UNIVERSITAT DE BARCELONA

Population structure and spatio-temporal modelling of biological attributes and population dynamic of nylon shrimp (*Heterocarpus reedi*) off central Chile (25°-36°S)

Estructura poblacional y modelamiento espacio-temporal de los atributos biológicos y la dinámica poblacional del camarón nailon *Heterocarpus reedi* (Decapoda, Caridea) frente a Chile central (25°-36°S)

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……A mi amada esposa Isabel y mis adorados hijos: Joaquin, Bruno y Lucas.

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Al término de este proceso durante el cual aprendí mucho más allá de mis expectativas y viví experiencias enriquecedoras, quisiera agradecer en primer lugar la amistad y apoyo del Director de esta tesis Dr. Joan B. Company, quien me invitó a realizar investigación más allá de los límites a los cuales estaba acostumbrado y cuyos resultados me llenan de satisfacción. De igual forma, todo mi agradecimiento a mi Tutor profesor Dr. Miquel Canals, quien confió desde el primer momento en este proyecto no obstante la distancia y de quien siempre recibí palabras de aliento y amabilidad.

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Resum

L'estructura poblacional dels recursos pesquers i l'impacte dels factors ambientals sobre la productivitat són processos importants a tenir en compte per a la gestió de les seves pesqueries. Els factors ambientals poden determinar l'èxit de la deriva larvària, l'estructura espacial de la població, així com les variacions de la biomassa. Tenint en compte aquests aspectes, s'haurien de considerar dos elements clau per a una explotació adequada i sostinguda de qualsevol pesqueria: les característiques biològiques de les espècies i com aquestes poden variar en el temps i en l'espai, essent necessària la millora de la comprensió d'aquests efectes, com varien, i com es relacionen amb els factors ambientals. No obstant això, els processos espacials rarament són considerats explícitament en la valoració i gestió de les poblacions d'invertebrats marins, més quan aquests aspectes són particularment importants en els processos de deriva larval actuant de principal mecanisme d'expansió d'una població. El concepte ecològic de metapopulations és àmpliament utilitzat i acceptat per a la comprensió de les poblacions marines de baixa mobilitat, i les seves implicacions haurien de ser considerades a la gestió pesquera.

En aquest treball es demostra l'efecte del medi en la distribució, abundància i estructura espacial de la població de la espècie de crustaci decàpode *Heterocarpus reedi* anomenada a Xile en castellà com a "Camarón nailon". S'ha mostrejat aquesta espècie a a la zona central de Xile (25 ° - 37 ° S) a partir de la informació obtinguda en campanyes oceanogràfiques de pesca d'arrossegament fets entre els anys 1996 i el 2011, així com de les característiques de l'aigua superficial (concentració de clorofil·la α i de la matèria orgànica dissolta). Els resultats van mostrar una separació geogràfica de la població a 32 ° S, on la densitat de gambes és més gran, així com també la concentració de clorofil·la α i la dissolució

de matèria orgànica, això darrer degut segurament a la presència d'afluents dels rius i zones d'aflorament costaner. En aquesta zona es concentra la major part de la població adulta i podria actuar com a població “font” i la seva influència en la deriva larvària explicaria tant la preponderància de juvenils en la zona nord així com una població menys abundant (població “pseudo-sumider”). A la zona sud, l'augment de mida de la població s'explica per un procés d'expansió espacial i batimètric a traves del temps, on la colonització i el creixement somàtic dels individus serien els principals mecanismes. Els períodes de condicions ambientals favorables explicarien les altes densitats de individus de l’espècie niló dos anys després. Aquestes condicions ambientals favorables podrien estar principalment relacionades amb la supervivència de les larves, l'èxit dels processos de reclutament i el posterior creixement somàtic.

D'altra banda, i amb l’objectiu de fer una verificació dels resultats dalt explicats, i basant-se en una font d'informació complementària, es van analitzar 17 anys de dades biològiques recollides en mostrejos pesquers del “camaron nylon” davant de la costa central de Xile. Es van analitzar aquestes dades utilitzant models lineals generalitzats (GLM) per tal de determinar els factors responsables dels canvis en la longitud del cefalotòrax, el pes del cos, la maduresa sexual i la proporció de sexes. Es va determinar una notable heterogeneïtat espacial en les característiques biològiques dels individus de *H. reedi*. Els individus en millor condició es van trobar al sud de la latitud de 32 ° S i aquesta millor condició es va relacionar amb les millors condicions ambientals i de menjar en aquesta zona. Per exemple, els individus són més grans, les femelles assoleixen abans el tamany de primera maduresa ($CL_{50\%}$), i les femelles madures són menys freqüents. Amb aquests resultats es presenta una base teòrica que pot guiar la

recerca sobre les poblacions de *H. reedi* tenint en compte les consideracions espacials en les futures mesures de conservació.

Finalment, per poder comparar diferents hipòtesis sobre l'estructura de la població i connectivitat espacial proposades al llarg d'aquest treball, es presenta un model de població basat en la talla i s'ha analitzat la informació biològica i pesquera disponible des de 1945. S'han tingut en compte tres hipòtesis en funció de la taxa de connectivitat de les dues subpoblacions, es a dir, les situades al nord i al sud de 32 ° S. Els resultats van mostrar que, estadísticament, diverses hipòtesi es poden fer servir per a explicar les dades disponibles. La hipòtesi més versemblant és la d'una metapoblació en la qual la zona sud actua com a població font o refugi reproductiu. Aquesta població determina parcialment o totalment l'arribada de reclutes a la zona nord i podria explicar l'augment d'aquesta població trobat a l'última dècada. Segons el nostre estudi, la hipòtesi de connectivitat espacial ha de ser contrastada només amb l'evidència empírica. Tenint en compte les implicacions per a la gestió pesquera, s'hauria de prestar una especial atenció a les condicions biològico-pesqueres que es registren al sud de 32 ° S, tenir especial precaució als nivells d'explotació pesquera i considerar aquesta zona (sud del 32 ° S) com a refugi reproductiu a Xile de l'espècie *H. reedi*.

Resumen

La estructura poblacional de los recursos pesqueros y el impacto de los factores ambientales sobre la productividad son procesos importantes a considerar para la gestión de sus pesquerías. Los factores ambientales pueden determinar tanto, el éxito de la deriva larval, la estructura espacial de la población, como las variaciones de biomasa. Teniendo en cuenta esto, deberían de considerarse dos elementos claves para una explotación adecuada y sostenida de cualquier pesquería; los atributos biológicos de las especies y cómo estos pueden variar en el tiempo y en el espacio, siendo para ello necesario mejorar la comprensión de estos efectos y cómo se relacionan con los factores ambientales. Sin embargo, los procesos espaciales rara vez constituyen una consideración explícita en la evaluación y gestión de las poblaciones de invertebrados marinos, más cuando son particularmente importantes en los procesos donde la deriva larval actúa como uno de los principales mecanismos de expansión de una población. El concepto ecológico de metapoblación es ampliamente utilizado y aceptado para la comprensión de las poblaciones marinas de baja movilidad, y sus implicancias deberían ser consideradas en la ordenación pesquera.

En este trabajo se muestra el efecto del medio ambiente sobre la distribución, abundancia y estructura espacial de la población camarón nailon (*Heterocarpus reedi*) frente a la zona central de Chile (25 ° -37 ° S), considerando la información de cruceros de pesca de arrastre realizados entre 1996 y 2011, y de variables ambientales de la superficie del mar relacionadas con la disponibilidad de alimento como es la concentración de clorofila-α y la materia orgánica disuelta. Los resultados mostraron una separación geográfica de la población de alrededor de 32 ° S, donde la densidad de camarones hacia el sur es mayor así como también la concentración de clorofila-α y la materia orgánica disuelta, esto último debido

probablemente a la presencia de afluentes de ríos y zonas de surgencia costera. En esta área, se concentraría la mayor parte de la población adulta y podría actuar como población "fuente" por lo que su influencia en la deriva larval explicaría tanto la preponderancia de los juveniles en la zona norte como el menor tamaño de su población ("población seudo-sumidero"). En la zona sur, el aumento del tamaño en la población se explicaría por un proceso de expansión espacial y batimétrica a través del tiempo, y donde la colonización y el crecimiento somático individuales habrían sido los principales mecanismos. Encontramos que los períodos de buenas condiciones ambientales explican las altas densidades del camarón nailon con un retraso de dos años, lo cual podría estar relacionado principalmente con la supervivencia de las larvas, el éxito del reclutamiento y el posterior crecimiento somático.

Por otra parte y con el fin de hacer una verificación cruzada de esta propuesta, y basado en una fuente de información complementaria, se analizaron 17 años de datos biológicos recogidos de pesca del camarón nailon frente a Chile central. Analizamos estos datos utilizando Modelos Lineales Generalizados con el objeto de determinar los factores responsables de los cambios en la longitud del caparazón, el peso corporal, la madurez y la proporción de sexos. Se determinó una notable heterogeneidad espacial en los atributos biológicos y donde las mejores condiciones físicas y reproductivas del *H. reedi* al sur de 32 ° S estarían relacionados con las mejores condiciones ambientales y de alimentos en esta zona. Por ejemplo, los individuos son más grandes y las hembras logran la primera madurez ($CL_{50\%}$) a mayor tamaño. Describimos un fundamento teórico que puede guiar la investigación sobre *H. reedi* y consideraciones espaciales en las futuras medidas de conservación.

Por último y con el fin de contrastar diferentes hipótesis de estructura de la población y la conectividad espacial propuesta a lo largo de este trabajo, propusimos un modelo de

población basado a la talla y analizamos la información biológica y pesquera disponible a partir del 1945 bajo tres hipótesis respecto de la tasa de conectividad de dos subpoblaciones, situadas al norte y al sur de 32°S. Los resultados mostraron que, estadísticamente, varias hipótesis se pueden utilizar para explicar los datos disponibles. La hipótesis más probable es la de una metapoblación en la cual la zona sur actúa como una población fuente o refugio reproductivo, y determina parcial o totalmente, la llegada de reclutas a la zona norte y explicaría el aumento de esta población registrado en la última década. De acuerdo con nuestro estudio, la hipótesis de la conectividad espacial debe ser fortalecida solo con evidencias empíricas y dadas las implicancias para la gestión de la pesquería, se debería prestar atención especial a las condiciones biológico-pesqueras que se registren al sur de 32°S, atender con precaución los niveles de explotación y considerar esta zona como refugio reproductivo del camarón nailon en Chile.

Abstract

The population structure of fishery resources and the impact of environmental factors over its productivity are important processes to be considered in fisheries management. Environmental factors could determine both, the success of larval drift as the population spatial structure and its changes of biomass. Considering this, two key elements in the adequate, sustained exploitation of any fishery should be considered; the biological attributes of the species and how these vary over time and space. Research is needed to obtain a more thorough understanding of these effects, how they vary, and how they relate to environmental factors. However, spatial processes rarely constitute an explicit consideration in the evaluation and management of marine invertebrate populations, but this is particularly important in processes in which larval drift acts as one of the main mechanisms of population expansion. The ecological concept metapopulation is widely used and accepted for understanding low-mobility marine populations, and its implications for fishery management purposes should be considered.

In this work we show the environmental effect over distribution, abundance and spatial structure of nylon shrimp population (*Heterocarpus reedi*) off central Chile (25°-37°S) from trawling surveys carried out between 1996 and 2011. Environmental variables considered where sea surface concentration of chlorophyll-*a* and dissolved organic matter. Results show a geographical separation in population around 32°S. Shrimp density is higher in the southern zone, where concentration of chlorophyll-*a* and dissolved organic matter are high due to presence of river tributaries and coastal upwelling zones. In this area, the bulk of the adult population is concentrated, which could act as "source" population and thereby its influence on larval drift could explain both, the preponderance of juveniles in the northern area as the

smallest size of its population ("pseudo-sink" population). In the southern area, a process of spatial and bathymetric expansion had driven the increase in population size over time, where the colonization and individual somatic growth had been the main mechanisms. We found that periods of good environmental conditions explain high densities of shrimp with a delay of two years, which might be related mainly with larval survival and enhanced recruitment and somatic growth.

In order to do a cross check of this proposal, and based on a complementary information source, 17 years of biological data collected from nylon shrimp fishery off central Chile were analyzed. We analyze these data using generalized linear models and determine the factors responsible for changes in carapace length, body weight, maturity, and sex ratio. better physical conditions and reproductive attributes of *H. reedi* south of 32°S would be related with the best environmental and food conditions at this zone. For example, individuals are larger, females are longer at first maturity ($CL_{50\%}$), and mature females are less prevalent. We outline a theoretical foundation that can guide future research on *H. reedi*. We also suggest that future conservation measures consider biological attributes within a spatial context.

Finally, in order to contrast different hypotheses of population structure and spatial connectivity proposed along this work, we proposed a length-based population model and analyzed the biologic and fishery information available since 1945 under three hypotheses, based on the connectivity rate of two subpopulations located to the north and south of 32°S. The results show that, statistically, several hypotheses can be used to explain the data. The most likely hypothesis is that of a metapopulation in which the south zone acts as a source population (reproductive refuge) and determines, partially or totally, the arrival of recruits in the north zone, thereby explaining the population increase over the last decade. According to our study, empirical evidence will strengthen the hypothesis of spatial connectivity and, given

the implications for managing the fishery of this resource, special attention should be paid to the biological-fishery conditions recorded south of 32°S, caution in its exploitation levels and consider this zone as reproductive refuge of nylon shrimp.

I. GENERAL INTRODUCTION AND OBJECTIVES

I.1. Shrimp catches in the world

According to the Food and Agriculture Organization of the United Nations (FAO, 2014), between 2011 and 2012, just over 80 million tons of marine resources were caught and landed in the world oceans. Of these, about 40% were made up of 23 fish species, including pelagic resources (engraulids, clupeids, scombrids) and some demersal species of the Gadidae family. Historically, these levels have remained stable since the early 1990s, a time when support for aquaculture increased worldwide. As the principle wild resources began to decline, more attention was given to the regulation of these fisheries (Fig. 1).

Finfish fisheries around the world have often been evaluated and regulated for purposes of stock recovery and/or more sustainable exploitation. However, whereas invertebrate fisheries have expanded rapidly (Figs. 2, 3) and become more economically important, current scientific knowledge of the state of the stock has been found to be insufficient, as was our understanding of the impact that fishing has on the ecosystems that sustain these fisheries. According to Anderson (2011), more scientific and administrative efforts need to be directed towards these resources in order to avoid negative impacts on ocean ecosystems and human welfare.

Berkes et al. (2006) and Anderson (2011) described the expansion of invertebrate fisheries, noting that crustaceans constituted ~35% of the catch (FAO, 2014), and that of these, shrimp were the most important species (52%). Worldwide, shrimp catches have exceeded 3.4 million tons per year and accounted for 7% of all species caught. However, in terms of value added, shrimp have had one of the highest shares of all marketed products. In 2006, the export value of shrimp (including farmed shrimp) reached 17%, followed by salmon (11%), groundfish (10%), tuna (8%), and cephalopods (4%).

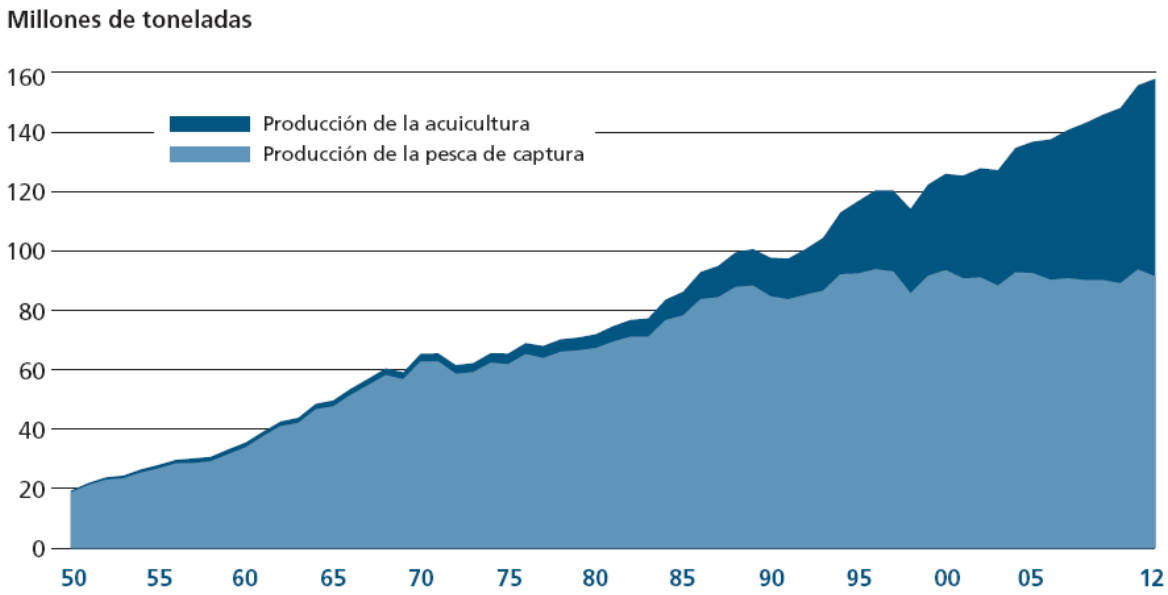

Figure 1. World production of fisheries (marine and inland) and aquaculture. (Source: FAO, 2014)

According to Gillet (2008), 60% of world shrimp production came from wild fisheries and the remaining 40% came from farms. Over half of the world shrimp catches came from China and four other Asian countries (FAO, 2014). Of the 300 known shrimp species, three families (Penidae, Caridae, Sergestidae) were the most important and six species accounted for over 83% of world catches. In terms of landings, *Acetes japonicus* (decapod, Peneidae) was the most important, with annual catches around 600,000 tons, or 20% of world shrimp catches (FAO, 2014). This species was followed by *Trachysalambria curvirostris*, with 13% (430,000 t), and *Pandalus borealis*, with 11% (380,000 t).

