b) Geographic variation of size at maturity across Atlantic and Pacific Oceans (pooled data). Geographic positions (x-axis) have been relativised (see Methods).

3.2. Scaling body size to density

Three models (linear, exponential, and potential), with similar AICc and AICw and negative relationships between Log Density and Log ML, were found for *E. braziliensis*, considering pooled data for oceans and clades (Figure 5, Table 1). The linear model was selected for parsimony not supporting the existence of differences in energy use at different body sizes.

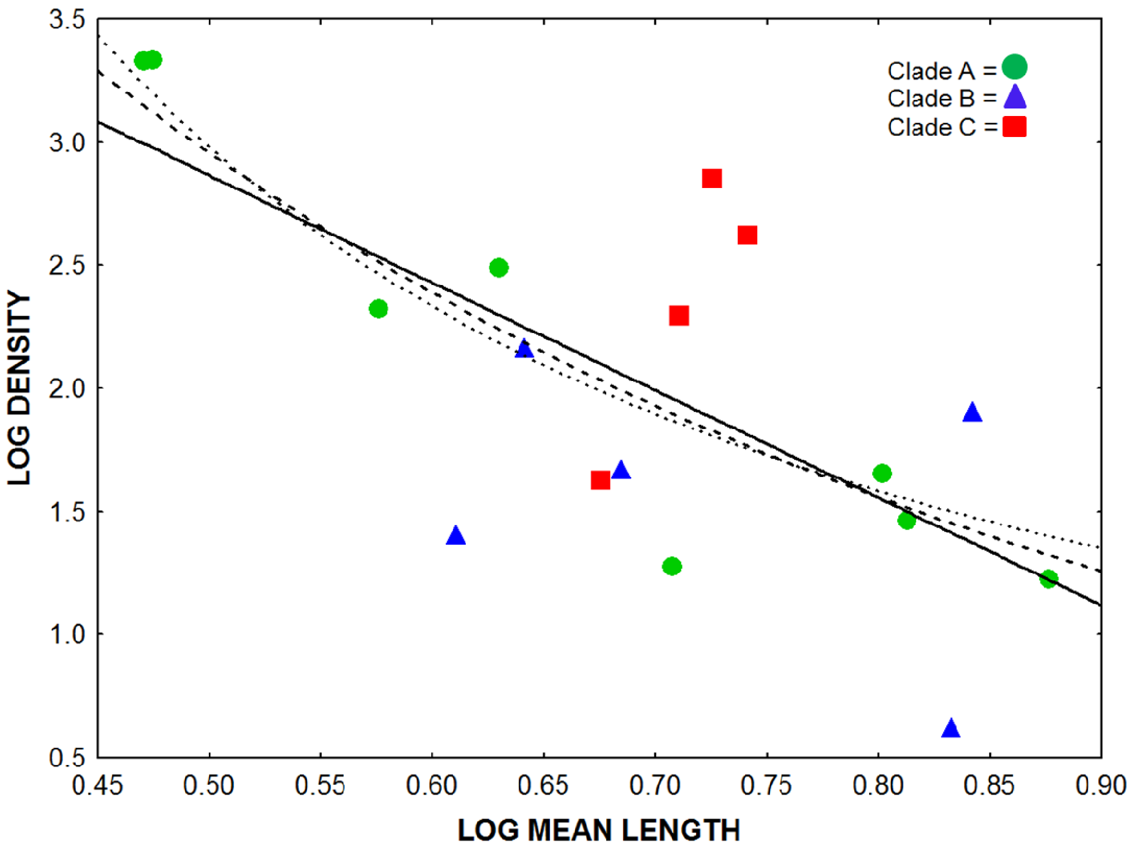

Figure 5. Log-log relationship between density and mean length across Atlantic and Pacific Oceans and clades (pooled data), where exponential (dotted line), linear (solid line) and potential (dashed line) models are also shown (see Table 1 for details).

3.3. Integrated rules analysis and the role of the environment

The path analysis model (Fig. 6, Table 2, Fig. B1-B7) showed that SST was a main component in the causal connection among latitude, body size and density. The Range Index determines temperature (1/K·SST), which in turn showed a single path connection and a positive relationship with body size. However, no direct connection between Range Index and body size was detected. Density was determined by the mean body size and also by Range Index. Path models that incorporated environmental variables showed a comparatively poor performance (Fig. B9, B10). The same holds true when using oceanographic variables and physical habitat as latent variables (Fig. B11, B12).

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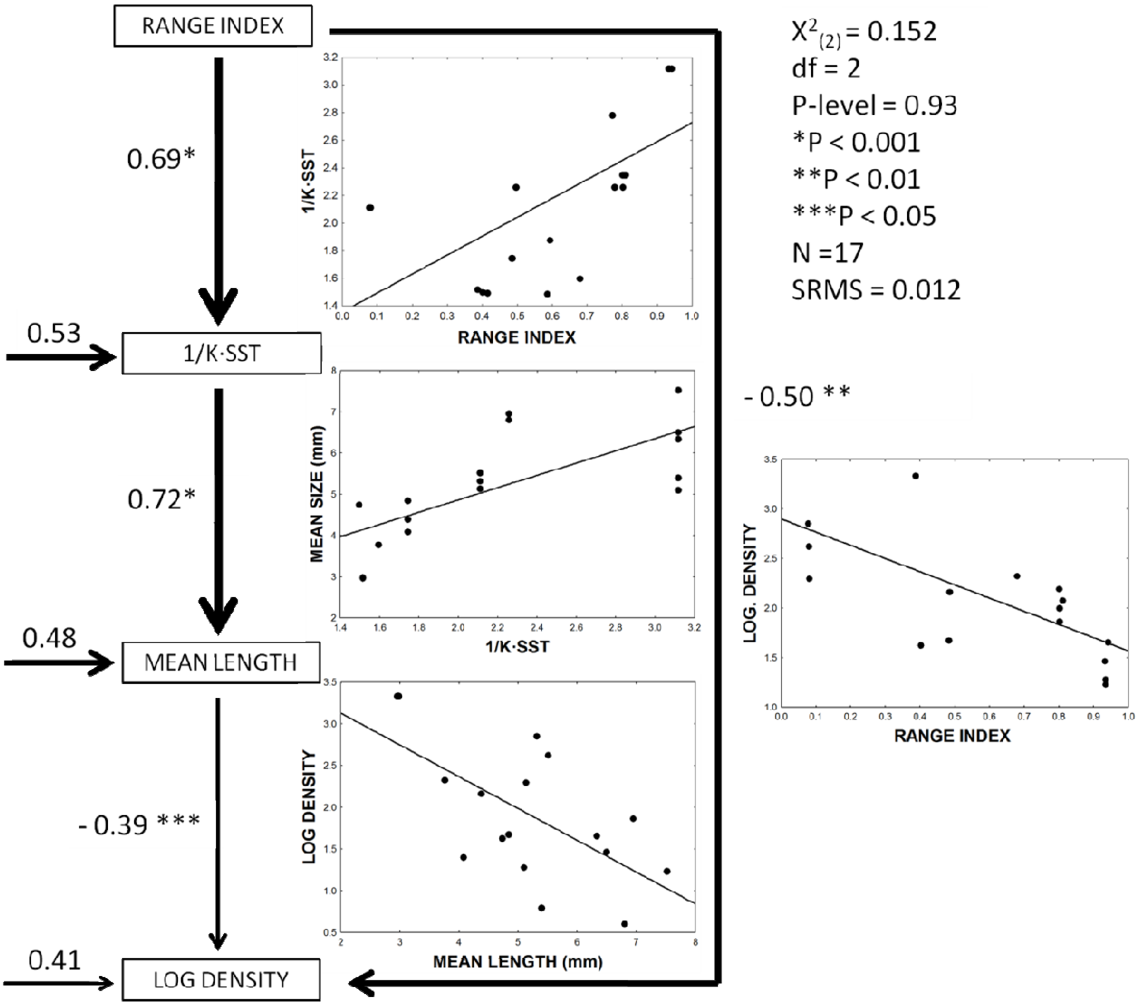

Figure 6. Causal connection among populations location within its range of occurrence (Range Index), Sea Surface Temperature (SST), body size (Mean Length) and density of the isopod *E. braziliensis*. Path values are standardized effect sizes and the arrow width is proportional to these effects. External arrows and related coefficients represent the amount of variance unexplained by the model; R^2 is determined by one minus the path coefficient. SRMS: standardized root mean square error.

Table 2. Model selection of path analysis of the evaluation of the putative role of SST (1/k·SST) in the connection among latitude (range index), body size (Mean Length) and log density of the isopod *Excirolana braziliensis*. AICc (corrected Akaike 's information criterion) and AICw (weight of evidence) are indicated.

Model	**df**	**AICc**	**AICw**
Fig. B.1	6	110.92	0.13
Fig. B.2	7	113.28	0.04
Fig. B.3	8	111.98	0.08
Fig. B.4	7	114.40	0.02
Fig. 5	**7**	**107.87**	**0.61**
Fig. B.5	8	111.85	0.08
Fig. B.6	9	116.79	0.01
Fig. B.7	7	114.40	0.01
Fig. B.8	8	117.40	0.01

4. Discussion

The isopod *E. braziliensis* followed the temperature size rule and the density-body size scaling, meaning bigger individuals with lower abundances found at low SST and high latitudes. Consequently, geographical changes were reported in life history parameters. The joint analysis of both rules revealed that SST, and consequently energetic-mediated mechanisms (Brown 2014), are main components in the causal connection between latitude, body size and density.

4.1. *TSR*

a) Latitude and SST

Tectonic configuration of America and its relationship with each oceanic gyre could explain the direct and strong relationship between latitude and SST. SST showed stable and tropical conditions between ca. 22°N in both oceans

(Mexico) to 20°S (Brazil) in the Atlantic Ocean and to 0° (Ecuador) in the Pacific Ocean. In the latter, southwards from 0°, the highest latitudinal SST change rate was registered due to the influence of the Humboldt current system. This zone resulted unusually cool for an ocean that is so close to the equator (Chaves et al. 2008). Cooling of the Atlantic Ocean occurred between 22º and 24ºS due to Southern Brazilian Bight upwelling in summer by Brazil current (Rio de Janeiro: Palma and Matano 2009), and the influence of Malvinas current southwards from 34°S (Piola et al. 2000; Ortega and Martínez 2007).

b) Body size and SST

An overall support was found for the TSR shown for mean and maximum length. The analysis deconstructed by ocean showed a higher maximum length-SST relationship for Atlantic populations, which could partially explained because clade B showed a higher slope than clades A (both oceans) and C. One explanation could be that southwards from Rio de Janeiro, *E. braziliensis* were found at intermediate and reflective beaches with coarse sediment, low local net primary production but with a safe supralittoral fringe (Martínez et al. 2017). In the Pacific Ocean, *E. braziliensis* were found at intermediate and dissipative beaches with very fine to medium size grain size (Martínez et al. 2017). These South Atlantic isopod populations showed drastic macroscale changes in life history traits, reaching the highest maximum lengths (11.0 and 12.5 mm) in this ocean where the effects of TSR could be enhanced by the abrupt change of local habitat. Bigger legs for a sensitive burrower isopod like *E. braziliensis* will foster a better burrow performance despite the coarse grain sizes of reflective beaches (Yannicelli et al. 2002). Another explanation could be that maximum length differences are located between 0° and 20°S where SST in the Atlantic Ocean is quite higher than those registered in the Pacific Ocean. In this latitudinal range, the Pacific Ocean showed the highest SD (SST) within isopod distribution where populations could experienced SST ranges close to 10°C. These differences between oceans can be explained due to the opposite oceanic gyres on both sides of the continent. This could be conditioning the maximum length of this isopod, probably related to anomalies in SST and also to the occurrence of ENSO (El Niño Southern Oscillation) events (see Fig. 2b;

Montesinos et al., 2003). These combined patterns could be also affecting the maximum body sizes of populations in the Pacific Ocean and partially explained differences between oceans.

c) Life history and SST

Life history parameters showed latitudinal gradients and strong relationships with SST throughout its distribution range. Except for maximum fecundity, these relationships followed a nonlinear trend with latitude similar to the trend reported for SST. Cirolanid isopods at high latitudes and low SST showed lower growth acceleration (K) and higher size at maturity, lifespan and maximum fecundity, as also shown by Cardoso and Defeo (2003, 2004). Thus, isopods at higher latitudes delay maturity, and allocate more resources to somatic growth. In this sense, higher body sizes for *E. braziliensis* had higher fecundity, through higher number and egg sizes at lower SST (Martínez and Defeo 2006). This covariation with body storage could be explained by the influence of maternal effects reflected in its body reserves (Glazier 2000). Moreover, bigger females with bigger brood-pouches, have more flexibility to increase brood size without decreasing egg size, and also present great efficiency in the packaging of bigger eggs (Glazier 2000b). *E. braziliensis* constitutes a semelparous and ovoviparous species with internal brooding (e.g. maternal care) (Klapow 1970, Martínez and Defeo 2006). This life history strategy probably represent a main determinant of the temperature-size relationship (Anguilletta et al. 2004 a), and of the density-body scaling for this isopod.

d) TSR and clades

E. braziliensis could be a close group of morphologically-related species (Hurtado et al. 2016) distributed over a wide latitudinal range in both oceans (Martínez et al. 2017). The independent evolution of these clades combined with phenotypic plasticity, could be simultaneously shaping the geographic trend in body size, population dynamics and abundance. Notably, in spite of the different evolutionary histories and variation in local conditions and interactions, both the density-body size scaling and the body size-temperature relationships were not related with clades or oceans. This consistency supports the view that the general mechanisms that operate at the population level are strong enough to be observed equally in different ecological and evolutionary scenarios.

4.2. Integrated rule analysis and environment

The individual and joint analysis (path analysis) of both ecogeographical rules revealed that SST was the main driver of the causal connection between latitude, body size and density. Despite the strong and direct effect of latitude on density, latent environmental variables (oceanographic variables, local habitat) showed very low causal link connection with density. This could be explained because primary production, salinity, tidal range and sand grain size, did not follow clear gradients with latitude. Moreover, high densities of *E. braziliensis* could result from a combination of local and regional physical variables (e.g. fine grain size, high primary production and SST: Martínez et al. 2017) not directly related to the geographical position. The strong and direct effect of latitude on density revealed that other factors not taken into account in the analysis like biological interactions (e.g. predation, interspecific competition), probably linked with latitude (e.g. Barnes 2002, Freestone et al. 2011) could play a role in shaping large-scale density patterns.

5. Conclusion

The temperature-size rule and the density-body size scaling hold for the isopod *E. braziliensis*. SST was the main driver of the causal connection between latitude, body size and density and explained geographical changes in life history parameters. Towards colder and temperate sandy beaches of both oceans, *E. braziliensis* had lower densities, larger sizes and higher growth acceleration, size at maturity, lifespan and fecundity. The great geographical adjustment of fecundity, jointly with parental care (internal brooding) could explain its high adaptation capability to environmental variations across its geographical range in both oceans. These responses are mostly driven by selection pressures towards very similar morphological forms, regardless of the reproductive isolation between them

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Appendix A. Bibliography where information of the isopod *Excirolana braziliensis* was taken. Latitude is in decimals.