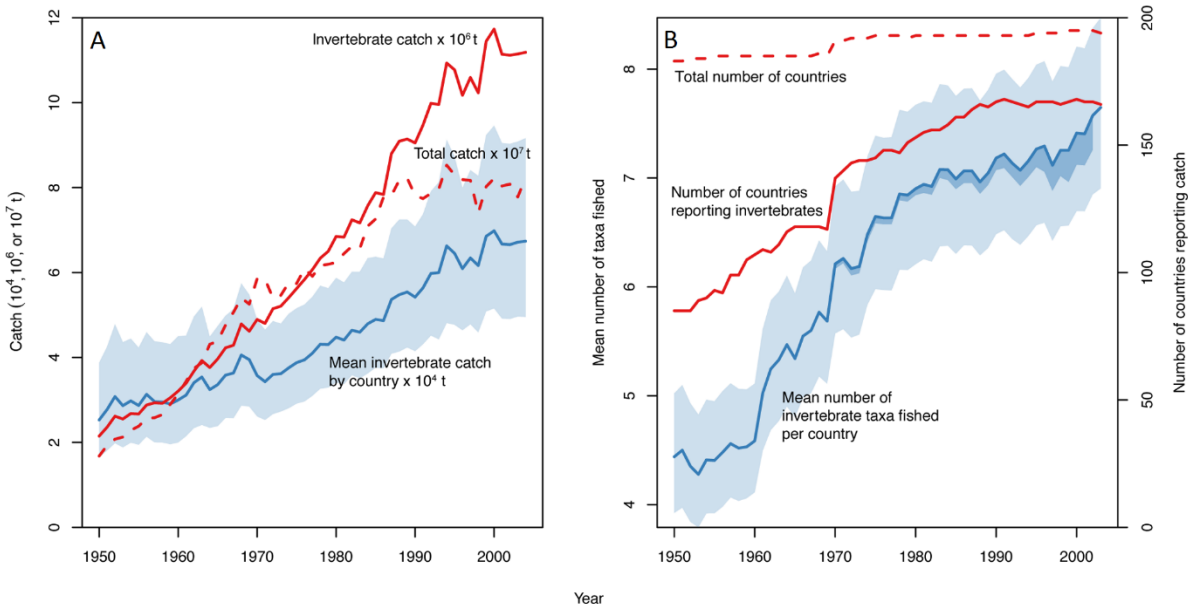

Figure 2. (A) Trends in invertebrate catch globally (red) and per country (mean and standard error assuming a log-normal distribution, blue). Trends in all finfish and invertebrate catch (total catch, dashed red) are included as a reference. (B) Trends in the number of countries reporting catch of invertebrates (solid red) and of all finfish and invertebrate species (total, dashed red, as a reference) since the 1950s, and number of invertebrate taxa (taxonomic groups or species) fished by country (mean and standard error assuming a negative binomial distribution, blue). Thickness of dark blue line approximates false increase due to increased reporting precision. (Source: Anderson, 2011).

I.2. Scientific research in shrimp fisheries

Significant progress has been made in our understanding of the life history and other biological aspects of the principle shrimp species. Although biological findings constitute the foundation of stock assessments in much of the research done on shrimp fisheries, Gillett (2008) was able to classify shrimp fishery research into several categories, including: fisheries monitoring and stock assessment, interdisciplinary research (biology, sociology, economics), improved economic efficiency through the development of bio-economic models and optimal exploitation strategies, and fishing gear design that reduces bycatch and minimizes the impact of trawling on the benthic community. Despite this, improving the management of these

resources remains challenging, particularly in terms of developing integrated assessment models consistent with the particular dynamics of these species.

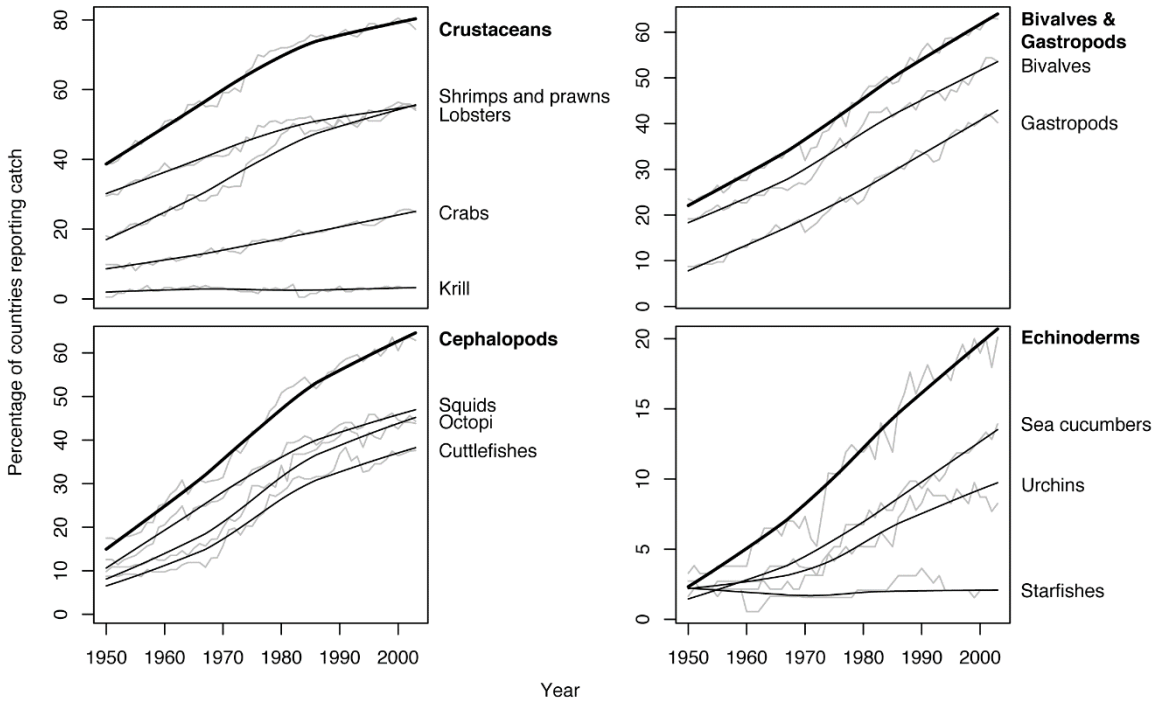

Figure 3. Expansion of invertebrate catch since the 1950s across taxa. Upper lines indicate total catch for each group and underlying lines indicate catch for subgroups. Dark lines represent smooth estimates obtained from a loess smoother (smoothing span 50% of the data). Light lines indicate the unfiltered catch trends (Fuente: Anderson, 2011).

Few studies have considered environment-resource integration in shrimp fisheries. The relationships between spatial and temporal shrimp distributions as well as their population characteristics (abundance, individual size), population structure, and environment are not well known. In particular, little is known about how river discharge and coastal upwelling affect early life stages of this resource. Some evidence of these relationships was reported in studies of Penaeid fisheries done in the waters of the Indo-Pacific (Grimes and Kingsford, 1996; Evans et al., 1997; Myers, 1998; Loneragan and Bunn, 1999) and the eastern Pacific (Mora-Lara et al.,

1984; Gracia, 1989; Mendo and Tam, 1993). Other research showed that dependence on the marine substrate, environmental characteristics, and exploitation determined changes in the abundance and distribution of decapod crustaceans (Diaz-Ochoa et al., 2004; Mujica, 2006; Encarnaçaô et al., 2013; Sancinetti et al., 2014) and biological parameters (Company et al., 2001, 2004; Araújo et al., 2014, among others) which is characteristic of discrete population units (Rufino et al., 2004; Fogarty & Botsford, 2006; Barria et al., 2011; Josileen, 2011; Sethi et al., 2013; Sal-Moyano et al., 2014, among others). These topics are addressed more fully in Chapters 1 and 2.

I.3. Nylon shrimp (*Heterocarpus reedi*) off Chile: biology and fishery

In Latin America, 17 shrimp species (10 penaeids, 7 carideans) have been identified as being the most commercially interesting (Wehrtmann et al., 2012). The nylon shrimp *Heterocarpus reedi* (decapoda, caridae) (Bahamonde, 1955) is one of the most important in terms of landings in the South Pacific. *H. reedi* is endemic to central Chile (25°-37°S) (Fig. 4). Catches exceeding 11,000 tons were recorded in the mid-1970s and 1990s for this fishery. At present and due to regulation, catches have stabilized around 4,000 tons per year (Fig. 5).

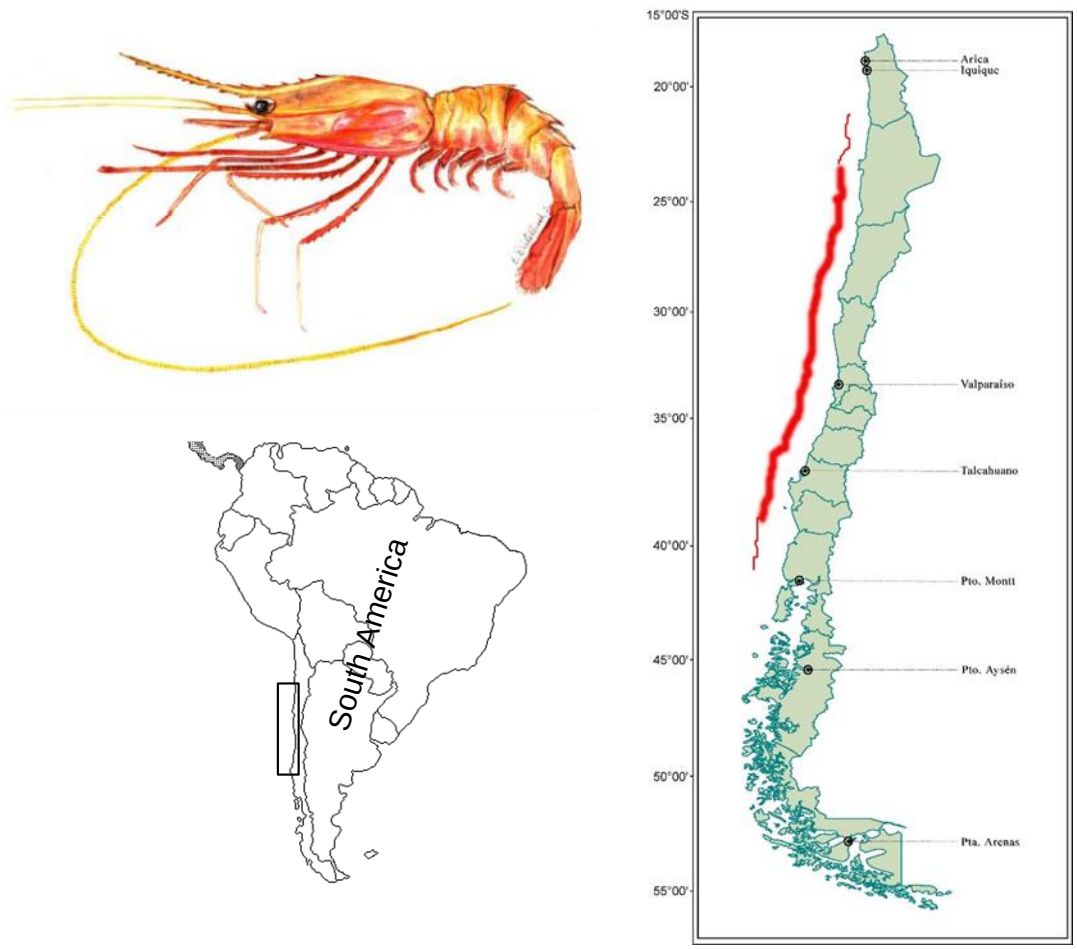

Figure 4. Geographical distribution of shrimp (*Heterocarpus reedi*) off the coast of Chile and its position on South America. The thickness of the red line represents the relative historical concentration of fishing effort. (Source: Arana, pers)

Nylon shrimp ranged in size from 10 to 40 mm carapace length (CL). Although the species showed no apparent dimorphism, females were relatively larger than males. *H. reedi* had a continuous distribution over the continental shelf and upper slope, mainly between 200 and 400 m depth. This habitat was heterogeneous, consisting of clay soils, sedimentary rock, sand, and mud. Two water masses coincided in the portion of the water column inhabited by *H. reedi*. Equatorial Subsurface Waters were low in dissolved oxygen, whereas Antarctic Intermediate Waters were cooler (10°-12°C) with relatively high salinity (34.5-34.9 g kg-1) (Silva, 2012). In the southern sector of the *H. reedi* distribution, an important contribution of

organic matter was generated by river tributaries (Canales et al., 2016a) and coastal upwelling (mainly in spring) (Silva & Valdenegro, 2003).

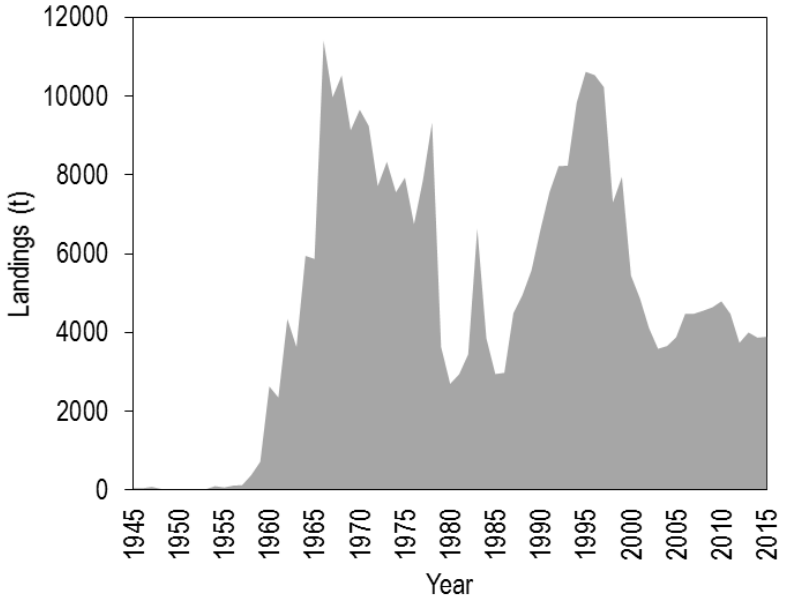

Figure 5. Nylon shrimp landings exploited off central Chile from 1955 to 2015

Nylon shrimp ranged in size from 10 to 40 mm carapace length (CL). Although the species showed no apparent dimorphism, females were relatively larger than males. *H. reedi* had a continuous distribution over the continental shelf and upper slope, mainly between 200 and 400 m depth. This habitat was heterogeneous, consisting of clay soils, sedimentary rock, sand, and mud. Two water masses coincided in the portion of the water column inhabited by *H. reedi*. Equatorial Subsurface Waters were low in dissolved oxygen, whereas Antarctic Intermediate Waters were cooler (10°-12°C) with relatively high salinity (34.5-34.9 g kg-1) (Silva, 2012). In the southern sector of the *H. reedi* distribution, an important contribution of organic matter was generated by river tributaries (Canales et al., 2016a) and coastal upwelling (mainly in spring) (Silva & Valdenegro, 2003).

Knowledge about the biological aspects of *H. reedi* was varied, scattered, and often limited to finite periods of time. Prominent early studies on the reproductive process, growth, and condition factor of nylon shrimp were done by Arana & Tiffou (1970), Bahamonde & Henriquez (1970), and Arana et al. (1976). Other noteworthy studies identified some small-scale migration and size structure patterns (Mistakidis & Henriquez, 1966; Arana & Nakanishi, 1971; Roa & Ernst, 1996; Canales et al., 1999, among others). The growth and natural mortality studies carried out for this decapod by Ziller (1993), Roa & Ernst (1996), and Canales et al. (1999) showed moderate growth (k=0.10 to 0.20), average maximum ages (7-9 years), and annual natural survival rates (~70%). Despite this last, many questions remain as to the quality of the information resulting from size compositions and their use as a fundamental element of analysis in the identification of age groups and longevity.

The referential scheme presented in Montenegro et al. (2014) covered the *H. reedi* life cycle from reproduction and spawning to the adult phase. After the eggs were released and hatched, the larval stage remained in the marine meroplankton for 6 to 8 months, followed by the onset of post-larval transformation. The time between spawning and the onset of the juvenile or pre-recruit stage was estimated to be one year, and the transition from recruitment[1] to maturity 2 to 3 years (Fig. 6). Montenegro et al. (2014) also noted a need for further studies of the biology and ecology of nylon shrimp in order to better understand its life cycle, despite documentation of some aspects of the adult stage (e.g., longevity, reproductive periods, mortality). These aspects are discussed further in Chapters II.1 and II.2 of this thesis.

[1] The smallest specimens that are, on average, susceptible to being exploited by the fishing gear

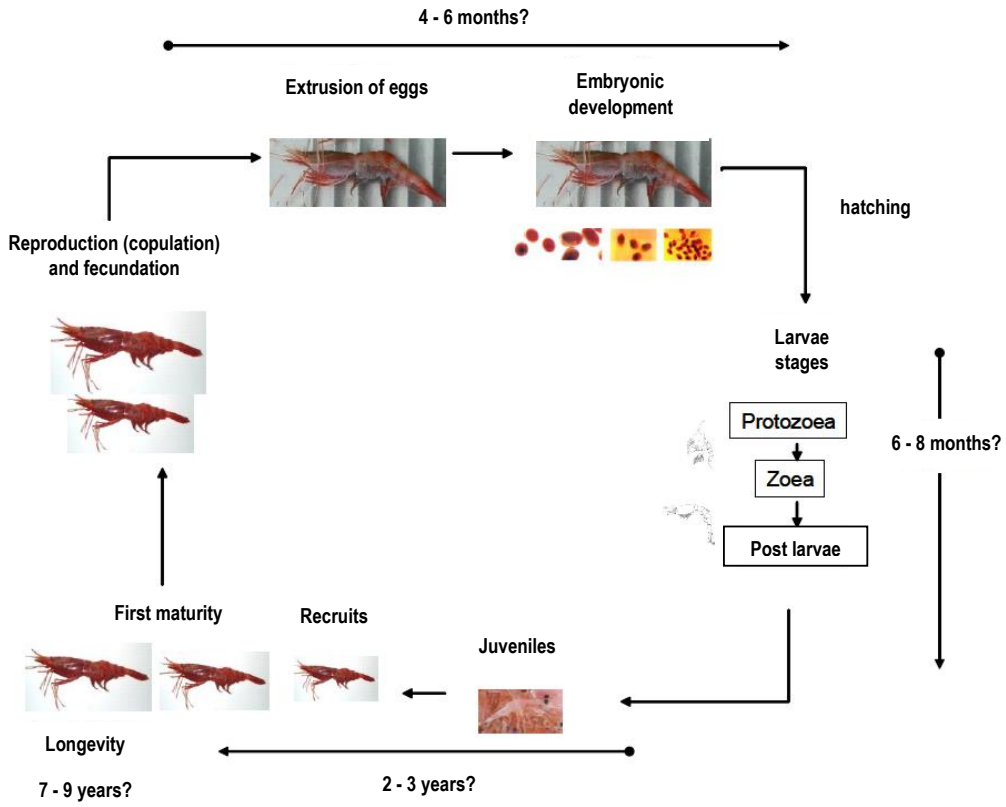

Figure 6. Theoretical schematic diagram of the life cycle of *Heterocarpus reedi.* (Fuente: Montenegro et al, 2014).

Nylon shrimp and two squat lobsters (*Pleuroncodes monodon*, *Cervimunida johni*) have the longest and most important history of exploitation and management of all Chilean demersal crustaceans. Nylon shrimp extraction began in the late 1940s, as part of the bycatch of the hake (*Merluccius gayi*) fishery. Now, the *H. reedi* fishery is developed by a largely small-scale industrial fleet of approximately 23 vessels averaging no more than 22 m length (Fig. 7).

Figure 7. Trawler fishing vessel dedicated to the exploitation of demersal crustaceans in Chile (up) and shrimp catch in a haul deployed on deck (down) (Source: Arana, com pers).

Chile's 1991 General Law on Fisheries and Aquaculture No. 18.892 administratively defined the nylon shrimp fishery as the area between 21°25'S and 38°28'S. In 1995, the fishery was declared fully exploited (MINECOM, 1995) and annual catch quotas were instated. As of 1998, a reproductive ban has been enforced between July and August of each year, covering the entire *H. reedi* distribution (MINECOM, 1998). Since 2004, the fishery has been managed under the 2001 Law of Maximum Catch Limits by Owner No. 19.713 (MINECOM, 2004). This law allocated and distributed the entire catch quota among the companies participating in the fishery. The *H. reedi* fishery is managed by the Chilean Undersecretary of Fisheries, in consultation with the Scientific Committee on Demersal Crustacean Resources (http://www.subpesca.cl), a multisector, decision-making, technical body responsible for approving the diagnoses of the resource based on the latest stock assessment and defining a range of acceptable biological catch (ABC) for the following year.

Management of this fishery relies on three independent sources of information: landings statistics from the National Fisheries Service (www.sernapesca.cl), tracking and monitoring of fishing activities from the Fisheries Development Institute (IFOP) (www.ifop.cl) since the early 1970s, and scientific trawling campaigns funded by the Fisheries Research Fund (FIP) (www.fip.cl) since the 1990s. The stock assessments and diagnoses conducted by IFOP are based on quantitative models (age-structured) of analysis that integrate biological knowledge of this species with other available information. These assessments assume the existence of two independent population units located north and south of the regional limit of 32°10'S (Montenegro et al., 2014). This matter is addressed in more detail in Chapter II.3.

Despite the existing research and management of nylon shrimp off Chile, our incomplete understanding of this resource translates into continued challenges for research

aimed at understanding: spatial-level population dynamics, interannual displacement patterns and bathymetric and latitudinal expansion, spatial connectivity between sub-populations, the relationship between abundance and environmental forcings, local characteristics of life history parameters, and the inclusion of all these aspects in size-structured alternative analytical models for purposes of fisheries management. These, ultimately, were the main motivating factors behind this doctoral thesis.

I.4. Dissertation objectives and contents

This thesis is organized as a collection of articles that are described at length in Chapters II.1, II.2, and II.3, and as a result of the generation of three articles, two of which have been published in ISI indexed journals and one that has been sent for review, as follows:

I.4.1. Objectives and presentation

This thesis aimed to advance our understanding of the spatiotemporal patterns of biological aspects and the population dynamics of nylon shrimp *Heterocarpus reedi* (Decapoda, Caridea) exploited off Chile. By emphasizing the species' biological attributes and its population structure, this work helped strengthen the scientific bases underlying the management of this fishery resource. The thesis was divided into three areas: (1) distribution, environmental variables, and population structure, (2) spatiotemporal changes in biological attributes, and (3) spatially explicit population modeling for purposes of fisheries management. In Chapter II.1, bathymetric and spatiotemporal patterns in the distribution of the species were presented

along with hypotheses as to the *H. reedi* population structure and the relationship between this structure and the environmental heterogeneity off Chile. In Chapter II.2, spatial and temporal patterns were identified for the main biological attributes (carapace length, weight, maturity, size-specific sex ratio) of nylon shrimp in relation to environmental conditions off Chile. Finally, in Chapter II.3, a model was formulated of the dynamics of the size-structured population in order to assess the hypothesis of population structure (spatial) also addressed in Chapter II.1. This was complemented by findings (patterns in biological parameters) identified in Chapter II.2, and estimates of previously unknown population parameters of spatial connectivity.

Detailed specific objectives of the thesis are given below by chapter:

Chapter II.1.

Information gathered over 13 years of "swept area" trawling campaigns carried out off Chile over the continental shelf and the edge of the continental slope was integrated in order: a) to understand the mechanisms of the nylon shrimp population expansion in relation to individual size, b) to identify spatial and bathymetric aggregation patterns, and c) to determine how abundance levels were related to environmental conditions over time. In this chapter, the specific objectives were:

i. To identify patterns of bathymetric and spatial segregation in the nylon shrimp distribution and its association with biological and environmental conditions off Chile.

ii. To characterize the mechanisms of spatial expansion in the nylon shrimp population off Chile.

iii. To propose a hypothesis for the population structure of nylon shrimp off Chile.

Chapter II.2.

Information from 17 years of biological sampling (1997-2013) of the nylon shrimp fishery off Chile was modeled in order to identify and characterize spatiotemporal patterns in the primary biological attributes of *H. reedi* (e.g., carapace length, weight, maturity, sex ratio) and their theoretical relationships with the conditions of the marine environment. The specific objectives of this chapter were:

iv. To identify spatial and temporal patterns in the main biological attributes (carapace length, individual weight, maturity, sex ratio) of nylon shrimp off Chile.

v. To propose relationships between the spatial patterns of the main biological characteristics of nylon shrimp and the environmental conditions off Chile.

vi. To determine the temporal variations in the size at first maturity of the nylon shrimp off Chile and how this relates to the environmental variables.

Chapter II.3.

In chapter 3, a statistical model was formulated for size-structured population dynamics in order to test the hypothesis of the population structure of nylon shrimp off Chile considering all available biological-fisheries information, the spatiotemporal characteristics of its spatial dynamics (Chapter II.1), and the spatial patterns of the biological attributes of this species (Chapter II.2). The specific objectives were:

vii. To evaluate the hypothesis of population structure (spatial) of the nylon shrimp off Chile through a statistical model of size-structured population dynamics.

viii. To determine the scale and composition of size at recruitment by area, the characteristics of the modal groups in the population, the level of spatial connectivity, and the fluctuations of the main population variables of the nylon shrimp off Chile.

ix. To suggest actions that tend to generate a sustainable exploitation of nylon shrimp off Chile based on the most likely population structure.

I.4.2. Methodological aspects and information sources

One pillar of this doctoral thesis is the integration and modeling of large amounts of information and data generated during decades of research and monitoring of the nylon shrimp fishery (*Heterocarpus reedi*) off central Chile. This is complemented by an analysis of some environmental variables related to the food supply (e.g., chlorophyll-α, dissolved organic matter) off south-central Chile. The following information sources were used:

- Fishing logbooks and biological samples from scientific trawls off Chile (central zone) between 1996 and 2011, funded by the Fisheries Research Fund of Chile (www.FIP.cl).
- Databases resulting from biological samples taken from the nylon shrimp fishery by the Fisheries Development Institute (www.IFOP.cl) at the main ports of landings in central Chile between 1997 and 2013.
- Digital records of absorption coefficients of chlorophyll-α and dissolved organic matter for the quadrant 26°-36°S; 70°-73°W, from September to December between 1997 and 2011. These months were chosen because they correspond to the period of greatest reproductive activity. These estimates were made using satellite telemetry models and

are available online in the electronic portal GIOVANNI (http://giovanni.gsfc.nasa.gov/giovanni/).

- Series of standardized landings and fishing yields (catch per unit effort, CPUE) taken, respectively, from the statistical yearbooks of the National Fisheries Service (www.SERNPESCA.cl) and public reports put out by IFOP.

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II. RESULTS

II.1. Population structure of nylon shrimp *Heterocarpus reedi* (Crustacea: Caridea) and its relationship with environmental variables off Chile

Canales, C.M, J.B. Company & P.M. Arana, 2016. Population structure of nylon shrimp *Heterocarpus reedi* (Crustacea: Caridea) and its relationship with environmental variables off Chile. *Latin American Journal of Aquatic Research*, 44(1): 144-154. DOI: 10.3856/vol44-issue5-fulltext-15

ABSTRACT. The population structure of fishery resources and the impact of environmental factors over its productivity are important processes to be considered in fisheries management. Environmental factors could determine both, the success of larval drift as the population spatial structure and its changes of biomass. In this paper we show the environmental effect over distribution, abundance and spatial structure of nylon shrimp population (*Heterocarpus reedi*) off central Chile (25°-37°S) from trawling surveys carried out between 1996 and 2011. Environmental variables considered where sea surface concentration of chlorophyll-*a* and dissolved organic matter. Results show a geographical separation in population around 32°S. Shrimp density is higher in the southern zone, where concentration of chlorophyll-*a* and dissolved organic matter are high due to presence of river tributaries and coastal upwelling zones. In this area, the bulk of the adult population is concentrated, which could act as "source" population and thereby its influence on larval drift could explain both, the preponderance of juveniles in the northern area as the smallest size of its population ("pseudo-sink" population). In the southern area, a process of spatial and bathymetric expansion had driven the increase in population size over time, where the colonization and individual somatic growth had been the main mechanisms. We found that periods of good environmental conditions explain high densities of shrimp with a delay of two years, which might be related mainly with larval survival and enhanced recruitment and somatic growth. The aim of this study was to understand the spatial-temporal variability of the nylon shrimp density.

Keywords: *Heterocarpus reedi*, nylon shrimp, abundance, distribution, environment, metapopulation, river tributaries.

Estructura poblacional del camarón nailon *Heterocarpus reedi* (Crustacea: Caridea) y su relación con variables ambientales frente a Chile

RESUMEN. La estructura poblacional de recursos de interés pesquero y el impacto de los factores ambientales sobre su productividad son procesos claves a considerar en la gestión pesquera. Los factores ambientales pueden determinar tanto el éxito de la deriva larval como la estructura espacial de la población y sus cambios de biomasa. Se muestra el efecto del medio ambiente sobre la distribución, abundancia y estructura espacial de la población de camarón nailon (*Heterocarpus reedi*) en Chile central (25°-37°S), considerando las variables ambientales de la superficie del mar y los cruceros de arrastre realizados entre 1996 y 2011. Los resultados muestran una separación geográfica de la población alrededor de 32°S. En la zona sur, la densidad del camarón es mayor, donde los altos niveles de concentración de clorofila-*a* y de materia orgánica disuelta se deben, entre otros, a la presencia de afluentes de ríos y a surgencia costera. En esta área, se concentra la mayor parte de la población adulta, que podría actuar como población "fuente" y por lo tanto, su influencia en la deriva larval podría explicar tanto la preponderancia de juveniles en la zona norte, como el tamaño más pequeño de su población (población "pseudo-sumidero"). En la zona sur, un proceso de expansión espacial y batimétrica habría impulsado el aumento de tamaño de la población a través del tiempo, donde los principales mecanismos habrían sido la colonización y crecimiento somático individual. Se determinó que los períodos de buenas condiciones ambientales explican las altas densidades de camarones con un retraso de dos años, aspecto que estaría relacionado principalmente con la supervivencia larval, reclutamiento y crecimiento somático. El objetivo de este estudio es comprender la variabilidad espacio-temporal de la densidad de camarón nailon.

INTRODUCTION

Nylon shrimp (*Heterocarpus reedi*) is a decapod crustacean (Caridea), distributed off the coasts of Chile, between 25° and 38°S, on clay, sedimentary rock, sandy and muddy bottoms. This species inhabit mainly the external border of the continental shelf and the upper slope, at a depth range that varies between 100 and 500 m. It can be found in the intersection area of Equatorial Subsurface Water (ESSW) and Antarctic Intermediate Water (AIW), which are cold (10-12°C) and saline (34.5-34.9) (Bahamonde & Henríquez, 1970; Arana, 2012; Silva, 2012). This species is described as a predatory detritivore with an omnivore diet (Andrade & Báez, 1980), while in its larval stage; the diet is mainly based on phyto and zooplankton. As described by authors such as Bahamonde & Henríquez (1970), Arana *et al*. (1975), and Roa & Ernst (1996), the carapace length (CL) of *H. reedi* varies in the range 15-40 mm, being the females larger than males and slightly predominant in the catches. Mature females carry eggs in the pleopods by a couple of month, within a reproductive season that takes place between May and December and whose peak is registered between June and September (Arana *et al*., 1975, 1976; Acuña *et al*., 1997). Mean size at maturity is reported between 24.3-25.1 mm CL (Arana & Tiffou, 1970; Arana *et al*., 1976; Canales *et al*., 1999). The presence of Caridea larvae in the plankton -with *H. reedi* being the most abundant species of the group-, has been reported in different areas (*e.g.,* Palma, 1980; Mujica *et al*., 2011), particularly in the middle of the southern spring, with the highest percentages on October.

The fishery of *H. reedi* is one of the oldest and most important among the group of demersal crustaceans in Chile, along with the red squat lobster (*Pleuroncodes monodon*) and the yellow squat lobster (*Cervimunida johni*). This resource started to be exploited in the 1950's,

with catches showing important fluctuations: the highest values around 10,000 annual tonnes in the middle of the 1990's, while the lowest has been recorded over the last decade around 4,000 ton yr^{-1}, due to regulations on fishing quotas caused by the reduction in the population of *H. reedi* (Wehrtmann *et al*., 2012).

One of the most important sources of scientific information is the trawling survey programme carried out since the mid-1990s. The data derived from these surveys allow to study changes in magnitude and spatial-temporal distribution of the population across years. Estimates of biomass of these surveys show important variations, whose highest increase is registered southward of latitude 32°S since 2006 (Acuña *et al*., 2012). This increase could have been facilitated, among others, by the reduction in exploitation levels, the closure of some fishing areas since 2000, and depletion of the common hake (*Merluccius gayi*), species that has been noted as an important predator of *H. reedi* (Arana & Williams, 1970; Bahamonde & Henríquez, 1970; Arancibia & Neira, 2008). In the same time period, northward of this parallel, estimates show a smaller population about half the biomass estimates in the south zone (Table 1).

The relationship between environmental variables and abundance have been reported in some crustaceans, *e.g.,* Loneragan & Bunn, 1999; Mujica, 2008; De Juan & Cartes, 2011; Encarnacão *et al*., 2013, but the relationship between spatial and temporal distribution in *H. reedi*, as well as the environmental aspects and those related to its population structure, are still under incipient research; particularly, and as an example, those related to the impact that environmental effects of river discharges and coastal upwelling could have on early life stages, given the evidence found on the studies of fisheries of penaeid crustaceans in waters of the Indian-Pacific (Grimes & Kingsford, 1996; Evans *et al*., 1997; Myers, 1998; Loneragan & Bunn,

1999) and in the Eastern Pacific (Mora-Lara *et al*., 1984; Gracia, 1989; Mendo & Tam, 1993). In this context, this paper summarizes the information collected by scientific surveys during thirteen years and surface environmental data coming from dissolved organic matter, detritus and chlorophyll-*a* obtained by satellite telemetry, aiming to study relationships between variations in distribution and abundance of *H. reedi*, regarding environmental conditions off Chile, and its connection with the population structure of this important crustacean.

MATERIALS AND METHODS

Survey information

The information used corresponds to records from trawling scientific surveys on the continental shelf off central Chile (25°30´, 37°30´S) between 1996 and 2011. The data were provided by the Fisheries Research Fund (FIP, for Fondo de Investigación Pesquera), corresponding to 6.400 geo-referenced trawling hauls (Fig. 1, Table 1). As reported by Canales & Arana (2010), these surveys have been conducted to assess the exploitable biomass of the *H. reedi* using the swept area method, conducted by commercial vessels and following sampling designs, such as systematic sampling where the hauls follow a set of parallel transect (each 10° of latitude) and perpendiculars to the coast (Canales & Arana, 2009), complemented since 2006 by an adaptive sampling strategy, where the number of transects is increased in those areas where a predefined minimum capture is obtained (Acuña *et al*., 2012). Sampling method has been throughout the time, in which vessels have had few technological innovation (Quiroz *et al*., 2005), which suggests that the fishing efficiency have not had major variations in time and thus without major

impact on catch rates as measures of relative abundance. For each trawling survey, hauls duration is standardized to 30 min and speed of 2.0-2.5 knots. The start and end position of each fishing haul were recorded, at the time of stop and turn on the cable winch of the fishing net.

These fishing surveys have been carried out during the second half of each year, and although one of the shortcomings in these have been the variations in the month of start and end of each survey (Table 1), the period -winter and spring at southern hemisphere- coincides with the season that intensifies the process of egg carrying by females of *H. reedi* (Arana *et al*., 1975; Acuña *et al*., 1997) and increases the flow of the main rivers that discharge in the area where this species inhabits. Given the above and that the reproductive period in this species is mainly extended in the second semester, for practical purposes, measurements of relative abundance and biological attributes of *H. reedi* derived from survey data assumed to be representative of reproductive activity peak.

Biological sampling recorded carapace length (CL), sex, and presence of eggs at pleopods of females and individuals weight. The information collected shows that, on the average, around 92,000 individuals have been analysed by survey, 60% of which were females (Table 1). It is important to highlight that the 2002 survey was particularly aimed at assessing three commercial decapod crustaceans at the same time (*Pleuroncodes monodon, Cervimunida johni* and *Heterocarpus reedi*), which required changes of the sampling design/strategy along with a significant increase in the number of fishing hauls, which could have explained some results shown later.

Environmental data

The geo-referenced environmental surface information was taken from free-access database, obtained from satellite telemetry available since 1997 in NASA-Giovanni Portals website,

particularly the data referred to absorption coefficients of organic matter and dissolved detritus (OMD), as well as the concentration of chlorophyll-*a* (Chl-*a*) between 1997 and 2011, under the assumption they represent indirectly the food availability for larvae and adults of *H. reedi*. This information was selected for the geographic quadrant 26°-36°S, 70°-73°W and represents the accumulated value between September and December of each year after the surveys were carried out (Table 1), coinciding with the peak of the reproductive cycle of this species and where both coastal upwelling as the effluents of rivers increase, both variation sources of OMD and Chl-*a*.

Table 1. Biomass of *Heterocarpus reedi* by zone and general details of assessment surveys carried out off Chilean coast between 1996 and 2011. In years, 1997, 2007 and 2010 surveys were not carried out. Zone 1: 24°00 -32°10'S, Zone 2: 32°10'-37°00'S, fp: female proportion.