Beach	**Country**	**Ocean**	**Latitude**	**Source**
Progreso	Mexico	Atlantic	21,27	11
Salina Cruz	Mexico	Pacific	16,17	15, 20
La Mancha	Mexico	Atlantic	19,60	11
Playa Cocal	Costa Rica	Pacific	9,43	14, 20
Airport Beach	Costa Rica	Atlantic	9,97	14
Las Lajas	Panama	Pacific	8,17	20
Naos island	Panama	Pacific	8,92	16, 32
Culebra island	Panama	Pacific	8,92	13, 17
Buenos Aires	Peru	Pacific	-8,15	2, 3
Las Delicias	Peru	Pacific	-8,18	2, 3
Huanchaquito	Peru	Pacific	-8,10	2, 3
Salaverry	Peru	Pacific	-8,23	2, 3
Cavancha	Chile	Pacific	-20,23	1
Playa Brava	Chile	Pacific	-20,23	1
Huayquique	Chile	Pacific	-20,28	1
Chauca	Chile	Pacific	-20,82	1
Chomache	Chile	Pacific	-21,07	1
Ike Ike	Chile	Pacific	-21,13	1
Boca del Diablo	Chile	Pacific	21,18	1
Playa Larga	Chile	Pacific	-21,32	1
Caleta Errázuriz	Chile	Pacific	-23,45	10, 33
El Apolillado	Chile	Pacific	-29,17	7,8
San Carlos	Chile	Pacific	-33,50	4
Mehuin	Chile	Pacific	-39,43	9, 22, 24
Matías	Chile	Pacific	-39,45	25
Curiñanco	Chile	Pacific	-39,73	25

Ronca	Chile	Pacific	-39,38	25
Calfuco	Chile	Pacific	-39,78	9
Fora	Brazil	Atlantic	-22,95	6
Bonita	Brazil	Atlantic	-22,98	6
Reserva	Brazil	Atlantic	-23,00	31
Sul	Brazil	Atlantic	-23,00	6
Grumari	Brasil	Atlantic	-23,05	5
Restinga da Marambaia	Brasil	Atlantic	-23,05	5
Prainha	Brazil	Atlantic	-23,08	19, 28
Barra da Tijuca	Brasil	Atlantic	-23,17	29, 30
Taquaras	Brasil	Atlantic	-26,98	8, 18
Barra del Chuy	Uruguay	Atlantic	-33,75	27
Pta diablo	Uruguay	Atlantic	-34,00	27
La Pedrera	Uruguay	Atlantic	-34,53	27
Santa Isabel	Uruguay	Atlantic	-34,57	27
Arachania	Uruguay	Atlantic	-34,60	27
Jignacio	Uruguay	Atlantic	-34,60	27
Santa Mónica	Uruguay	Atlantic	-34,85	27
Punta Negra	Uruguay	Atlantic	-34,90	27

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APPENDIX B

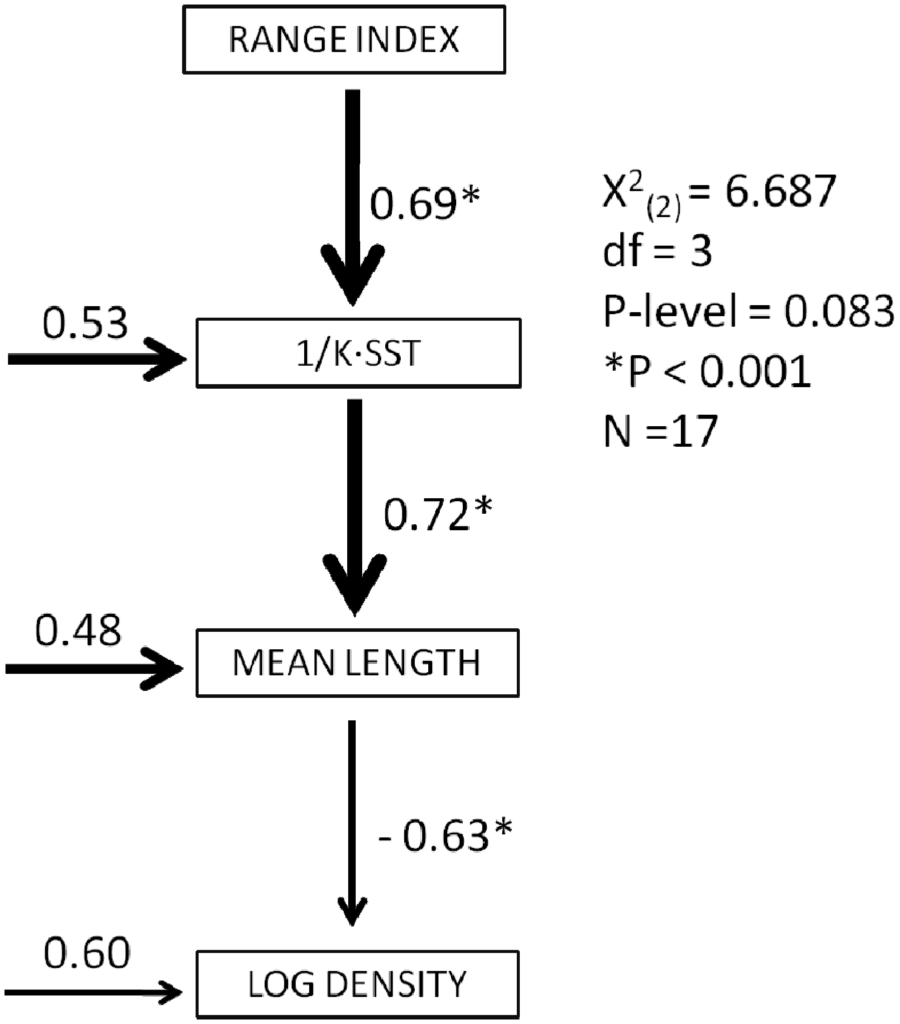

Figure B.1. Evaluation of the putative role of SST (1/k·SST) in the connection among latitude (range Index), body size (Mean Length) and log density of the isopod *Excirolana braziliensis*. Path values are standardized effects, with 0 meaning no causal link and 1 a complete causal link and a value of 0 mean no causal link. Arrow width represents the strength of the causal link. External arrows represent variances unexplained by the model, and the explained variance for endogenous variables, R^2 is represented by one minus the path coefficient.

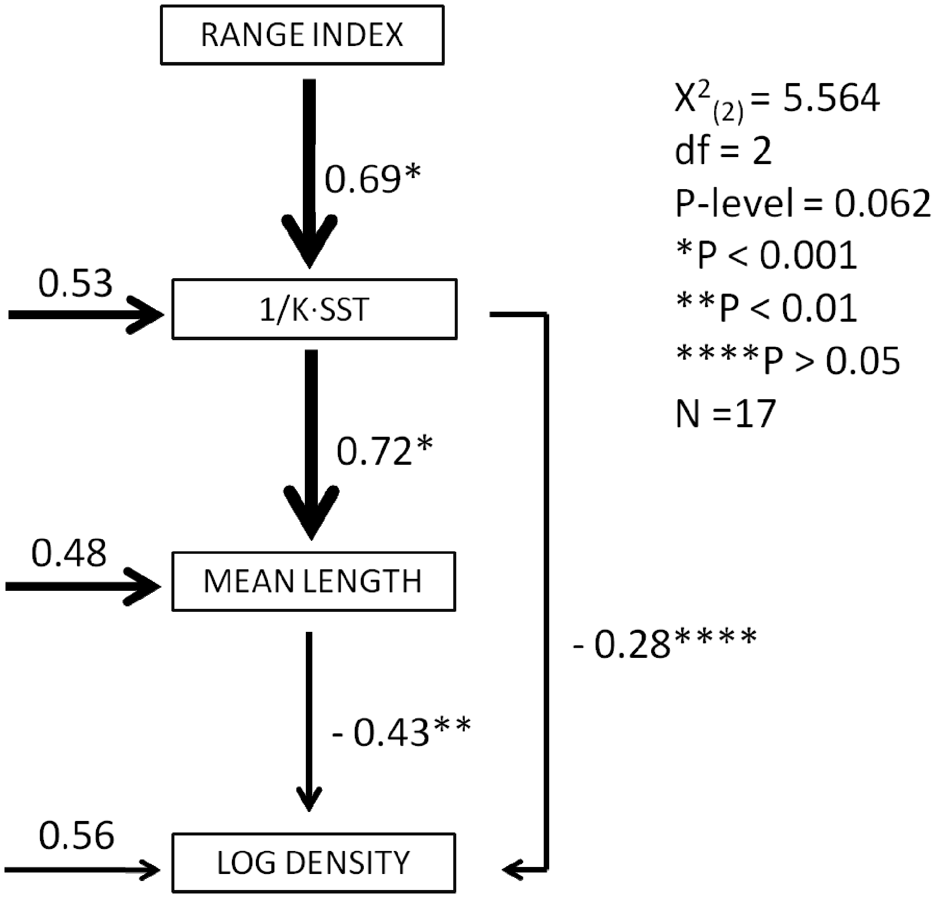

Figure B.2. Evaluation of the putative role of SST (1/k·SST) in the connection among latitude (range Index), body size (Mean Length) and log density of the isopod *Excirolana braziliensis*. For further references see Fig. A.1.

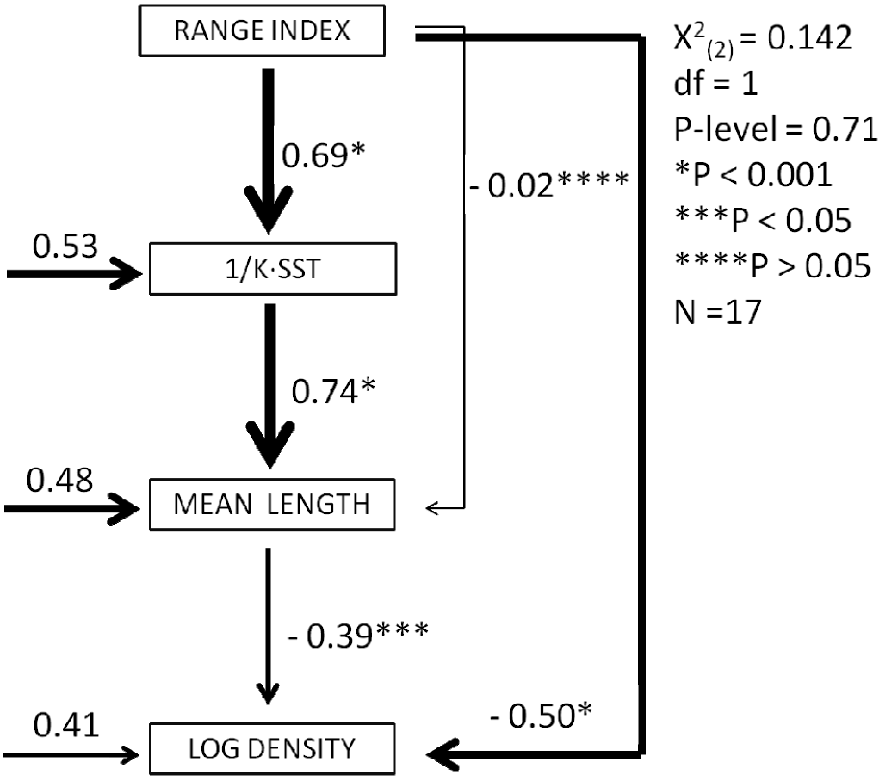

Figure B.3. Evaluation of the putative role of SST (1/k·SST) in the connection among latitude (range Index), body size (Mean Length) and log density of the isopod *Excirolana braziliensis*. For further references see Fig. A.1.

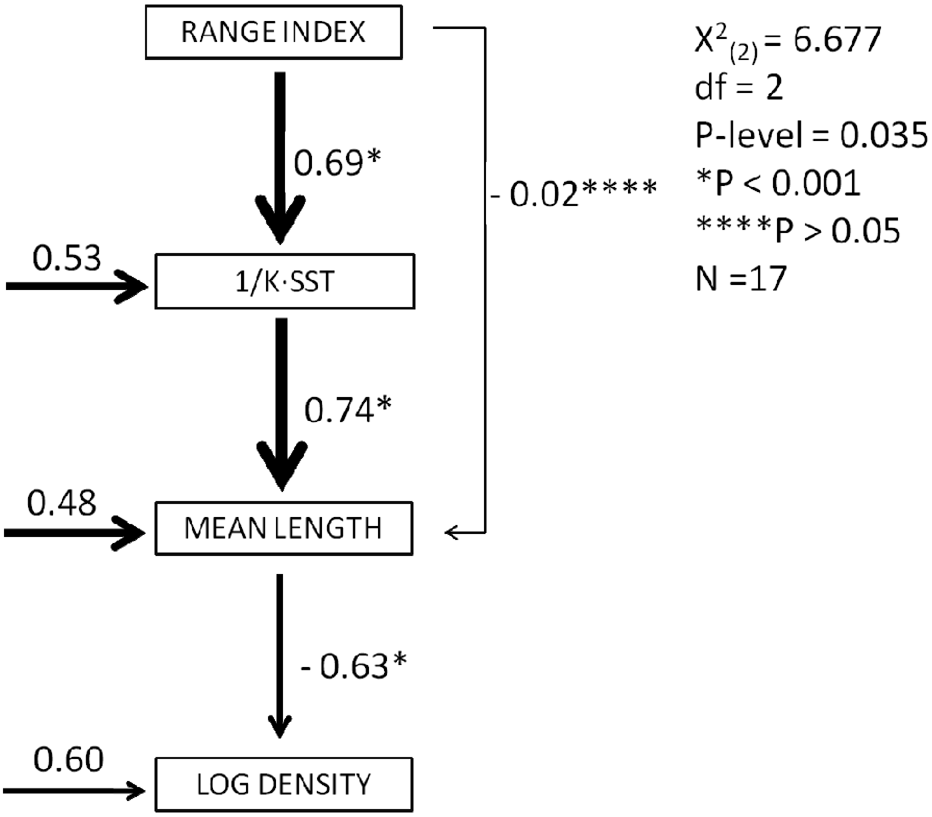

Figure B.4. Evaluation of the putative role of SST (1/k·SST) in the connection among latitude (range Index), body size (Mean Length) and log density of the isopod *Excirolana braziliensis*. For further references see Fig. A.1.

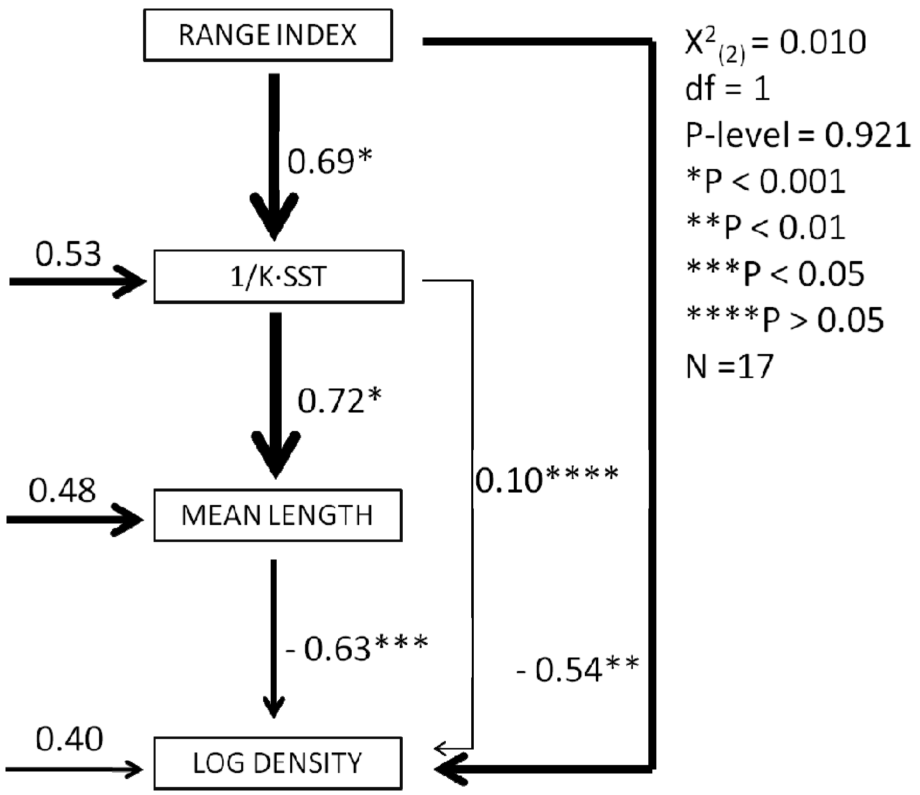

Figure B.5. Evaluation of the putative role of SST (1/k·SST) in the connection among latitude (range Index), body size (Mean Length) and log density of the isopod *Excirolana braziliensis*. For further references see Fig. A.1.