Year	Biomass (t)		Hauls	Effort	Biological samples		Depth (m)		Latitude (°S)		Period	
	Zone 1	Zone 2	(n)	(km)	(n)	(fp)	(min)	(max)	(min)	(max)	start	end
1996	24 557	10 873	297	400	74 587	0.45	170	440	25.9	38.5	May	Aug
1998	2 593	6 809	274	456	36 415	0.70	46	649	21.6	38.2	Aug	Dec
1999	876	20 872	248	439	18 449	0.67	122	505	21.7	38.5	Jul	Sept
2000	725	21 086	780	1 427	152 816	0.65	74	604	23.0	37.0	Jun	Oct
2001	3 224	19 575	348	740	23 989	0.58	84	617	21.7	38.3	Jun	Jul
2002	8 348	18 256	1 156	2 308	97 860	0.66	51	584	23.0	37.0	Aug	Oct
2003	7 465	18 079	442	805	266 416	0.63	148	497	23.0	36.7	Aug	Sept
2004	8 281	21 545	502	855	151 041	0.60	120	562	23.0	36.9	Jul	Sept
2005	14 382	27 561	562	1 235	208 964	0.57	110	640	25.2	37.0	Jul	Aug
2006	19 486	37 111	407	376	19 045	0.50	118	648	24.2	36.7	Oct	Dec
2008	15 809	28 772	515	531	54 991	0.51	125	518	25.3	36.7	Jun	Dec
2009	27 718	38 058	490	513	49 567	0.56	108	575	25.1	36.7	Aug	Nov
2011	23 515	35 048	379	538	39 662	0.56	131	652	25.2	36.7	Oct	Dec

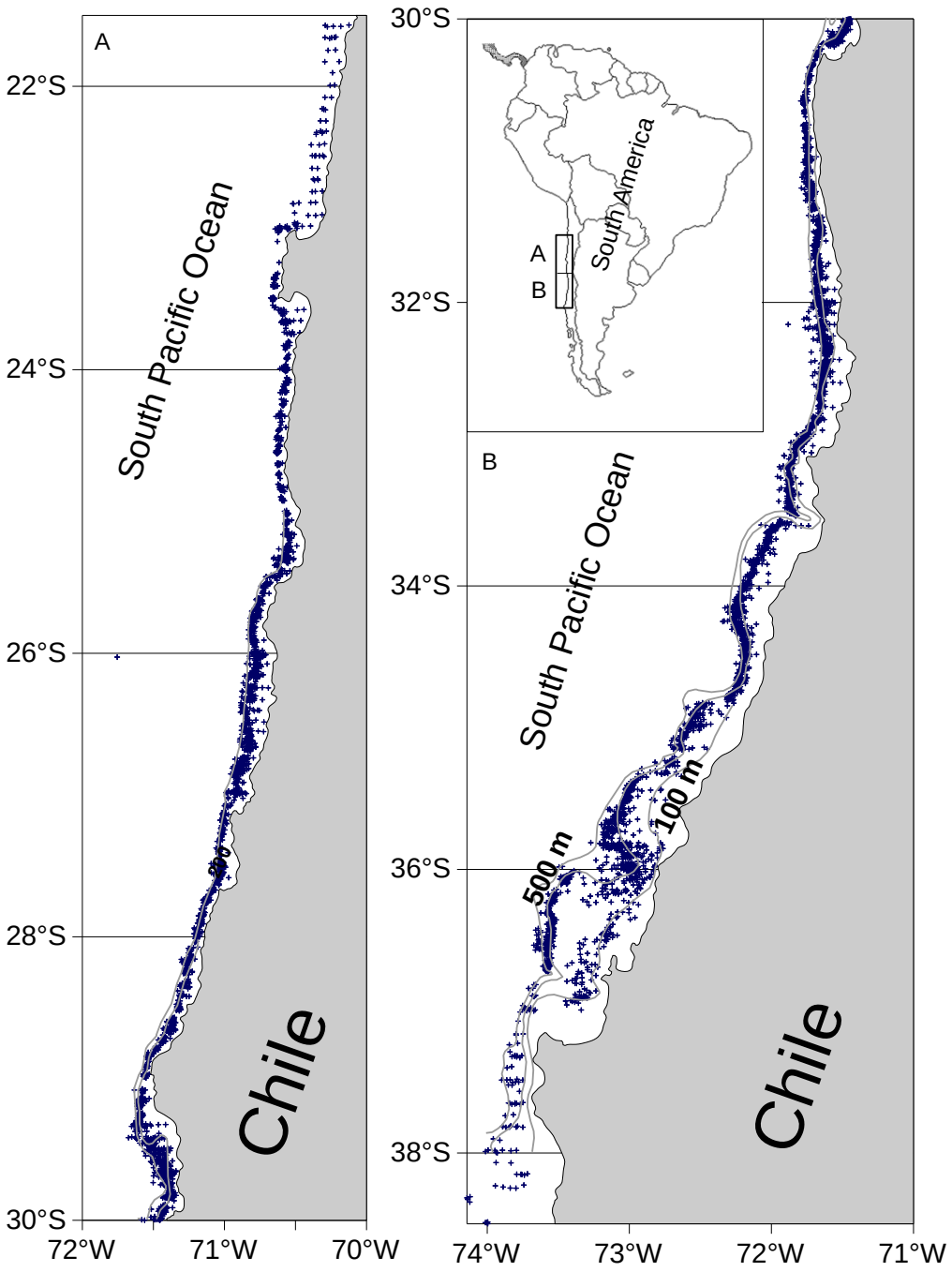

Fig. 1. Study area and geographic location of fishing hauls (dots) of *Heterocarpus reedi* in trawl surveys carried out at the central southern zone of Chile between 1996 and 2011.

Abundance index

As a measure of relative abundance, the ratio between the catch (kg) and the linear distance travelled on every fishing haul was considered. The advantages of this measure are: it is independent of net-opening performance, it is standardized to the distance travelled by the vessel, and it is not influenced by the criteria of time or effective hauling (Canales & Arana, 2010). The distance travelled in linear kilometres is measured once the geographic coordinates of start and end of the haul are known through the Haversine equation, $D = 2\,R\,asin\sqrt{a^2 + b^2\,cos(\mathrm{lat}_1)cos(\mathrm{lat}_2)}$, where a=sin[0.5(lat_2-lat_1)] and b=sin[0.5(long_2-long_1)], where lat and long represent latitude and longitude, respectively, both converted to radians; sub-indices 1 and 2 refer to the respective variable measure at the beginning and end of the fishing haul; while R = 6,371 corresponds to the radius of the Earth measured in km.

Exploratory analysis

In order to explore abundance patterns and link them with depth and environmental conditions, both the fishing hauls information (abundance and CL) as environmental data were stratified by year, geographic latitude (each 30 nautical miles) and depth range (each 100 m). For each of these nodes (year-latitude-depth), a simple average was computed with the purpose to represent in a discrete scale, changes in abundance, individual size (CL) and environmental variables (OMD and Chl-*a*). From this, a kriging representation was used to explore spatial-temporal patterns in the data and summarize the extensive information available. On the other hand, and in order to explore the relationship between environment and shrimp abundance, a

correlation analysis was conducted between anomalies of environmental variables and anomalies of relative abundance of *H. reedi*, with a temporal lag between 0 and 3 years.

The use of anomalies was preferred because more accurately describes climate variability over larger areas, and they give a frame of reference that allows more meaningful comparisons between locations and more accurate calculations of environmental trends. These anomalies for each year were calculated as A=(V-E(V))/E(V) where $\bar{V}$ represents the average of the interest variable for each year while E(V) corresponds to the expected value represented here by a simple average. The Pearson correlation coefficient was used as statistic, while its significance level was verified with Pyper & Peterman (1998) methodology, who proposed a critical correlation (r*) based on an effective sample size (N*), used as hypothesis test considering the autocorrelation degree of the explanatory variables (OMD and Chl-*a*). The analysis was also complemented by *F*-Fisher and *P*-value tests.

RESULTS

Environmental conditions and *H. reedi* distribution

The surface distribution of organic matter and dissolved detritus (OMD) and Chl-*a* between 1997-2011 showed concentration zones near the affluent of the main rivers and at coastal upwelling areas mentioned by Silva & Valdenegro (2003), and Moraga *et al*. (2001), and as a result of this, a higher number of OMD and Chl-*a* concentration areas were registered southward of 32°S (Fig. 2). The accumulated value of OMD and Chl-*a* per latitude and year (Sept-Dec) shows three foci near the coast and located around the 30°S (Elqui River), 33°30'S (Maipo and Rapel

rivers) and 35°S (Mataquito and Maule rivers) respectively (Fig 2). The spatial-temporal variability of these indices show that southward 32°S the highest concentrations of OMD and Chl-*a* were recorded in 2000 and 2004-2007, while north and off the Elqui River (30°S) high concentrations were recorded in 2002, 2006-2007 and 2010-2011 (Fig. 2).

In terms of *H. reedi* depth distribution, the bathymetric information shows that the highest *H. reedi* abundance (>50 kg km-linear^{-1}) is located in depths of 200-400 m and between the 25°30' and 37°00'S, showing a pattern in which, at a lower latitude, the foci of highest abundance are obtained at deeper depths (Fig. 3). The temporal variations in the bathymetric range indicate that since 2004, the abundance has gradually expanded towards higher depths, reaching a peak in 2008.

In addition, across most of years analysed, an important discontinuity is observed in the abundance of *H. reedi*, whose reference points are around parallel 32°S. The increase in abundance reported since 2006, affected all the distribution area, but the increase southward 32°S was the most important reaching maximum values over 220 kg km-linear^{-1} in 2009 around the 33°S, and after in 2011 near the 35°30´S (Fig. 4a). In the southern zone, the displacement of the isopleth of 120 kg km-linear^{-1} registered a gradual northward movement according to the increase of abundance from 2006 around 35°S, to near 32°S in 2011 (Fig. 4a).

Spatial-temporal changes in size composition

In general, larger individuals have been found south 32°S reaching over 27 mm CL as average, while in the north zone, size of *H. reedi* has varied almost always below the 25 mm CL (Fig. 4b). The information shows an important spatial-temporal dynamic in this variable southward 32°S, where isopleths of 25 and 26 mm CL show a displacement in the south-to-north axis since 2001,

similar to the behaviour of the isopleth of relative abundance of 120 kg km-linear^{-1} mentioned above. This situation coincides with the increase of population abundance and is explained by the individual somatic growth alongside the contribution of juveniles located towards the borders of the population expansion. An example of this, is the gradual increase that shows the average CL through years at the 34°-36°S latitudinal range, which goes up from 24 mm in 2000 to 28 mm CL in 2011 (Fig. 4b). Is important to note that in this species the growth rate is moderate (Roa & Ernst, 1996), so that the mean CL by year is enough robust to minimize the impact of lack of temporal coincidence at the survey period, as was described earlier.

Relative abundance *vs* sea surface environmental variables

Since 2006 and particularly southward 32°S, both the relative abundance of *H. reedi* as the environmental variables (OMD and Chl-*a*) have registered positive anomalies, but with different inter annual variability and some temporal lag between them (Fig. 5). In spatial-temporal terms, the environmental and population abundance distribution suggest a spatial correlation, which not only means latitudinal coherence in the concentration nuclei of this species, but also episodes where favourable environmental conditions are followed by high abundances of *H. reedi*.

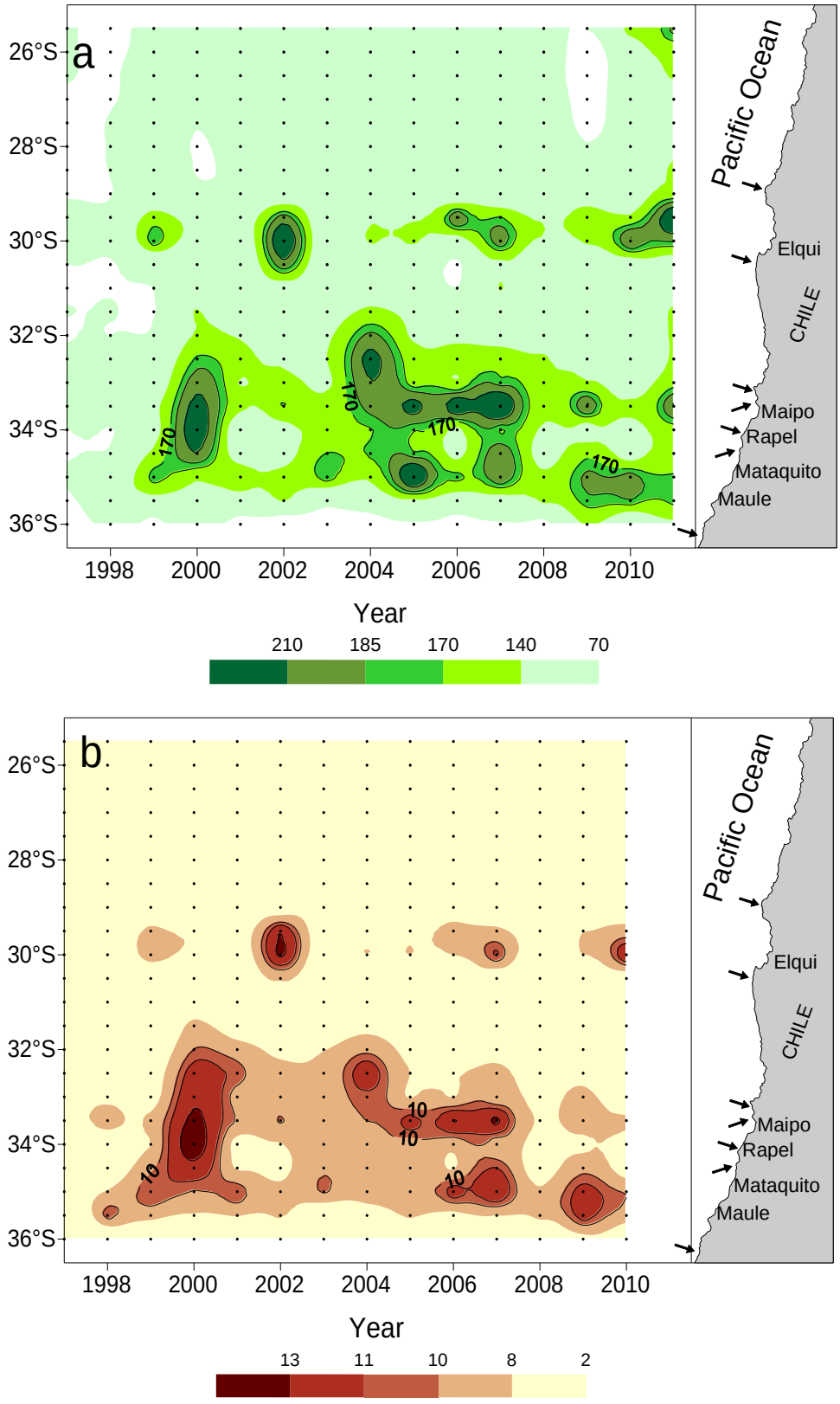

Fig. 2. a) Isopleths of absorption coefficient of chlorophyll-*a* concentration (mg m^{-3}) and b) organic matter and dissolved detritus (m^{-1}). Dots represent the information nodes. Over the map the main river names are displayed. The black arrows correspond to main upwelling zones.

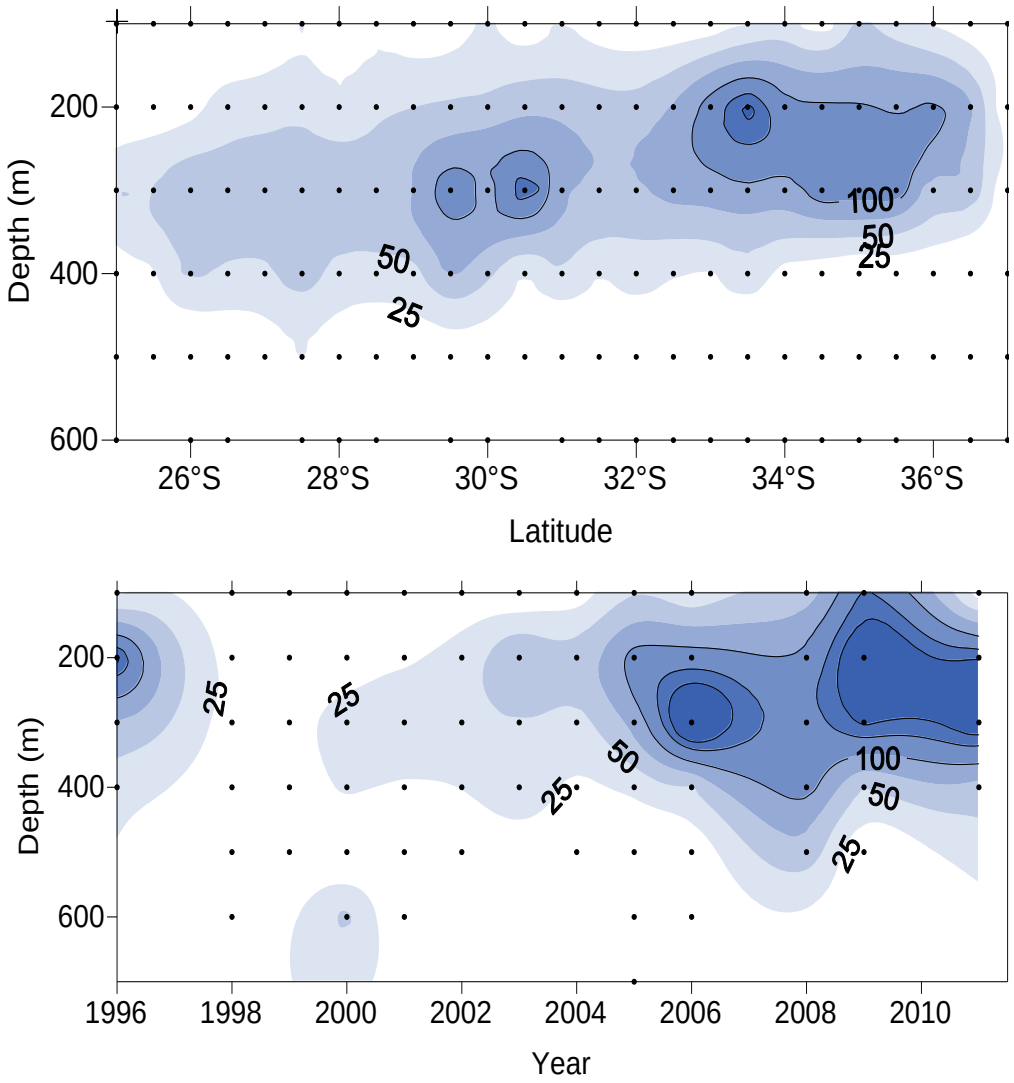

Fig. 3. Isopleths of abundance (kg km-lineal^{-1}) of *Heterocarpus reedi* estimated in surveys using swept area method by depth, latitude, and year. Dots represent the information nodes.

Different year-lags were analyzed (0-3 years). The partial correlation analysis shows that the highest level of linear relationship (0.43-0.67) between the environmental variables and the population abundance southward 32°S are obtained when a 2-year lag is considered (Table 2). This situation improves significantly when the survey of 2002 (year 2000 for environmental variable) is addressed as an out layer and excluded from the analysis, in which case the annual variability of relative abundance of *H. reedi* presents a considerable and significant positive correlation with respect to the anomalies of OMD and Chl-*a*, reaching coefficients of r = 0.78 (*P*-value = 0.0086, *F* = 11.93) and r = 0.86 (*P*-value = 0.0012, *F* = 24.06) respectively (Fig. 6). The significance level is also confirmed because the correlation coefficients are larger than the critical correlation (r^*) of Pyper & Peterman (1998), estimated in 0.75 (N^* = 3.67, $t_{(0.975,11)}$ = 2.02) for OMD and 0.79 (N* = 2.90) for Chl-*a*. Here, two probable reasons could explain the lack of a relationship between the environmental conditions in 2000 and the abundance of *H. reedi* in 2002: modifications in the survey sampling design as mentioned earlier, or the population inelasticity to respond the large positive environmental anomaly recorded in 2000.

Table 2. Autocorrelation's coefficients for explanatory variables and Pearson's correlation coefficients of environmental variables organic matter and dissolved detritus (OMD) and chlorophyll-*a* (Chl-*a*) vs *Heterocarpus reedi* abundance in zone 32°-36°S for two analysis cases. In bold the highest scores are indicated.

				Correlation coefficients			
	Autocorrelation coefficients			All data		Excluding year 2000	
lag (yr)	OMD	Chl-*a*	Abundance	OMD	Chl-*a*	OMD	Chl-*a*
0	1.00	1.00	1.00	-0.15	0.29	0.15	0.49
1	-0.05	0.18	0.89	-0.05	0.36	0.15	0.51
2	-0.58	-0.49	0.89	**0.43**	**0.67**	**0.78**	**0.86**
3	-0.29	0.00	0.93	0.24	0.57	0.43	0.70

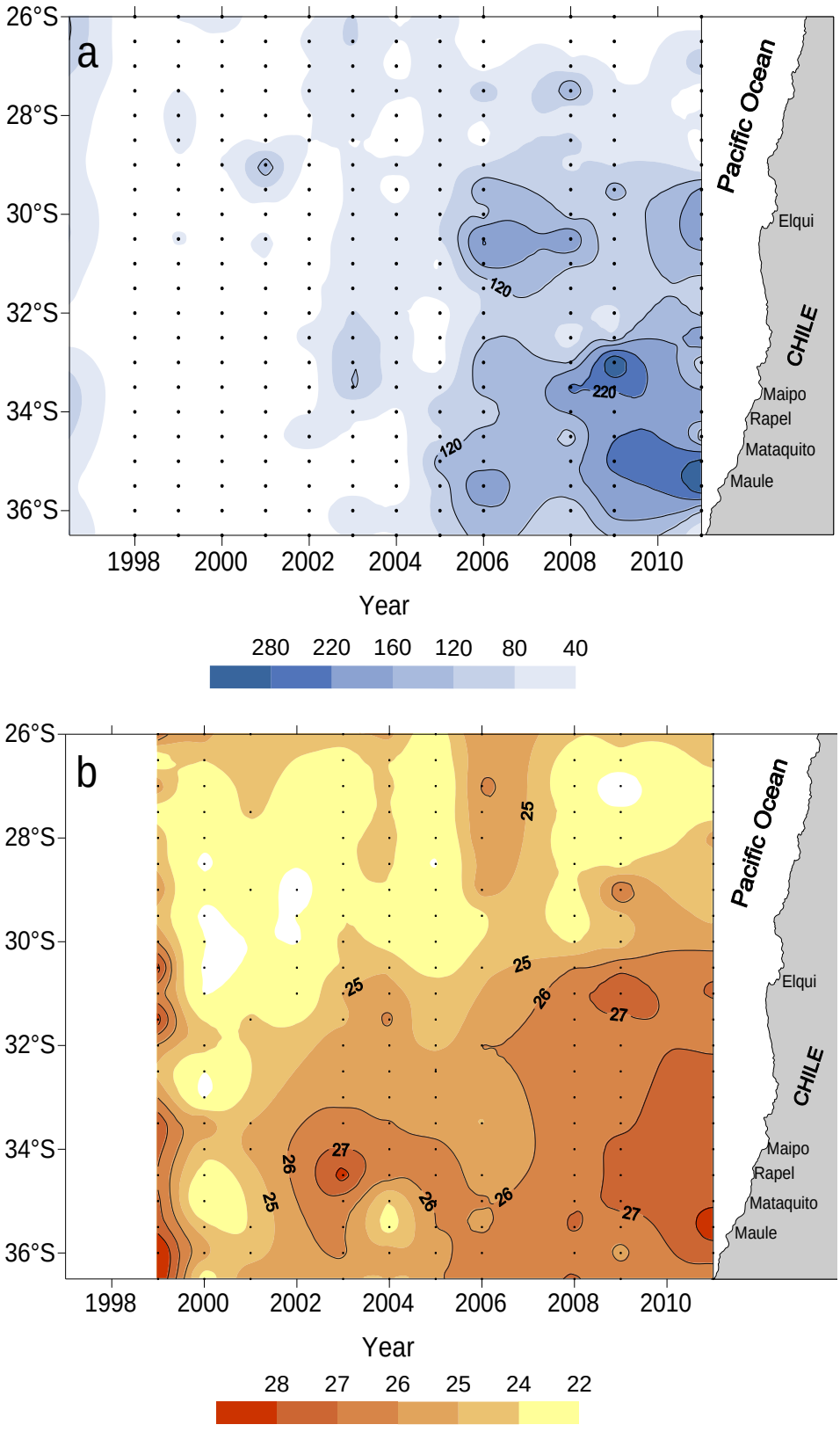

Fig. 4. a) Isopleths of abundance (kg km-lineal^{-1}), and b) mean carapace length (mm) (both genders) of *Heterocarpus reedi* estimated in surveys using swept area method by latitude and year. Dots represent the information nodes.

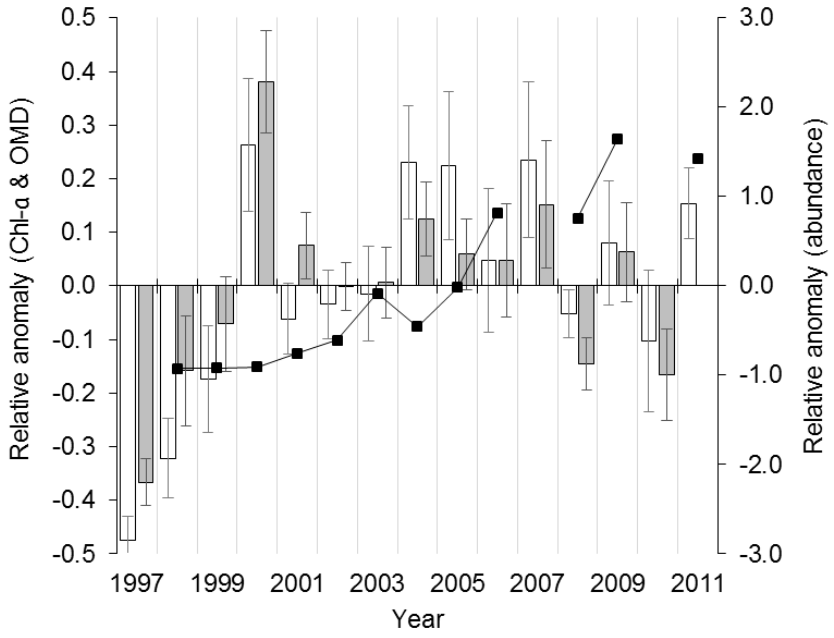

Fig. 5. Anomalies of environmental variables and abundance of *Heterocarpus reedi* by year in zone 32°-36°S. The white and gray bars represent Chl-*a* and organic matter and dissolved detritus (OMD), respectively. The black line corresponds to shrimp abundance. Error bars represent two times the standard error.

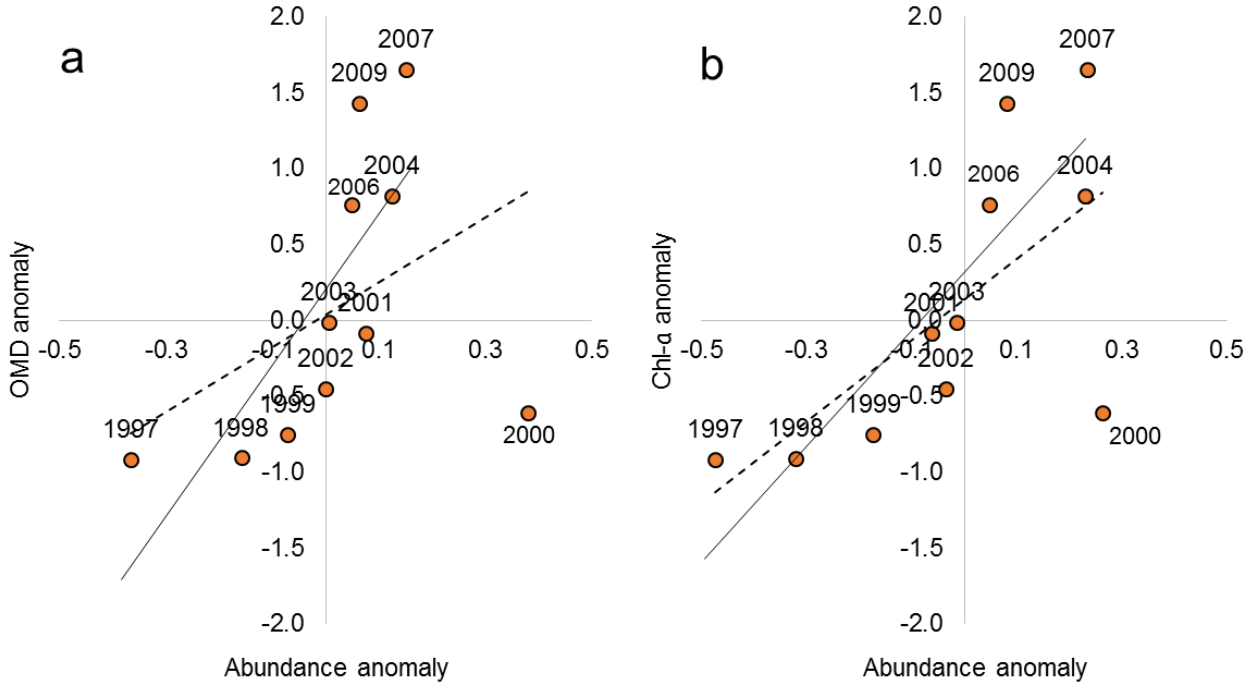

Fig. 6. Linear relationship between anomalies of shrimp abundance *Heterocarpus reedi vs* a) organic matter and dissolved detritus (OMD), and b) chlorophyll-*a*. (Chl-*a*) Environmental variables are delayed two years relative to the abundance anomalies. The year labels are related to environmental variables. Continuous line represents the situation when year 2000 is excluded from analysis.

DISCUSSION

The highest increase of population biomass of *H. reedi* over the last years is registered since 2006, mainly southward 32°S (Table 1), increase that was joined by the south-to-north geographic expansion through a colonization of less dense areas and expanding the range of its bathymetric distribution (Figs. 3, 4). This agreed with report in Roa & Bahamonde (1993), who observed the same orientation in the population expansion of red squat lobster (*Pleuroncodes monodon*) at the central-southern zone of Chile. The colonisation of areas as expansion mechanism of populations has been extensively discussed on the scientific literature (*e.g.*, Rockwood, 2006), and particularly on crustaceans decapods by authors such as Fogarty & Botsford (2006), Fëlix-Hackradt *et al*. (2010) and Lavesque *et al.* (2010).

The main nuclei of aggregations of the *H. reedi* were located nearby the mouths of rivers and upwelling zones, which is a characteristics in other coastal decapods by Haas *et al*. (2001); Medina-Reyna (2001); Ramírez-Rodríguez *et al*. (2003) and Carvalho *et al*. (2011). In this context, at the southern area of the distribution of *H. reedi* where the main river effluents and upwelling zones are located (southward 32°S), a significant correlation between abundance and concentrations of OMD and surface Chl-*a* was found (Table 2, Fig. 6). This correlation was maximum (r = 0.78-0.86) when a two-year lag was considered among the variables, which coincides with the age at which the shrimp reach around 11.5 mm CL size (*e.g*., Ziller, 1993; Roa & Ernst, 1996; Canales *et al*., 1999) and starts to be available at recruitment zone and/or fishing gear. Similar findings have been reported by Company *et al*. (2008) and Díaz-Ochoa & Quiñones (2008), who found important correlations with temporal lags, between environmental variables and abundance of depth crustaceans.

The possible explanation to the relationship found is that, when there are good surface environmental conditions of OMD and Chl-*a*, derived probably from the discharge of rivers and the coastal upwelling mentioned above (Fig. 2), the conditions would be favourable for feeding and spawning of adults and for the survival of larvae and post-larvae. Later, these would settle following the course of the larval drift and would recruit to the fishing gear or zone as juveniles of two years old. As a consequence of the south-to-north direction of the Humboldt Current System (Glantz, 1998; Lorca *et al*., 2004; Fuenzalida *et al*., 2008; Silva, 2012), whose mean maximum surface speed can be higher than 15 cm s^{-1} (Fuenzalida *et al*., 2008), larvae could be transported more than one thousand km in three months, which would explain the direction and orientation of the spatial expansion of the *H. reedi* population indicated above.

One of the most important differences in the population characteristics is the predominance of adults (>25 mm de CL) southwards 32°S (Fig. 4b), where most biomass increases are explained by somatic growth and a higher abundance, thus constituting the bulk of the parental population. Here, the absence of main predators as common hake (Arancibia & Neira, 2008) could have facilitated a faster growth in the shrimp population. Following the idea of Pulliam (1988), Hanski & Gilpin (1997), and Hanski (1998), this area could be compatible with the concept of “source habitat”, while the zone northward 32°S could receive part of the contribution of larval drift coming from the southern zone, conforming a “pseudo-draining habitat”, which may explain the lower population size and the higher presence of juveniles in that area. In this context, Rockwood (2006) indicated that a heterogeneous quality of the habitat can generate larger and more productive populations as a source of migrants towards poorer zones, and that the spatial expansion and colonization in decapods is ruled by the process of larval dispersion (Epifanio *et al*., 1984; Ernst *et al*., 2005; Fogarty & Botsford, 2006, 2007).

Therefore, both the dynamics of length compositions as the spatial patterns in the population abundance suggest that the *H. reedi* could constitute a metapopulation, with at least two sub-populations located northward and southward of 32°S. The most important of them would locate between the mouths of Maipo and Maule rivers (33°43'S-35°18'S), and the smallest one with a nucleus located between the mouths of Elqui River and Punta Lengua de Vaca (30°23'-31°12'S). This proposal of population structure could be complemented by the basin model of McCall (1990), in which there is a central nuclei with the highest density of individuals, and the population growth is generated by the "overflow" of biomass toward areas less dense. In this model, advection it is one of the mechanisms described and therefore larval drift could give support to the metapopulation hypothesis. Another evidences were given by Acuña *et al*. (1997), who investigated morphometric aspects in *H. reedi* and found out significant differences between the sample coming from the region Caldera-Coquimbo (27°03'-29°58'S) and from the region Quintero-Tomé (32°46'-36°35'S). These authors complemented their results with a genetic analysis, determining that population heterogeneity would be explained by a migratory process along the spatial distribution, but at rates that are insufficient to revert the effect of dispersive-genetic factors.

CONCLUSIONS

The extensive amount of information analysed in this paper, which was obtained from thirteen years of trawling surveys on *H. reedi* off Chile, correlated with data of environmental variables (Chl-*a* and OMD) obtained through satellite telemetry, shed light on aspects of population dynamics of this species. Noticeable patterns in environmental conditions along shrimp

distribution were identified, mainly in those areas close to rivers mouth and upwelling zones southward 32°S, which would be related with fluctuations in abundance and distribution of *H. reedi*.

This evidence was supported by good correlation levels between abundance and distribution of environmental variables, and whose explanation could be given by the relationship between good environmental conditions, larval survival success and its later settlement before to reach the recruitment size at two years old. The shrimp population is likely to be constituted by a metapopulation structure with at least two subunits located each north and southward 32°S, and whose connectivity would be explained by larvae drift through Humboldt Current System in south-north direction, situation very relevant for fishery management when them are considered as independent stock units. In this sense, given the level of relationship found between the environmental variables and the abundance of the *H. reedi*, including the population structure, it is concluded that is need to further investigate and strengthen this evidence, since this could become as a forecasting tool in the management of this fishery when poor environmental anomalies be detected. To reinforce that, also it is suggested to develop a more detailed research on the early development stages of this crustacean related to its larval drift along the coast of Chile and its dependence with environmental factors.