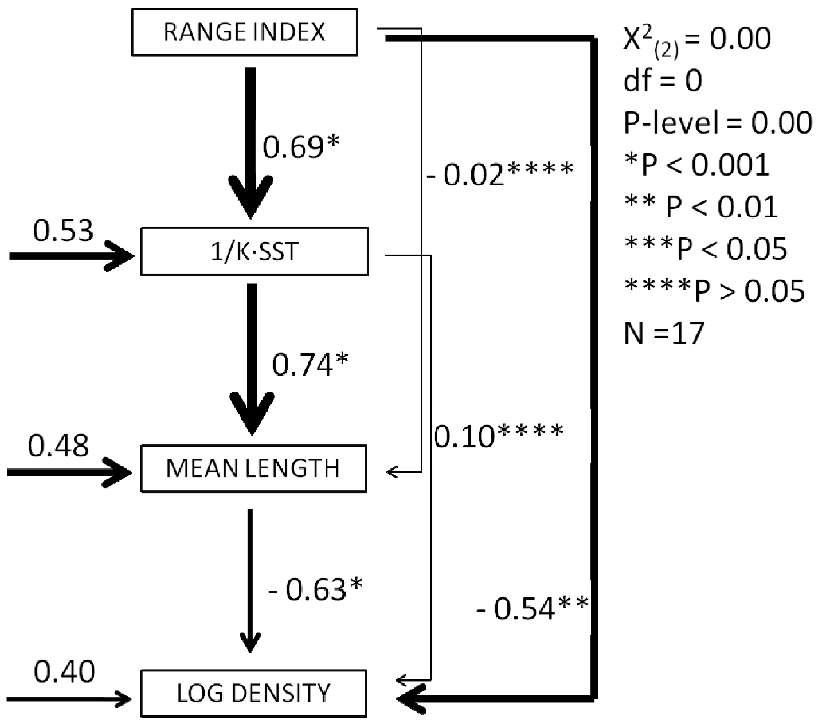

Figure B.6. Evaluation of the putative role of SST (1/k·SST) in the connection among latitude (range Index), body size (Mean Length) and log density of the isopod *Excirolana braziliensis*. For further references see Fig. A.1.

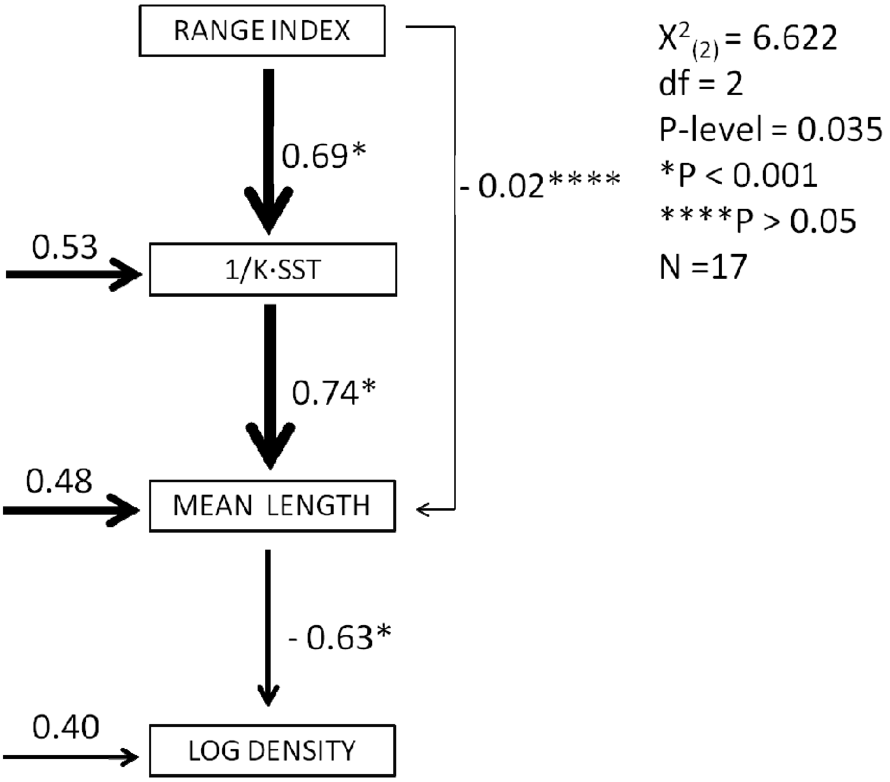

Figure B.7. Evaluation of the putative role of SST (1/k·SST) in the connection among latitude (range Index), body size (Mean Length) and log density of the isopod *Excirolana braziliensis*. For further references see Fig. A.1.

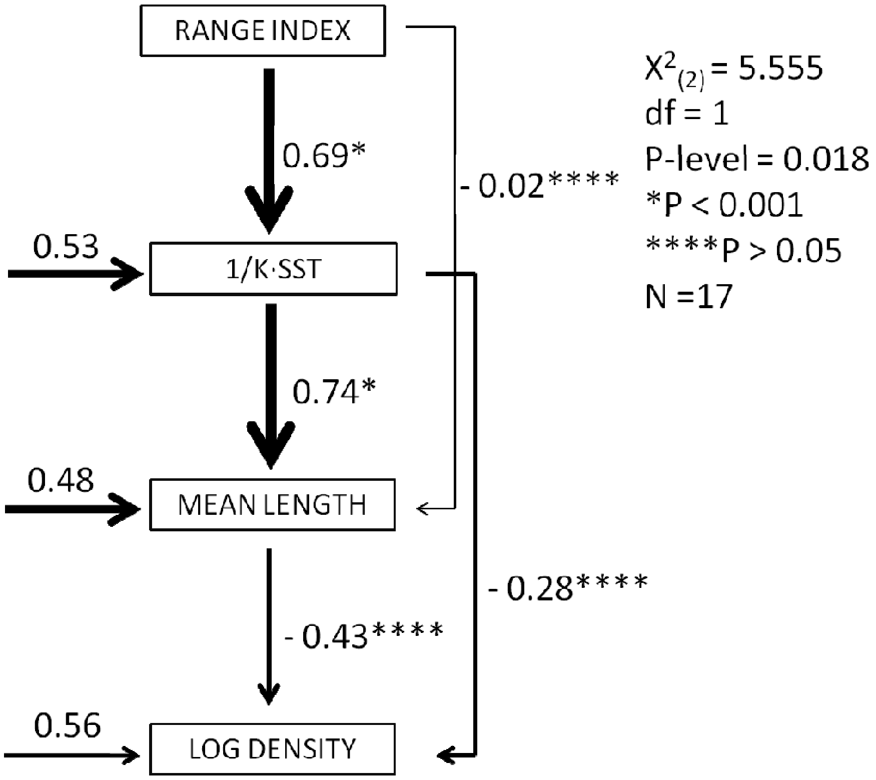

Figure B.8. Evaluation of the putative role of SST (1/k·SST) in the connection among latitude (range Index), body size (Mean Length) and log density of the isopod *Excirolana braziliensis*. For further references see Fig. B.1.