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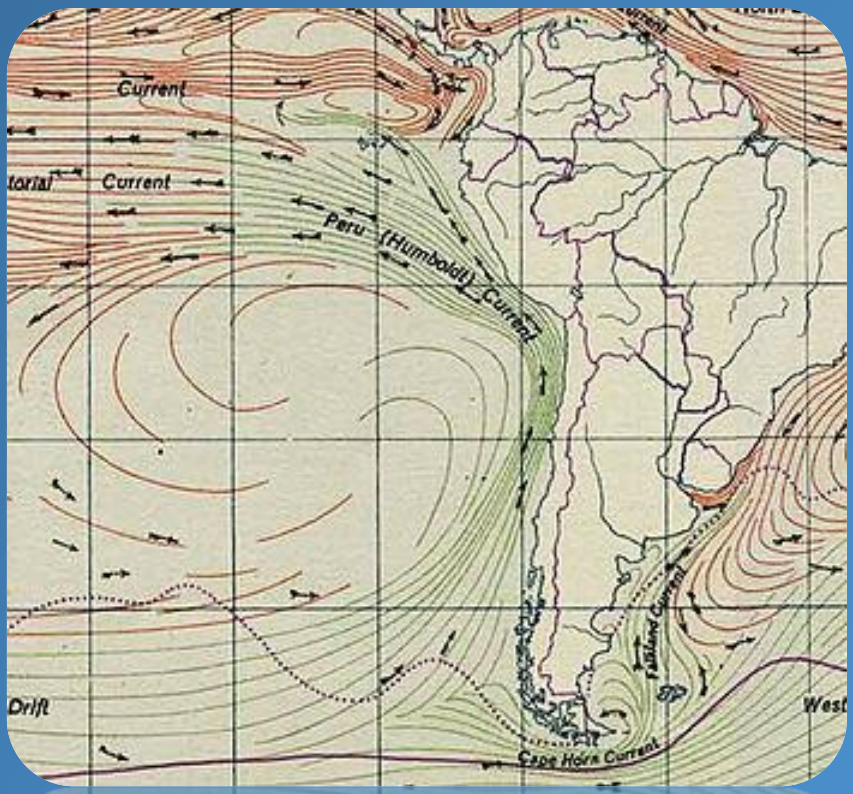

II.2. Spatio-temporal modelling of the maturity, sex ratio, and physical condition of nylon shrimp *Heterocarpus reedi* (Decapoda, Caridea), off Central Chile

Canales, C.M, J.B. Company & P.M. Arana, 2016. Spatio-temporal modelling of the maturity, sex ratio, and physical condition of nylon shrimp *Heterocarpus reedi* (Decapoda, Caridea), off Central Chile. *Fisheries Research.* 179 (2016) 1–9. http://dx.doi.org/10.1016/j.fishres.2016.02.001

ABSTRACT

Two key elements in the adequate, sustained exploitation of any fishery should be considered; the biological attributes of the species and how these vary over time and space. Research is needed to obtain a more thorough understanding of these effects, how they vary, and how they relate to environmental factors. For 17 years, biological information has been collected for *Heterocarpus reedi* (nylon shrimp) caught off central Chile (25-37°S). Here, we analyze these data using generalized linear models and determine the factors responsible for changes in carapace length, body weight, maturity, and sex ratio. The environmental and alimentary conditions are better south of 32°S, and this is probably associated with the better physical condition and reproductive attributes of *H. reedi* there. For example, individuals are larger, females are longer at first maturity ($CL_{50\%}$), and mature females are less prevalent. We outline a theoretical foundation that can guide future research on *H. reedi*. We also suggest that future conservation measures consider biological attributes within a spatial context.

Keywords:

Heterocarpus reedi, generalized linear models, maturity, spatial distribution, sex ratio

1. Introduction

Important changes in the abundance and distribution of many marine benthic species are determined by substrate, environmental characteristics, and exploitation (e.g., Loneragan and Bunn, 1999; Diaz-Ochoa et al., 2004; Encarnaçaô et al., 2013; Sancinetti et al., 2014; Canales et al., 2016). These factors also affect seasonal differences in, and the persistence of, biological parameters (e.g., Company et al., 2001, 2004; Araújo et al., 2014) and may even give rise to discrete population units or metapopulations (e.g., Fogarty and Botsford, 2006; Josileen, 2011; Sethi et al., 2013; Sal-Moyano et al., 2014).

Heterocarpus reedi (nylon shrimp) is one of the most important decapod crustaceans exploited in central Chile (25-37°S), with catches of ~4,000 tons year^{-1}. This species is distributed continuously on the continental shelf and upper slope, between 200 and 400 m depth (Fig. 1), occupying a heterogeneous habitat made up of clay soil, sedimentary rock, sand, and mud. The water column in this area contains both equatorial subsurface waters, which are low in dissolved oxygen, and Antarctic intermediate waters, which are cool (10-12°C), but have relatively high salinity (34.5-34.9 g kg^{-1}) (Silva, 2012). In the south of the study area, river discharge (Canales et al., 2016) and coastal upwelling (mainly in spring) (Silva and Valdenegro, 2003) lead to important amounts of organic matter.

Our understanding of the biology of *H. reedi* is varied. Much information is restricted to finite time periods, for example the early works on reproductive process, growth, and condition factor of *H. reedi* (Arana and Tiffou, 1970; Bahamonde and Henríquez, 1970; Arana et al. (1976). Those authors suggested, among other things, probable spatial heterogeneity in length at first maturity as a response to environmental conditions. Nonetheless, research that

extends the space-time dimension or that focuses on other biological attributes (e.g., physical condition, sex ratio, length at maturity) and their variations in time and space remains limited.

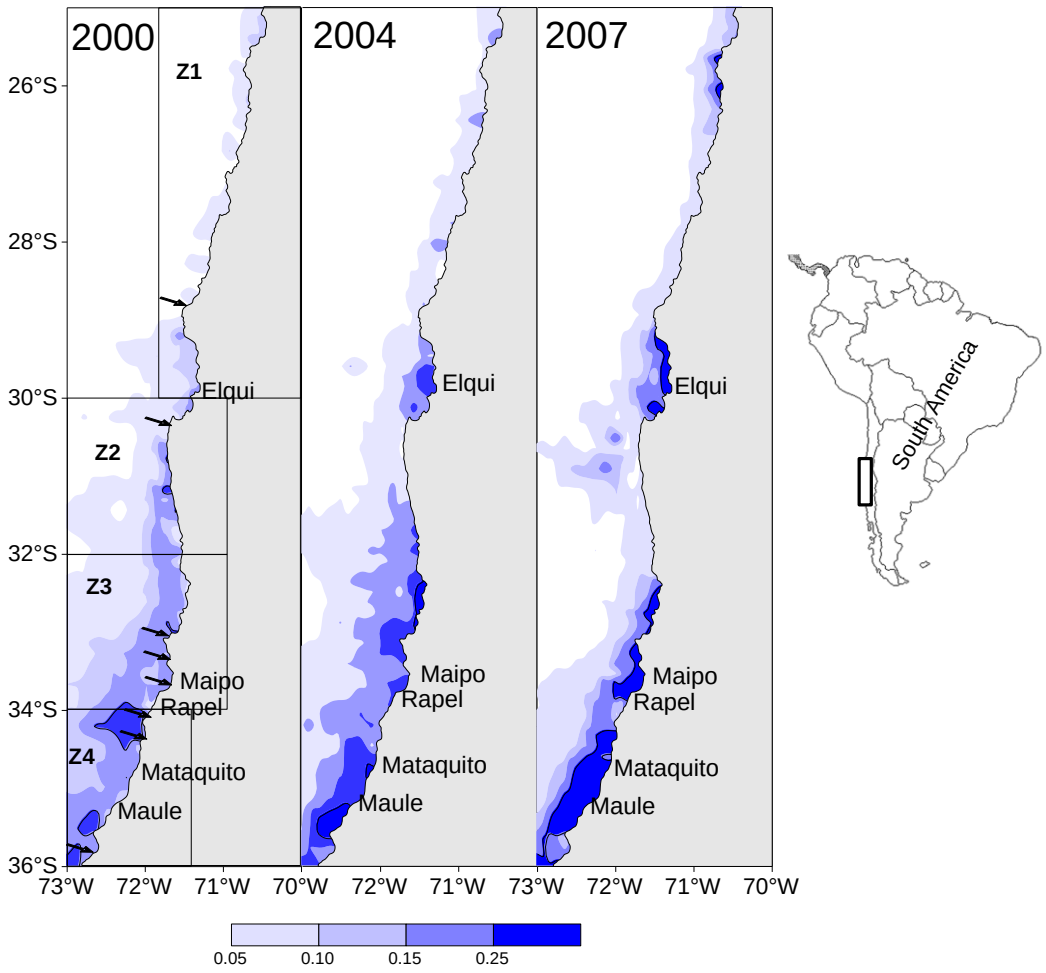

Figure 1. Study zone and distribution of cumulative organic matter and dissolved detritus between September and December in three years, with the main river names are displayed. The black arrows indicate the main upwelling zones. The rectangles make reference to subzones of analysis.

We analyzed 17 years of biological information gathered while monitoring the extraction activities of *H. reedi* to understand the patterns and trends of the factors and variables that determine the spatio-temporal changes in its biological attributes, maturity state, physical condition, body length, and sex ratio. Our results contribute to understanding the spatial heterogeneity of these attributes as affected by the environmental conditions observed off the coast of Chile between 1997 and 2013.

2. Materials and methods

2.1. Data source

Biological samples were taken by the Fisheries Development Institute (Instituto de Fomento Pesquero, IFOP). Samples were taken in south-central Chile (25°-36°S) between 1997 and 2013, as part of a program that not only monitors fishing activity at the main landing ports and processing plants, but also performs on-board sampling. The individuals used for biological samples were selected to represent, in a nonrandom manner, the greatest size range possible. Specimens were taken from the final haul of each fishing trip, allowing us to measure variables that would have been difficult to measure on land (e.g., body weight, morphometric measurements). Statistically, this sample was consistent with prior studies that showed, for example, weight and state of maturity to be heavily dependent on individual carapace length. Because of this, more observations should be made at either end of the size frequency spectrum. For each individual, we recorded: the date and geographic location of capture, sex, carapace length (CL) in millimeters, and total wet weight in grams. For females, the

reproductive status (mature or immature) was also recorded, as determined by the presence or absence of eggs in the abdomen.

2.2. Statistical analysis

We used Generalized Linear Models (GLM; McCullagh and Nelder, 1989) to analyze four biological response variables (CL, individual weight, maturity, sex ratio), in the same sense as several other authors have used GLM to analyze maturity at size (or age) and the sex ratio (e.g., ICES, 2008; Lambert et al., 2009; Wheeler et al., 2009; Stewart et al., 2010). The models were specified and fit using the language and environment for statistical computation and graphics R (R Development Core Team, 2009). An analysis of deviance was used to evaluate the importance and significance of each predictor variable included in the model. This was complemented by an Akaike Information Criterion (AIC) analysis (Akaike, 1974), which was used to evaluate the relative increase of AIC after excluding specific terms from the full model through the *drop1* function included in R language.

This analysis considered four factors as discrete predictor variables: year (Y), quarter (Q), zone (Z), and sex (M: male, F: female, MF: mature female); and carapace length (CL) as a continuous predictor variable. The models describing the proportion of mature females, total females, and body weight included CL. While analysis focused on model main effects, the first-order interaction defined by quarter*zone also was evaluated to know if seasonality of some dependent variable is determined by spatial influences (zones). Other interactions were not considered to avoid decompensation of the design matrix. Both CL and the logarithm of weight were assumed to be normally distributed (Gaussian error model) with link functions "log" and

"identity", respectively, whereas the proportions (of mature and of total females) were assumed to have a binomial distribution with a "logit" link function (Table 1).

Only females (126,252 individuals) were used for the analysis of the proportion of mature individuals. Maturity was designated as a binary variable (p) according to the presence (1) or absence (0) of eggs in the pleopods. After fitting the model and regardless of the year, the length at first maturity was calculated in each zone and for quarter (Q*) with the highest proportion of mature females, using the estimator $\mathrm{CL}_{50\%} = \beta^{-1}(-\alpha + \bar{Y} + Q^{*} + Z)$, where α is the model intercept and β is the coefficient CL. $\bar{Y}$ is the average of year factor coefficients, including value zero for reference treatment (first level of each factor). Similarly, for the analysis of the proportion of females in the samples, the same statistical attributes of the maturity model were considered, but this time applied to all the individuals measured. The binary response variable corresponded to presence (p=1) or absence (p=0) of females in the samples.

Table 1. Generalized Lineal Models used to describe variability of carapace length (CL), weight, maturity and sex ratio of *Heterocarpus reedi*.

Response variables	Error	Link	Predictor variables
CL	Gaussian	Log	Year+Quarter+Zone+Sex
log(weight)	Gaussian	Identity	Year+Quarter+Zone+Sex+log(CL)
Maturity	Binomial	Logit	Year+Quarter+Zone+CL
Sex ratio	Binomial	Logit	Year+Quarter+Zone+CL

3. Results

3.1. Preliminary data treatment

The information was classified by year, quarter, and zone (Z1: 25°-30°S; Z2: 30°-32°S; Z3: 32°-34°S; Z4: 34°-36°S) (Fig. 1), considering both the latitudinal distribution of the fishery and whether or not sufficient observations were made in each stratum. A total of 295,000 individuals were collected and measured during the study period. Of these, 52% were females and 21% of those were mature. The highest incidence of maturity (45%) was recorded in the third quarter (July-September) of each year (Fig. 2). Due to the low spatial representation of the samples taken between 2000 and 2002 (Fig. 2), these data were discarded from the maturity analysis, reducing the sample size to ~126,000 individuals.

In general, the H. reedi carapace length (CL) measured between 10 and 40 mm CL, averaging nearly 25 mm CL and 7.25 g. Females were more prevalent in catches over 26 mm CL and were, on average, larger than males (up to 38 mm CL vs. about 33 mm CL) (Fig. 3a). The prevalence of ovigerous females was greater during the third quarter, with mature individuals starting at 22 mm CL and reaching a maximum incidence of 80% at lengths >30 mm CL (Fig. 3b). It is likely that not all mature females were included in the count because the larger individuals may have released their eggs before sampling.

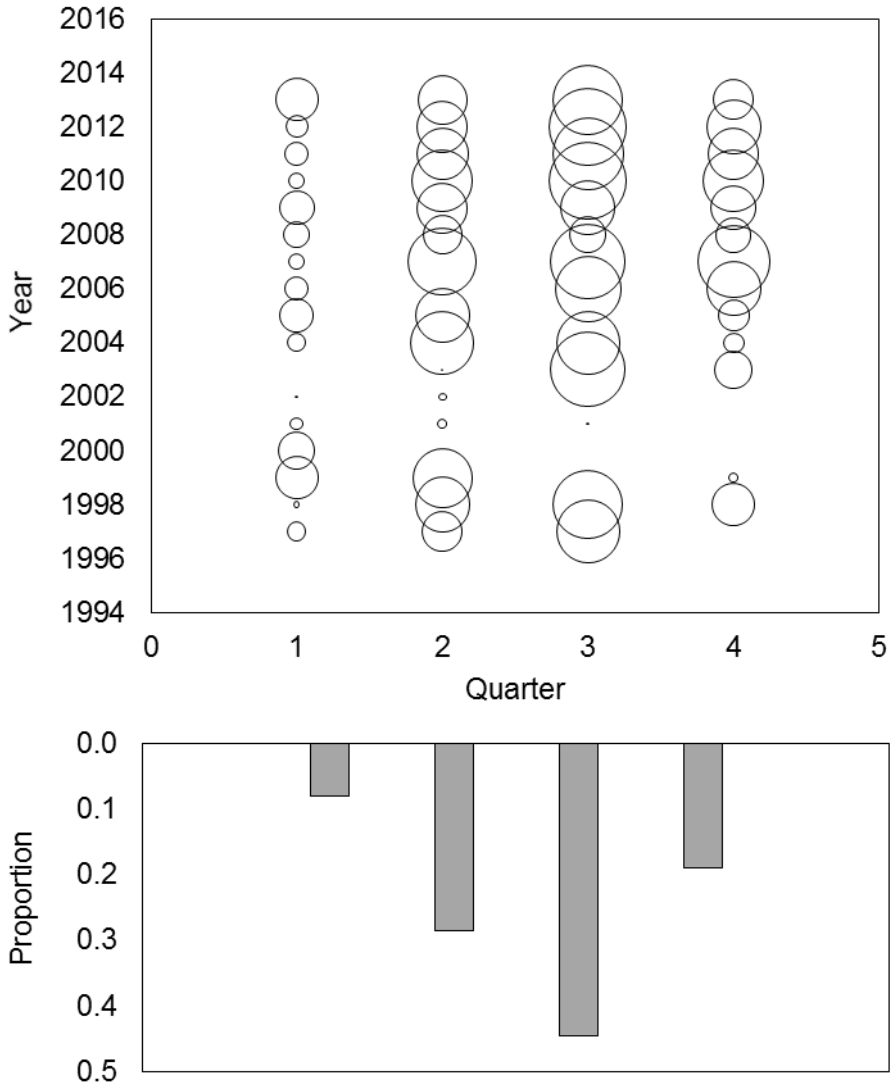

Figure 2. Proportion (average) of mature females of *Heterocarpus reedi* by year and quarter. The bubble size represents the relative importance within the year, estimated by dividing the number of mature females by the number of total females each quarter and year. The bars represent the expected value across the years.

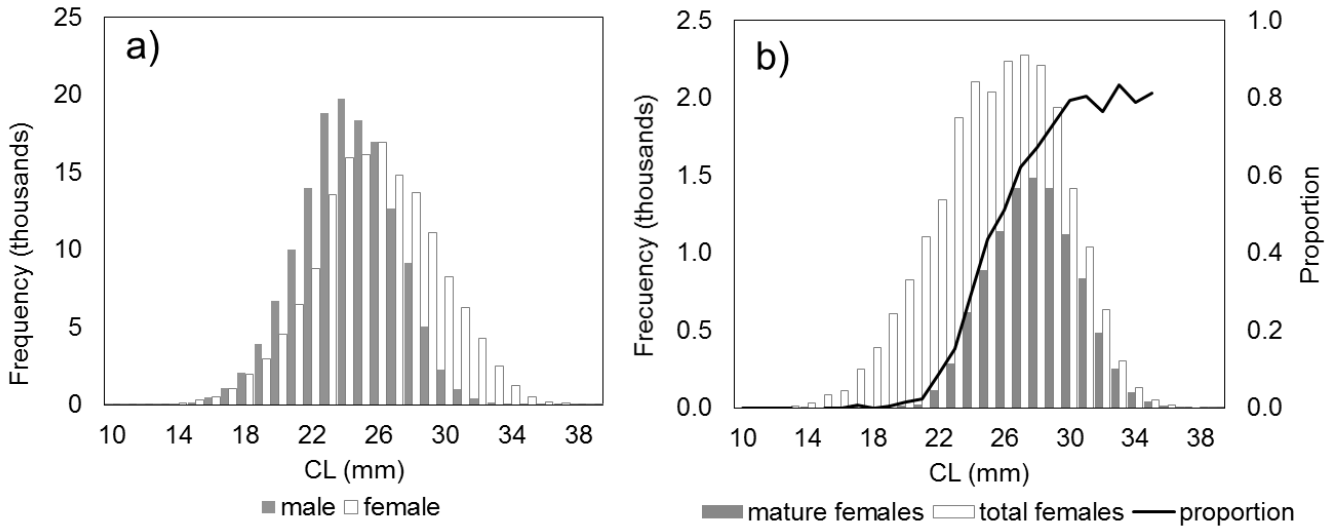

Figure 3. Histogram of carapace length (CL) of biological samples of *H. reedi*. (a) Males (n = 142,927) and females (n = 152,000), (b) mature females (n = 10,249) and total females (n = 23,005) measures in the third quarter of each year. The solid line represents the proportion of mature females.

3.2. Model fit diagnostics

The models fitted the data adequately both in variability and trend (left panels Fig 4). For CL and W, normal quantile-quantile plots (qq-plot) and studentized residuals were considered, while only deviance residuals were considered for the logistic models. The qq-plots for CL and W suggested that the assumed error model appears adequate (center panels Figs. 4a, 4b), while the studentized residuals did not show significant trends against the predicted values (right panels Figs. 4a, 4b). For logistic models the same situation was observed (center panels Fig. 4c, 4d), where there no trends in residuals within each groups (binary response), and the

dispersion diagram between predicted values against residuals shows an expected profile, with two curves with monotonic decrement around zero (right panels Figs. 4c, 4d).

3.3. Carapace length and body weight

According to the GLM models, all the factors considered were significant (Table 2). In particular, the main factors determining the variability of *H. reedi* carapace length (CL) and body weight were sex ($p<0.001$, $F=16.1e3$) and zone ($p<0.001$, $F=7.3e3$); and CL was the co-variable in the GLM for body weight (Table 2).

The GLM coefficients showed that the average length and weight of *H. reedi* individuals increased significantly from north to south. The individuals from Z4, the southernmost zone, were, on average, 12% longer and heavier than those from Z1, the northernmost zone (Table 2, Fig. 5b). Overall, females were 4% longer and heavier than males. Likewise ,and irrespective of the CL, the coefficients of the model indicated that berried (mature) females weighed 16% more than resting females (Fig. 5d), whereas the coefficient of the length-weight ratio ($b=2.90$, s.e.=0.002) indicated negative allometric growth for *H. reedi* ($b<3$) (Table 2).

Seasonally, both CL and body weight decreased significantly towards the second and third quarters of each year (Fig. 5a), coinciding with the period of greatest reproductive activity (Fig. 2). Annually, CL growth was found to follow a linear trend (slope>0, p-value=0.00035), particularly from 2007 to 2013, while in the weight's model, the annual effect shows that this can vary independently to body size (Figs. 5c), as for example, when annual variations of condition factor occur. In these GLMs, the first-order interaction (quarter*zone) had few contribution in the model's deviance explanation (ΔAIC<1%).

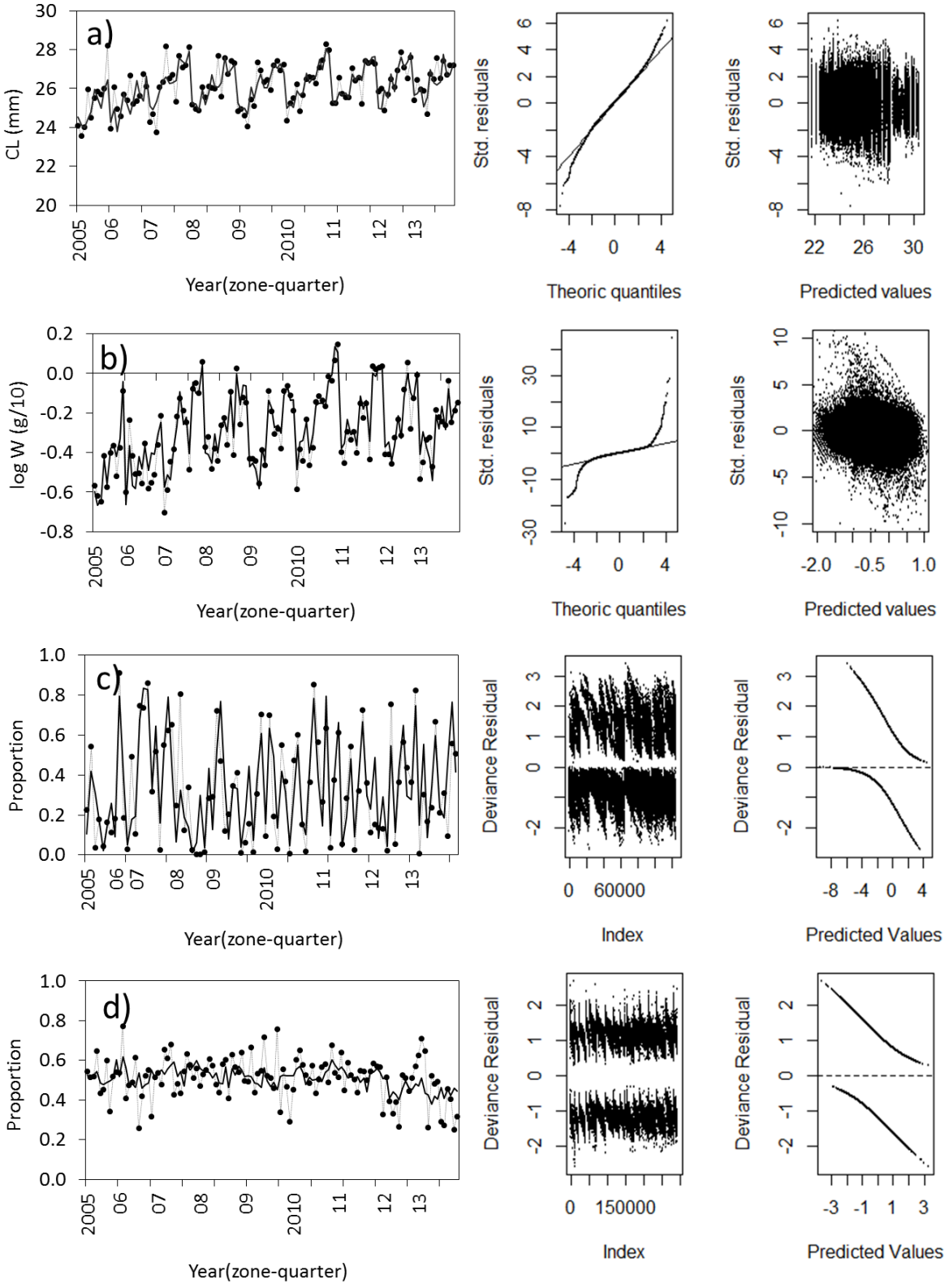

Figure 4. Model fit diagnostics. Each row corresponds to a different variable: a) carapace length (CL), b) log-weight (W), c) maturity ratio, d) females proportion. Left panels represent the average values by year, zone and quarter (the line is the model fit and the dots are data), where time scale was reduced for improve visualization of model fit. The center panels show respectively the normal quantile-quantile plots for CL and logW, whereas the plots in the 3th and 4th rows are residuals over time. The right panels how the residuals versus the predicted values.

Table 2. Main statistics of generalized linear models applied to carapace length (CL), log(weight), maturity, and sex ratio of *Heterocarpus reedi*. ΔAIC shows the porcentual increment of AIC when from the full model a predictor variable is excluded.

		Response variable											
Predictor		Carapace length			log(weight)			Maturity			Sex ratio		
variable	Level	ΔAIC	Coeff.	*t*	ΔAIC	Coeff.	*t*	ΔAIC	Coeff.	*t*	ΔAIC	Coeff.	*t*
Intercept			3.142	2482.4		-7.527	-976.2		-9.277	-109.9		-3.862	-97.2
Quarter (Q)		0%			1%			21%			0%		
	Q2		-0.029	-52.3		-0.033	-44.9		2.170	94.4		-0.013	-1.3
	Q3		-0.031	-45.8		-0.042	-45.9		3.462	127.1		0.050	4.1
	Q4		-0.013	-22.9		-0.008	-10.6		1.506	63.2		0.001	0.1
Zone (Z)		2%			8%			6%			0%		
	Z2		0.032	41.3		0.017	16.5		-0.830	-27.6		-0.261	-18.4
	Z3		0.068	110.7		0.069	82.1		-2.028	-73.2		-0.469	-40.9
	Z4		0.093	147.1		0.125	141.4		-1.361	-55.8		-0.417	-34.0
Year		1%			5%			4%			1%		
Sex		2%			11%								
	F		0.042	95.1		0.032	53.7		-	-		-	-
	MF		0.122	182.1		0.181	179.8		-	-		-	-
CL			-	-		-	-	10%	0.263	95.1	5%	0.180	130.9
log(CL)			-	-	187%	2.907	1210.3		-	-		-	-
Z*Q		0%			1%			5%			0%		

AIC: Akaike Information Criterion. F: females. MF= mature females.

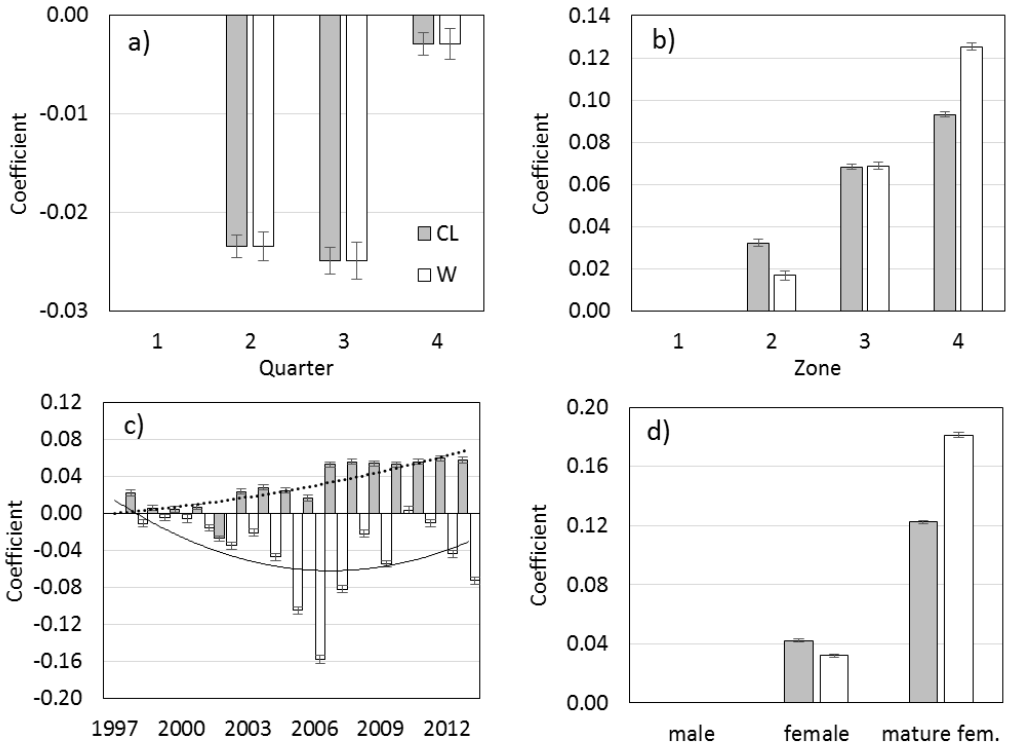

Figure 5. GLM's coefficients related to carapace length (gray bars) and individual weight (white bars) for *H. reedi*. The effects are: (a) quarter, (b) zone, (c) year, and (d) sex. The trend lines represent the annual factor by year (c).

3.4. Maturity and sex ratio

According to the GLM that described both the variability of maturity and the proportion of females, CL and quarters were the most relevant and significant variables in the model ($F>12E3$, $p<0.001$, $\Delta AIC>5\%$). The magnitude of the coefficients revealed that the third quarter was the most influential in the proportion of mature females (Table 2, Fig. 6a). The proportion of mature females decreased significantly from north to south, particularly south of 32°S (Z3, Z4) (Fig. 6b). The results also indicated, though with less influence on the model, that the annual effect on the proportion of gravid *H. reedi* females was variable and increasing over time (Fig. 6c). Also, a small but significant AIC variation ($\Delta AIC=5\%$) was observed when the quarter*zone

interaction was excluded from full model, it that might suggest that shrimp maturity depends on spatial and temporal covariates.

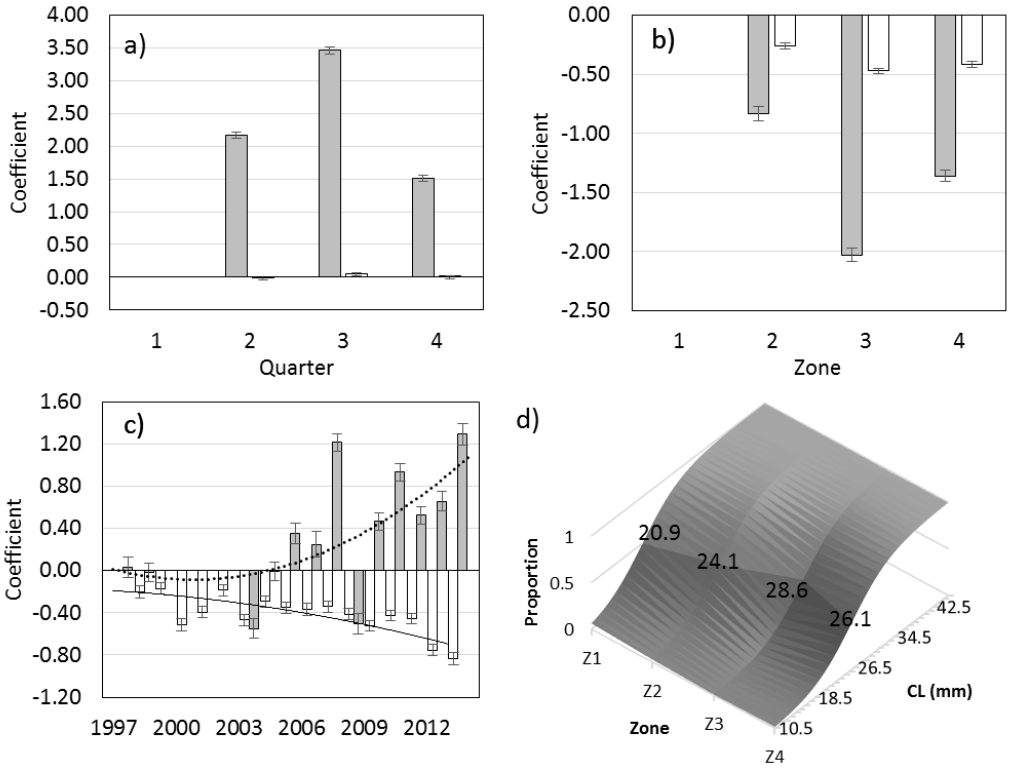

Figure 6. GLM's coefficients related to maturity (gray bars) and the proportion of females (white bars) for *H. reedi*. The effects are: (a) quarter, (b) zone, and (c) year. The trend line represents the annual factor by year (c). Panel (d) show the maturity ogive by zone where are included the $CL_{50\%}$ estimations.

Taking the third quarter to be the period when reproductive activity peaked for *H. reedi*, estimates of size at 50% maturity ($CL_{50\%}$) were significantly different between zones. North of 32°S, $CL_{50\%}$ ranged from 24.1 mm (Z2) to 20.9 mm CL (Z1), whereas south of 32°S, $CL_{50\%}$ was significantly higher, ranging from 28.6 mm (Z3) to 26.1 mm CL (Z4) (Fig. 6d). These data explain the greater proportion of gravid females observed in the north, since the lower

the $CL_{50\%}$ value, the greater the fraction of mature individuals for the size ranges considered. Combining all years and zones, the model that described the proportion of maturity at size for *H. reedi* during the third quarter was P(CL)=exp(-6.53 + 0.26 CL)/(1+exp(-6.53 + 0.26 CL)), in which the parameter -6.53 was the sum of the value of the GLM intercept plus the average of the coefficients of the factors of the model: year, zone, and third quarter. $CL_{50\%}$ was estimated to be 24.9 mm CL (Fig. 7a). Annually, the results suggested a negative trend for $CL_{50\%}$ (r^2=0.65, p=0.005), as this fell by 32% between 2008 and 2013 (Fig. 7b, 7c).

With respect to the sex ratio (female), CL was the most important variable (ΔAIC=5%). Two other factors, Zone (F=483) and Year (F=95), had a lesser, albeit still significant influence on the model, indicating a lower proportion of *H. reedi* females south of 32°S (Fig. 7b). When combining all the factors, the logistic relationship between CL *vs.* sex ratio showed that females were dominant in the population (>50%) beginning at 25 mm CL; this figure was similar to the $CL_{50\%}$ reported earlier (Fig. 7a).

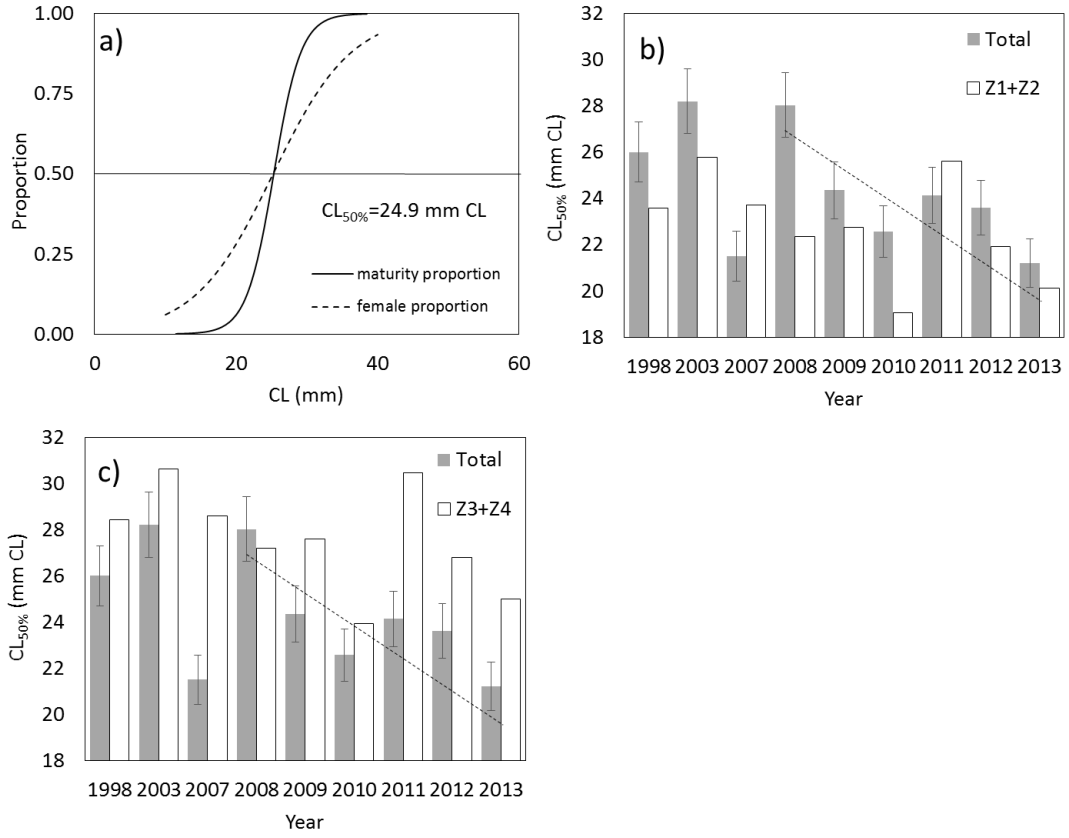

Figure 7. (a) Proportion of mature females by size of *H. reedi* in the third quarter, for all years and combined zones, plus the proportion of females by size. In panels b) and c), comparative annual changes in maturity size (CL50%) by zones: total vs Z1+Z2 combined (b), total vs Z3+Z4 combined (c). The dotted line represents the annual trend, and error bars show the 95% confidence interval.