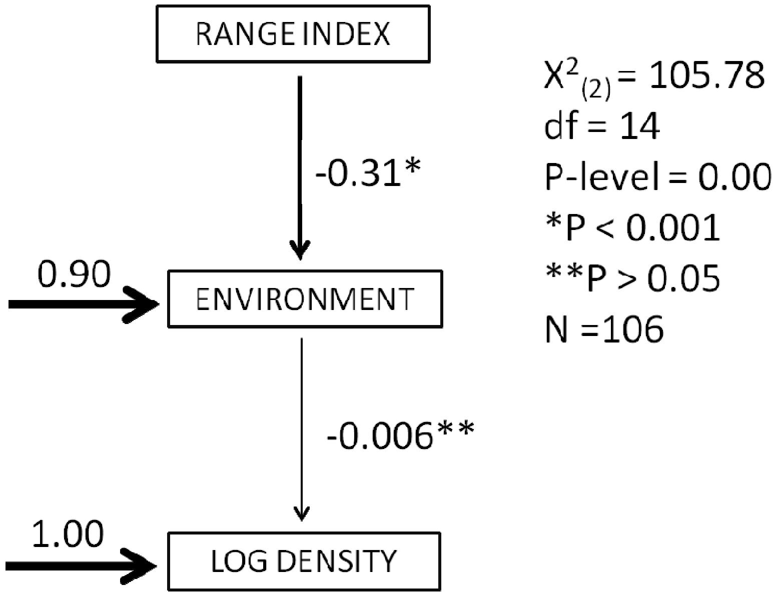

Figure B.9. Evaluation of the putative role of Environment (Oceanographic variables and physical habitat) in the connection among latitude (range Index) and log density. Path values are standardized effects, with 0 meaning no causal link and 1 a complete causal link and a value of 0 mean no causal link. Arrow width represents the strength of the causal link. External arrows represent variances unexplained by the model, and the explained variance for endogenous variables, R^2 is represented by one minus the path coefficient.

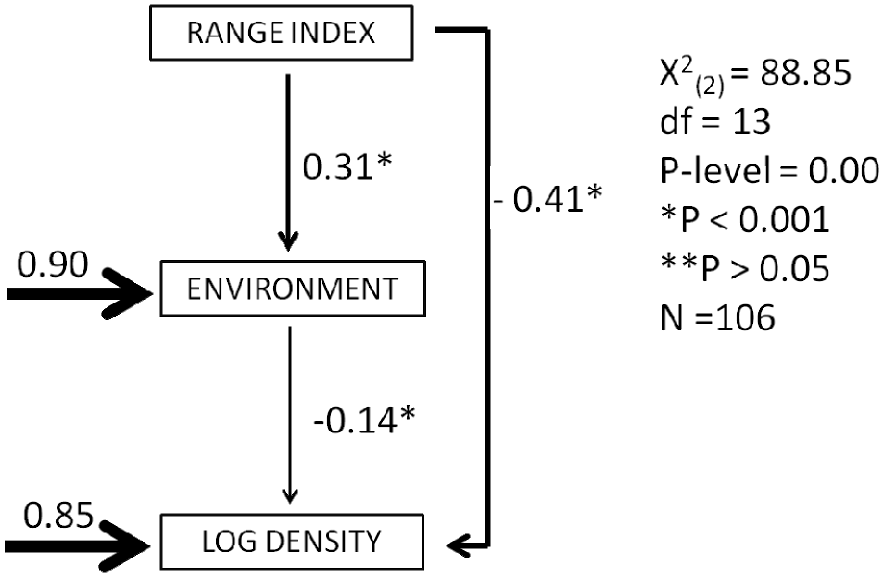

Figure B.10. Evaluation of the putative role of Environment (Oceanographic variables and physical habitat) in the connection among latitude (range Index) and log density. For further references see Fig. B.9.

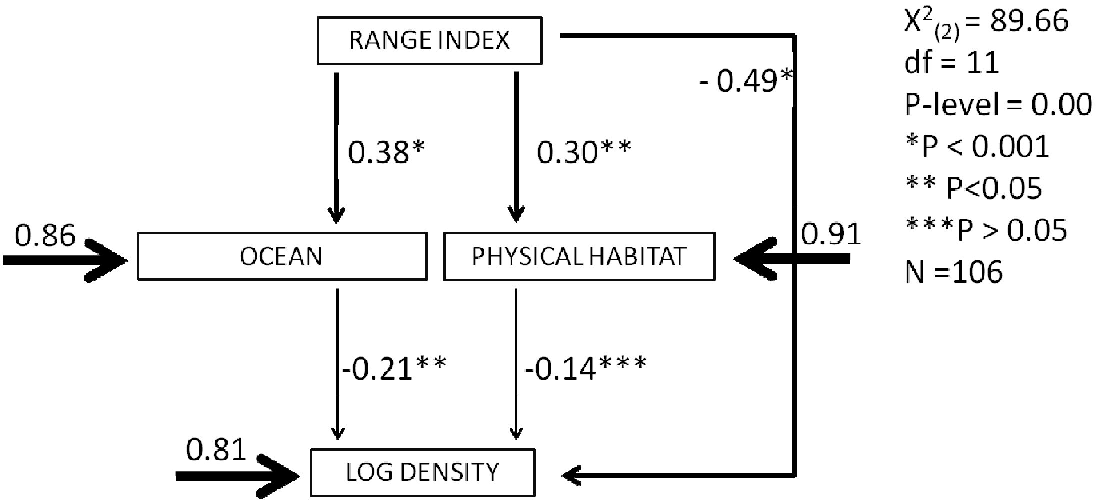

Figure B.11. Evaluation of the putative role of oceanographic (OCEAN) variables and physical habitat in the connection among latitude (range Index) and log density. Path values are standardized effects, with 0 meaning no causal link and 1 a complete causal link and a value of 0 mean no causal link. Arrow width represents the strength of the causal link. External arrows represent variances unexplained by the model, and the explained variance for endogenous variables, R^2 is represented by one minus the path coefficient.

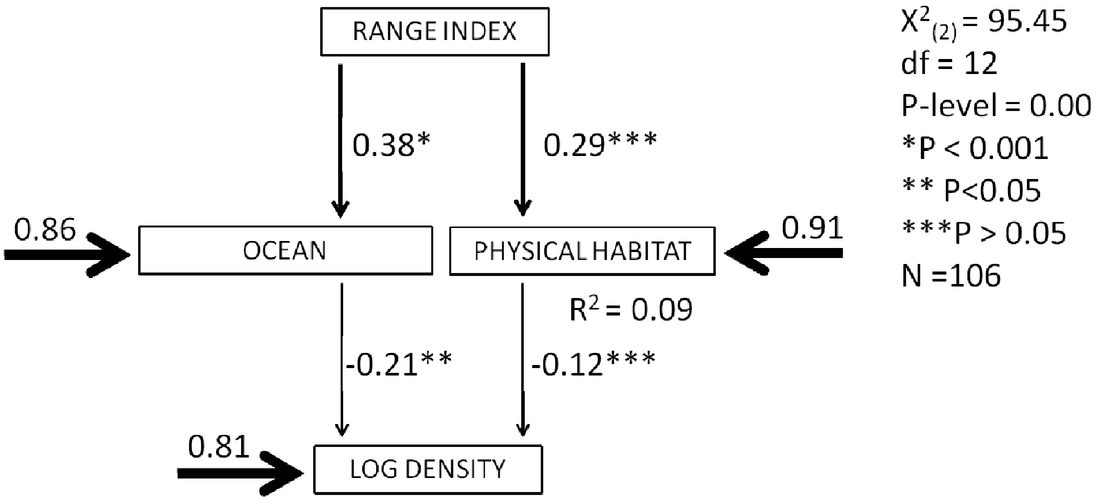

Figure B.12. Evaluation of the putative role of oceanographic variables (OCEAN) and physical habitat in the connection among latitude (range Index) and log density. For further references see Fig. B.11.

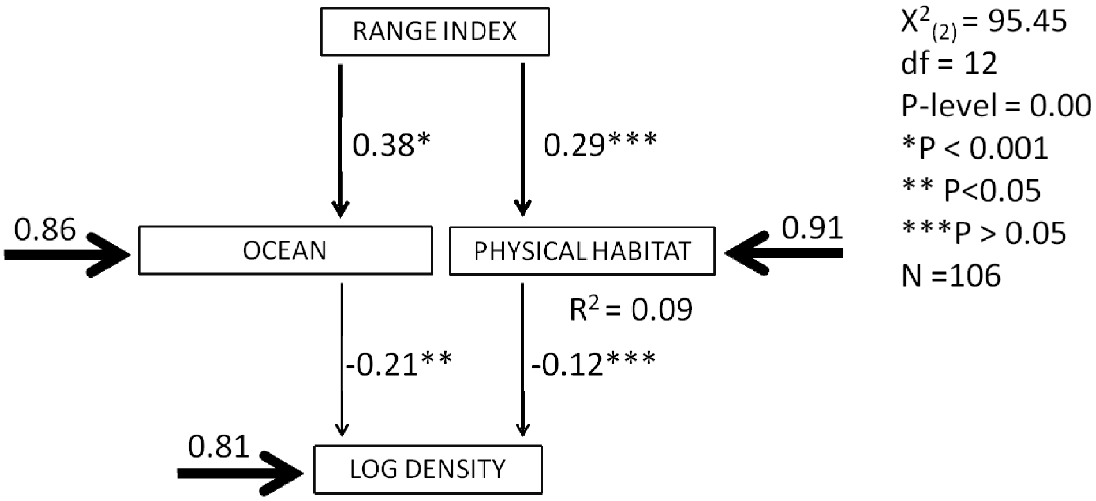

Figure B.11. Evaluation of the putative role of oceanographic variables (OCEAN) and physical habitat in the connection among latitude (range Index) and log density. For further references see Fig. B.10.

4. DISCUSIÓN GENERAL Y CONCLUSIONES

En la tesis se evaluaron tres reglas ecogeográficas: la regla de abundancia central (ACH) (Capítulo 2), la relación temperatura-tamaño corporal (TSR) y el escalamiento densidad-tamaño corporal (Capítulo 3), y varias hipótesis auxiliares para el isópodo *E. braziliensis.* Los resultados mostraron que el gradiente geográfico (e.g. latitud), el tamaño corporal, y la abundancia y sus patrones de distribución geográfica pueden conformar un triángulo de inter-relaciones (Fig. 4.1). En este sentido, los patrones geográficos de la abundancia de *E. braziliensis* estarían determinados por: 1) los centros de nicho ambiental y gradientes morfodinámicos locales; y 2) la tasa metabólica debido a su dependencia térmica y su efecto en la demanda de recursos, conectando las reglas temperatura-tamaño corporal (TSR) y el escalamiento densidad-tamaño corporal.

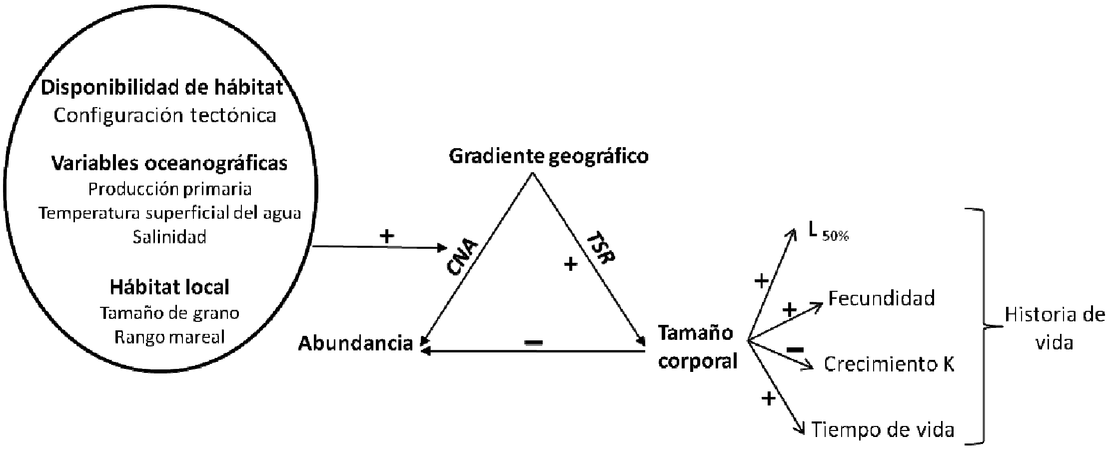

Figura 4.1. Diagrama esquemático que muestra las relaciones entre la regla de temperatura-tamaño corporal (TSR) y los parámetros de historia de vida, el escalamiento densidad-tamaño corporal, y el rol de los centros de nicho ambiental (CNA) en la abundancia de *E. braziliensis*. Esta figura no pretende abarcar toda la complejidad de los patrones de la abundancia de esta especie sino esquematizar las diferentes interconexiones abordadas en la tesis y sus resultados.

4.1 Rol de los centros de nicho ambiental y los gradientes morfodinámicos

Los patrones de abundancia de *E. braziliensis* mostraron tendencias opuestas entre océanos. Las desviaciones o la congruencia con las expectativas de la ACH son no obstante esperados en base a las hipótesis auxiliares: la disponibilidad de hábitat (playas arenosas), la adecuación de hábitat (sensu Capítulo 2) o variables oceanográficas (sensu Capítulo 3), y las características del hábitat físico. Dichos patrones determinarían la presencia de uno o varios centros de nicho ambiental a lo largo de su distribución geográfica (Capítulo 2) (Fig. 4.1). Dichos centros están determinados por: 1) la disponibilidad de hábitat (playas arenosas) operando a una escala de paisaje y dada por la configuración tectónica continental y los giros oceánicos; 2) variables oceanográficas (producción primaria, la temperatura superficial del agua y la salinidad) ;y 3) el tamaño de grano y rango mareal, que conforman dos de las variables más importantes para describir las características del hábitat específico de este isópodo: las playas arenosas (Capítulo 2, Fig. 4.1). Las probabilidades de ocurrencia y las abundancias más altas, que se registraron en zonas de surgencias costeras, con alta temperatura del agua y en playas disipativas (granos finos, baja pendiente y alta producción primaria local), indican que los efectos combinados de las condiciones regionales y locales son más determinantes que la ubicación geográfica.

Brown (1984) postuló que las mayores abundancias de una especie y/o para especies ecológicamente similares, están relacionadas a un centro geográfico y ecológico, disminuyendo hacia los extremos de su rango de distribución geográfico, conformando una distribución gaussiana (ACHg). A tales efectos, asume una autocorrelación espacial de los requerimientos ecológicos de la especie (nicho multidimensional, Hutchinson 1957). Los mecanismos que se invocaron para esta hipótesis incluyen la tolerancia fisiológica (Brown 1984), la dinámica fuente-sumidero de las poblaciones (Pulliam 1988), los compromisos en varios componentes de la aptitud física a lo largo de un único gradiente ambiental (McGill 2003), y agregación o multiplicación hacia el centro geográfico de las respuestas fisiológicas de muchas dimensiones del nicho hutchinsoniano (Brown et al. 1995). Con base en los 4 mecanismos mencionados, McGill y Collins (2003) proponen que la abundancia sigue un patrón de pico y cola con varios picos de muy alta abundancia, que caen rápida y suavemente a una larga cola de abundancia de uno a dos órdenes de magnitud más baja que los picos. Estudios más recientes en ambientes terrestres (Yañez-Arenas et al. 2012) y Martínez-Meyer et al. (2013) proponen una hipótesis de abundancia central (ACHe) pero donde los patrones geográficos de abundancia de las especies están determinados por las condiciones ecológicas (teoría de nicho) de los sitios de ocurrencia y no por su posición geográfica. En este sentido, las mayores abundancias se registrarían en las poblaciones más cercanas al centroide del nicho y disminuirían monótonicamente hacia los bordes del hipervolumen.

Los resultados de esta tesis indicarían que la presencia de los centros de nicho ambiental junto a los gradientes morfodinámicos locales a lo largo de la distribución geográfica conformarían los patrones geográficos de la abundancia de *E. braziliensis.* Ambos factores podrían generar los diferentes patrones de abundancia (normales, rampas, de bordes), incluyendo la ausencia de patrón en playas arenosas. La presencia de centros de nicho ambiental explicaría las máximas abundancias de este isópodo en ambos océanos. En este sentido, estos centros pueden ser más relevantes para la biología de la población de las especies que las distancias desde el centro o centroide del rango geográfico. Dichos centros están muy vinculados a zonas de alta producción primaria, la cual representó casi el 75% en la modelación predictiva de distribución de *E. braziliensis* en ambos océanos. Asimismo, en las zonas de surgencia o de descargas de agua dulce se registraron las mayores abundancias de esta especie y determinaron los patrones geográficos de la misma (Capitulo 2: Figuras 1 y S1). De los trabajos que analizan patrones geográficos de abundancia en ambientes costeros, incluyendo 25 poblaciones de invertebrados marinos (e.g. Sagarin y Gaines 2002, Rivadeneira et al. 2010, Fenberg y Rivadeneira 2011, Tam y Scrosati 2011, Baldanzi et al. 2013, Fenberg et al. 2014), 23 presentan las abundancias más altas en zonas de alta producción primaria, generadas principalmente por surgencias costeras o por la combinación con descargas de agua dulce (Townsend 1991, Bustamante et al. 1995, Dugdale et al. 1997, Figueroa y Moffat 2000, Zaytsev et al. 2003, Whitney et al. 2005). Estas surgencias costeras o afloramientos localizados se generarían: 1) a partir del desplazamiento de aguas costeras más cálidas fuera de plataforma y la entrada de agua más fría y con mayor cantidad de nutrientes por vientos paralelos o perpendiculares a la costa (Bakun 1990); o 2) por el efecto conjunto del relieve del fondo y la curvatura de la línea de costa (Brink 1983) (e.g. puntas rocosas, Cabo Frío, Rio de Janeiro).

La temperatura superficial del agua es importante para los centros de nicho ambiental. En este sentido, esta variable le siguió en importancia a la producción primaria en la modelación predictiva de distribución de *E. braziliensis* en ambos océanos (Capítulo 2: Fig. S1), dado por el gradiente geográfico norte-sur, y por el efecto que éste tiene en la producción primaria, ya que la tasa máxima local de producción primaria es mayor en zonas de aguas más cálidas (Moore y Abbott 2000). El rol del hábitat local y la presencia de playas disipativas (e.g. grano fino) en los centros de nicho ambiental son esenciales para la existencia de altas abundancias de especies en playas arenosas. Los gradientes morfodinámicos locales que se conforman a lo largo de la distribución geográfica de *E. braziliensis* son responsables de los rangos de abundancia en similar latitud o posición geográfica (por ejemplo, Defeo y Martínez 2003, Caetano et al. 2006). Este gradiente generaría condiciones ambientales óptimas y subóptimas para este isópodo y terminaría de configurar los patrones de abundancia a lo largo de su rango geográfico. El gradiente morfodinámico en playas arenosas es similar al papel de la exposición a las olas (protegidas y expuestas) en las poblaciones de costas rocosas (ver Bertness et al. 2006, Blamey y Branch 2009, Tam y Scrosatti, 2011; 2014).

Los límites de rango geográfico en ambos océanos para *E. braziliensis* fueron congruentes con los límites de las provincias biogeográficas debido a los efectos combinados de la disponibilidad del hábitat, las corrientes de superficie por flujo de una vía o por convergencia que afectarían la capacidad de dispersión, y las restricciones fisiológicas definidas por la temperatura superficial del agua que determinarían la viabilidad poblacional a partir de cierta posición geográfica. La disponibilidad del hábitat constituye un factor clave para determinar patrones geográficos y límites de especies del intermareal rocoso del Océano Pacífico en America (Fenberg y Rivadeneira 2011, 2019, Fenberg et al. 2014).

4.2 TSR, escalamiento tamaño corporal-densidad e historia de vida

El isópodo *E. braziliensis* siguió la relación temperatura-tamaño corporal (TSR) y también su hipótesis auxiliar, la relación entre la temperatura y los parámetros de historia de vida (ver Fig 4.1). El análisis individual del escalamiento densidad-tamaño corporal mostró que *E. braziliensis* no presentaría diferencias sistemáticas en el uso de energía entre clases de tamaño corporal. Esto sugiere que el aumento en demanda energética a mayores tamaños es compensado con una reducción en la densidad de individuos. El análisis en conjunto de la relación temperatura-tamaño corporal (TSR) y el escalamiento densidad-tamaño corporal identificó a la temperatura superficial del agua como un potencial origen causal de la conexión entre la latitud o "gradiente geográfico" (sensu Hawkins y Diniz-Filho 2004), el tamaño del cuerpo y la densidad (como estimador de abundancia) (Capítulo 3). Los resultados de estas inter-relaciones implican encontrar un mayor tamaño corporal en latitudes altas, con menor temperatura superficial del agua y abundancia de isópodos. Como consecuencia se reportaron cambios latitudinales significativos en los parámetros de historia de vida *E. braziliensis*, encontrándose mayores tasas de crecimiento, menor talla de madurez sexual, longevidad y fecundidad en latitudes bajas (Capítulo 3) (ver Fig. 4.1). En particular, el ajuste geográfico de la fecundidad, conjuntamente con el cuidado parental interno (ovoviviparidad) podrían explicar su alta capacidad de adaptación a las variaciones ambientales a lo largo de su rango geográfico en ambos océanos. Estas respuestas son impulsadas principalmente por presiones de selección hacia formas morfológicas muy similares, independientemente del aislamiento reproductivo entre ellas.

Existen ocho especies del género *Excirolana* desde Canadá hasta el sur de Chile y Argentina. Entre ellos, *E. braziliensis* tiene el rango geográfico más amplio con una gran adaptación a diferentes tipos de playas: expuestas a protegidas y de macro a micromareales (Capítulo 2). Esta especie sobrevive en playas arenosas de zonas muy urbanizadas, de gran uso turístico y contaminadas con hidrocarburos (Betz et al. 1982, Gomez-Veloso et al. 2011, Vieira et al. 2012). Además, puede recuperarse rápidamente de impactos naturales como los tsunamis mediante la rápida colonización desde poblaciones cercanas (Jaramillo et al. 2012). *E. braziliensis* es un consumidor primario que puede ocupar la zona supralitoral de las playas arenosas, constituyendo la especie congenérica que se encuentra más alejada de la zona de inundación (Capítulo 2). Definitivamente, esta especie o el complejo de especies con similitud morfológica, mostró una serie de atributos ecológicos que explican su viabilidad en un hábitat estresante como las playas de arena, alcanzando una distribución muy amplia en el continente para una especie con desarrollo directo. En este sentido, deben completarse los estudios filogeográficos para esta especie y realizar una revisión taxonómica del género *Excirolana* (ver Hurtado et al. 2016, Capítulo 2). Además, estos estudios deberían complementarse con más información ecológica teniendo en cuenta su gran distribución geográfica, a efectos de comprender cómo *E. braziliensis* está respondiendo tanto a la variabilidad como al cambio climático. Esto es importante pues las playas de arena constituyen uno de los principales ecotonos entre los ecosistemas terrestres y acuáticos, y la zona supralitoral donde este isópodo habita constituye la última frontera entre estos dos grandes dominios.

4.3. Conclusiones

Los centros de nicho ambiental (alta producción primaria y temperatura superficial del agua, y playas disipativas) serían los responsables de las máximas abundancias a lo largo del rango geográfico. Dichos centros, conjuntamente con los gradientes morfodinámicos locales que generan condiciones ambientales óptimas y subóptimas para este isópodo a lo largo de su distribución geográfica, conforman los patrones geográficos de la abundancia de *E. braziliensis.*

El análisis individual del escalamiento densidad-tamaño corporal sugiere que el aumento en la demanda de recursos con el escalamiento de la tasa metabólica-tamaño corporal determina un aumento en la competencia que limitaría la abundancia de las poblaciones de *E. braziliensis.*

Las relaciones temperatura-tamaño corporal (TSR) y densidad-tamaño corporal identifican a la temperatura superficial del agua como el principal impulsor de la conexión causal entre la latitud o "gradiente geográfico", el tamaño corporal y la abundancia de *E. braziliensis*. En latitudes altas, donde la temperatura superficial del agua es menor, las poblaciones de este isópodo presentaron mayor tamaño corporal y fueron menos abundantes. Como consecuencia se reportaron cambios latitudinales significativos en los parámetros de historia de vida de este isópodo, encontrándose, menores tasas de crecimiento y mayores tallas de madurez sexual, longevidad y fecundidad en latitudes altas.

El análisis de las 3 reglas ecogeográficas y sus hipótesis auxiliares resultaron fundamentales para la comprensión de los patrones de abundancia de este isópodo, así como para entender las causas de su amplia distribución geográfica en ambos océanos de América.

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