4. Discussion

The main biological attributes of *H. reedi*, particularly those related to physical condition and maturity, showed significant spatial and temporal heterogeneity, as evidenced through biological information obtained with samples taken from commercial catches over the course of 17 years. The spatial pattern for the physical conditions of *H. reedi* could be related to environmental heterogeneity observed along its distribution, which among others could determine food availability. Similar findings have been reported in other marine decapods, where bottom conditions seem explain seasonal and spatial differences in some biological parameters (e.g., Company et al., 2001, 2004; Encarnaçaô et al., 2013; Sancinetti et al., 2014). In our analysis area, north of 32°S there is a semi-desertic weather, low precipitations and a narrow continental shelf, while south, several tributary rivers and coastal upwelling zones contribute with important amounts of organic matter and detritus, and probably determining an important food source (Canales et al., 2016) (Fig. 1). Both individual CL and weight differed significantly on spatial and seasonal scales, with individuals of both sexes being longer and in better physical condition south of 32°S, although these conditions were largely reversed in the third quarter, coinciding with the peak of the reproductive process. Weight loss during the reproductive process can be attributed to increased energy consumption while carrying eggs (females) or producing sperm (males) (Bauer, 2004), to the detriment of energetic investments in individual growth. In common with Gaete and Arana (1986), Anger (1998), Paschoal et al. (2013), and Grabowski et al. (2014), the males in this study were smaller than the females and, starting at 25 mm CL, the females made up a larger proportion of the *H. reedi* population. Also,

further investigations seem be necessary to evaluate the apparent relationship between maturity, zone and quarter.

The proportion of females in the samples showed no significant seasonality and, therefore, no apparent connection to the reproductive process. Instead, a weak geographic pattern was observed: the relative predominance of females decreased gradually from north to south, and was heavily dependent on CL. An early study by Gaete and Arana (1986) that looked at the sex ratio of *H. reedi* reported that females were dominant with no significant differences between months. Those authors also found that females were predominant in the size ranges over 25 mm CL, corroborating the findings of the present work.

Many aspects relative to the maturity of *H. reedi* have already been well documented (e.g. Arana and Tiffou, 1970, Bahamonde and Henríquez, 1970, Arana et al., 1976, Canales et al., 1998). Our results for the period of greatest reproductive activity and size at maturity $CL_{50\%}$ (24.9 mm CL) were similar to those found in previous works: 25.5 mm CL (Arana and Tiffou, 1970), 24.3 mm CL (Canales et al., 1998), and 25.1 mm CL (Arana et al., 1976). Our results also confirmed the spatial pattern suggested by Bahamonde and Henríquez (1970), where length at maturity $CL_{50\%}$ increased significantly from north to south. Tuck et al. (1997), Kuhulmann and Walker (1999), and Queiroz et al. (2013) described variations of this parameter in other regions of the world. Those authors offered different explanations for this phenomenon: from the impact of overexploitation of the larger individuals of a population, which would reduce the average length at age, to the importance of habitat in determining life parameters as a result of discrete population units. In the case of *H. reedi*, the latter may be the more likely scenario since commercial fishing does not seem to have generated significant changes in the

population structure, given the low level of exploitation recorded in the last decade (Montenegro et al., 2014) and the increased biomass reported by Acuña et al. (2012).

Queirós et al. (2013) noted that spatial variations of $CL_{50\%}$ were not yet well understood, but were related to recruitment and hydrodynamic conditions (Hill et al., 1997), sediment characteristics (Campbell et al., 2009), and food availability (Tuck et al., 1997). According to Canales et al. (2016), *H. reedi* has a heterogeneous population structure, with the greatest densities and largest individuals located south of 32°S, where the food supply and probably the sediment quality were greater, in turn, determining the larger sizes of $CL_{50\%}$ mentioned above. The better quality of the habitat may lead to delayed maturity, allowing individuals to allocate more of their energy consumption to growth and, thereby, explaining why few large individuals were found north of 32°S and why females in that area were smaller at maturity. As indicated by Kuhlmann and Walker (1999), latitudinal differences in $CL_{50\%}$ result in implicit changes in the growth patterns and could have important implications for management of *H. reedi* fisheries since the level of fishing mortality that would allow sustainability of this resource depends on both the maturity ogive and life history parameters.

Our results also showed annual trends in key biological attributes. For example, the proportion of mature females has been greater since 2008, in response to a decline in $CL_{50\%}$ observed in the same period. Such changes in biological parameters have often been related with environmental stress factors and exploitation. Indeed, both Phillip (2013) and Zheng (2008) noted that temperature, food, and population density may have led to changes in $CL_{50\%}$. This situation was also studied by Castilho et al. (2007), who established, for example, that the characteristics of the rearing period for *Artemesia longinaris* were correlated with the availability of food for the potential larvae of this decapod. Those authors indicated that $CL_{50\%}$

was the result of a process of reproductive adaptation to the aforementioned environmental factors. For *H. reedi*, Canales et al. (2016) provided environmental indicators associated with the area south of 32°S, showing a suggested decrease in the anomalies of chlorophyll-a and organic matter dissolved since 2008, which could explain in some way the decline in $CL_{50\%}$ mentioned above.

5. Conclusion

This research identified spatio-temporal patterns in the main biological attributes of *H. reedi*, the causes of which seemed to be determined mainly by environmental factor related to the habitat. Better conditions in the southern portion of the distribution area could explain the higher $CL_{50\%}$ and the presence of individuals in better physical condition, thereby suggesting that future studies of *H. reedi* growth parameters and natural mortality be conducted on a similar spatial scale. Finally, our results support the hypothesis of the *H. reedi* population structure proposed by Canales et al. (2016): in brief, the *H. reedi* population structure is spatially heterogeneous, particularly north and south of 32°S. This reveals the importance of considering these characteristics when developing future conservation and fisheries management measures.

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II.3. Using a length-based stock assessment model to evaluate population structure hypotheses of nylon shrimp *Heterocarpus reedi* (Decapoda, Caridea) exploited off central Chile

Canales, C.M, J.B. Company & P.M. Arana (*in press*). Using a length-based stock assessment model to evaluate population structure hypotheses of nylon shrimp *Heterocarpus reedi* (Decapoda, Caridea) exploited off central Chile. *Fisheries Research.*

ABSTRACT

Spatial processes are rarely considered explicitly in the evaluation and management of marine invertebrate populations. This is particularly true when larval drift acts as one of the main mechanisms of population expansion. The ecological concept metapopulation is widely used and accepted for understanding low-mobility marine populations. This study uses a length-based dynamic analysis model for nylon shrimp (*Heterocarpus reedi*) exploited off central Chile (25°-37°S) to contrast various hypotheses of population structure and spatial connectivity. The two subpopulations studied are located to the north and south of 32°S. The model is fitted to the historical fishery data (from the mid-1940s to the present), the results of monitoring of fishing activities (1970s-present), and research surveys (1990s-present). Statistically, several hypotheses can explain the data. The most likely hypothesis is that of a metapopulation in which the south zone acts as a source population (reproductive refuge) and determines, partially or totally, the recruits in the north zone, thereby explaining the population increase over the last decade. Empirical evidence will strengthen the hypothesis of spatial connectivity and special attention should be paid to the biological-fishery conditions recorded south of 32°S given the implications for managing the fishery for this resource.

Keywords:

Heterocarpus reedi, stock assessment, migration, metapopulation, length-based model

1. Introduction

The spatial attributes of populations are not often explicitly considered in the classical approach to stock assessment used for marine invertebrates. Instead, the discussion focuses on the size of the spatial scales of analysis, presuming that the principal biological processes (e.g., spawning and larval settlement) occur within these limits (e.g., Legendre, 1993; Tuck and Possingham, 1994; Caddy and Defeo, 2003). However, larval drift has been identified as the main mechanism of expansion for many decapod crustacean populations (Fogarty and Botsford, 2006). Thus, the influence of nearby areas defined as reproductive refuges or sources (Walters, 1998; Caddy, 1999) should be considered when explaining variations in this type of marine resource. Not knowing the levels of spatial connectivity specific in a metapopulation could, for example, provide an incorrect perception about the poor recruitments in a specific zone, when really this are a function of a nearby source population that has been overexploited. (Orensanz and Jamieson, 1998; Caddy and Defeo, 2003).

Data for nylon shrimp (*Heterocarpus reedi*) date back to the mid-1940s and constitute one of the longest data sets available for a decapod crustacean exploited off Chile's central coast (25°S-37°S) (Fig. 1). The commercial fleet that fishes nylon shrimp is made up of small-scale industrial trawlers and concentrates operations between 200 and 400 m depth over the continental shelf and the upper edge of the slope (Bahamonde and Henríquez, 1970; Arana et al., 1976; Arana, 2012). *H. reedi* has a continuous latitudinal distribution with largely bathymetric and meridional migratory cycles (Arana et al., 1975). The nylon shrimp aggregations seem to depend on river mouths and have a juvenile-led population expansion from south to north. Moreover, they are likely influenced by the Humboldt Current System, which moves in a general south-to-north direction at the surface and acts as an advective

mechanism for eggs and larvae. Thus, Canales et al. (2016b) proposed a metapopulation population structure with two sub-populations: one north and one south of 32°S. In this set-up, the south zone acts as the main habitat or *source* population.

The *H. reedi* fishery is administered as if it were two independent stock units separated at 32°10'S. Stock assessments consider each of these stock units to be closed and rely on a model that integrates age-structured dynamics with size observations (Montenegro et al., 2015) similar to the A-SCALA model proposed by Maunder and Watters (2003). An analysis of the data - mainly the signals found in abundance indices from the commercial fishery and scientific trawling surveys - reveals that population variations between these zones are similar, suggesting some level of correlation and/or spatial connectivity (Montenegro et al., 2015).

In this paper, we analyze the data and historical information for the nylon shrimp using a length-based population dynamics model (e.g., Sullivan et al., 1990; Punt and Kennedy, 1997; Zheng and Siddeek, 2011; Turnock and Rugolo, 2011). We evaluate probable relations between spatially neighboring sub-populations and determine whether the information used in the stock assessment can be explained by more than one hypothesis of the population structure. Our results permit evaluation of the implications that this situation could have on management of this resource and contributes to our understanding of the *H. reedi* biological-fishery data from a novel analytical perspective.

2. Materials and methods

2.1 Study area and data analyzed

We use data from three independent sources: landing statistics recorded by the Chilean National Fisheries Service (SERNAPESCA), fishing activities as monitored by the Fisheries Development Institute (Instituto de Fomento Pesquero, IFOP) since the early 1970s, and scientific trawling surveys funded by the Fisheries Research Fund (Fondo de Investigación Pesquera, FIP) since the 1990s. These data cover the area where *H. reedi* is distributed and fished (northern central Chile), but are divided into two zones separated by the latitude 32°S (Fig. 1). For modeling purposes, we consider the series of landings back to 1945, length frequencies (combined sexes) for the commercial landings and scientific surveys combined, the standardized series of annual catch per unit of effort (CPUE) (tons per hour of trawling) (Montenegro et al., 2015), and annual indices of relative abundance (catch in kg per linear km trawled) calculated from the fishing logs during scientific surveys (Canales et al., 2016b) (Table 1).

For each survey, the abundance index is calculated by zone and year using the ratio estimator (Cochrane, 1978), where the density of shrimp (kg km^{-1}) in a given zone (z) and year (y) corresponds to the ratio of the sum of the landings of all hauls made in a given zone and year, to the sum of the individual linear distances trawled for all hauls made in the same zone and year. The seasonal and technological considerations of this indicator are ignored because, in general, the surveys are conducted during the second half of the year, are based on stratified

designs, and use vessels with similar operational characteristics (Canales and Arana, 2010; Canales et al., 2016b).

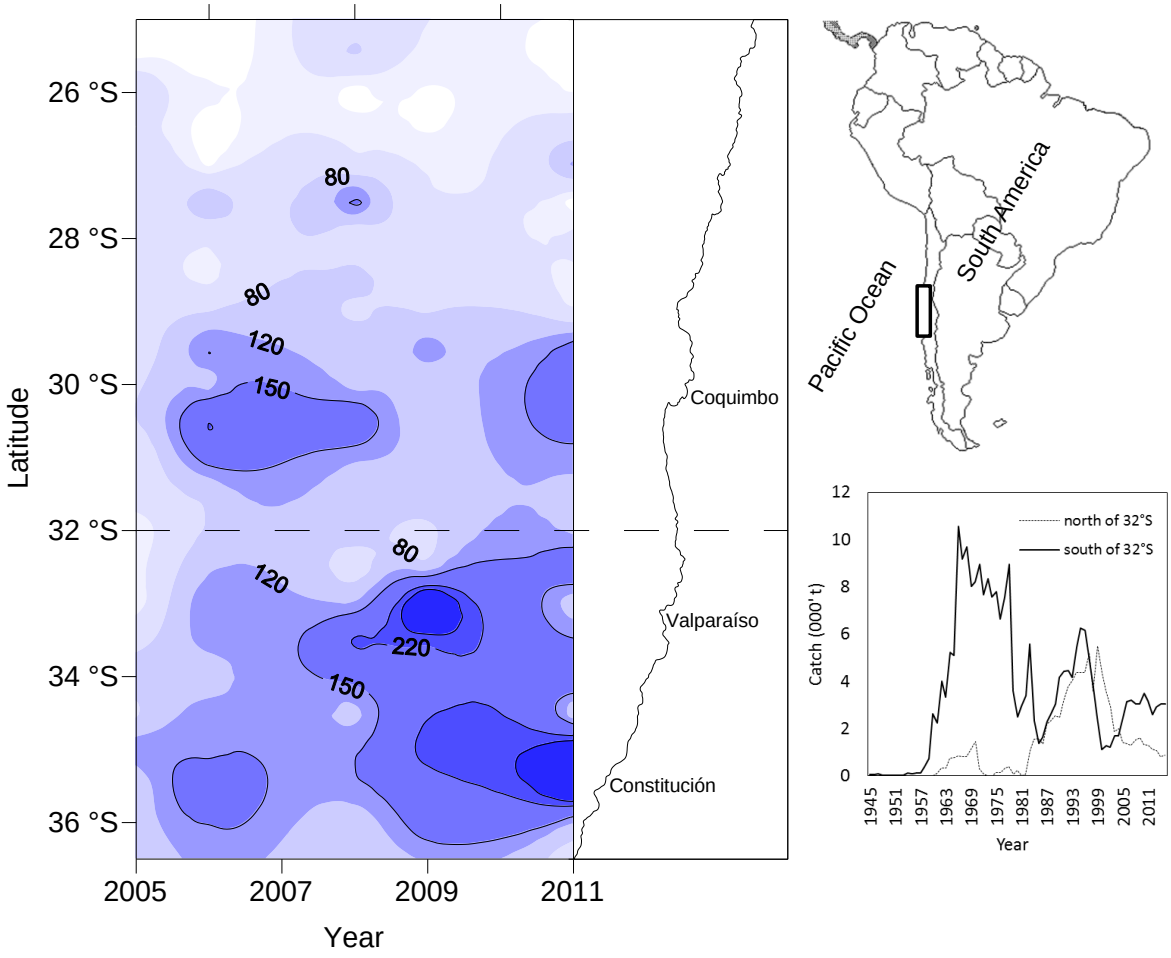

Fig. 1. Spatial distribution and catches of nylon shrimp (*Heterocarpus reedi*) off Chile. In the map, contour lines represent the density isopleths (kg km^{-1}) estimated from scientific survey data (source: Canales et al. (2016)). The horizontal dashed line (32°S) represents the hypothetical spatial separation of the population.

2.2 *Biological parameters*

The biological parameters of *H. reedi* such as growth, the proportion maturity at size, and weight at size are assumed to be the same between years but to differ by zone (Canales et al., 2016a) (Table 1). The growth parameters by zone were estimated outside the model based on an analysis of modal compositions (Fournier et al., 1990; Guayanilo et al., 1994; Canales and Arana, 2009) from size frequencies from the commercial fishery and scientific surveys. The natural mortality rate was fixed at M = 0.36 yr^{-1} (Montenegro et al., 2015), and assumed to be invariant between years, sizes, and zones.

Table 1. Years of available information and biological parameters of nylon shrimp (Heterocarpus reedi) by zone (north (n) and south (s) 32°S) used for stock assessment.

	Northward 32°S (n)	Southward 32°S (s)
Catches	1961-2015	1945-2015
Length compositions	Fleet: 1970-71; 1984-86; 1993-2014 Surveys: 1999-2006; 2008-2009; 2011-2012	Fleet: 1970-1981; 1984-1987; 1989-1990; 1992-2015 Surveys: 1999-2006; 2008-2009; 2011-2012
Abundance indexes	Fleet: 1969-1971; 1974-1975; 1978-1979; 1981-2014 Surveys:1998-2006; 2008-2009; 2011	Fleet: 1968-1978; 1980-2000; 2002-2015 Surveys: 1998-2006; 2008-2009; 2011
Maturity proportion at-length (50%-95%)	22.0 mm - 33.0 mm CL	27.0 mm - 36.0 mm CL
Coefficients of weight-at-length relationship	a=5.19E-4, b=2.91	a=5.67E-4, b=2.91
Growth parameter [(1)]		
l_∞ *(mm)*	41.1	42.3
k (yrs^{-1})	0.14	0.15
Lo (mm)[(2)]	20.1	18.2
Sr[(3)]	2.0	1.8

(1) Estimated outside the model, (2) Mean carapace size of the first modal-group, (3) standard error of the first modal-group

2.3 Population model

The model of the population dynamics was implemented using AD Model Builder (C++) (Fournier et al., 2012) and is based the models proposed by Sullivan et al. (1990), Punt and Kennedy (1997), Zheng and Siddeek (2011), Haddon (2011), and Turnock and Rugolo (2011), amongst others. Recruitment in this model is distributed over a range of sizes and occurs at the start of the year after the survivors of fishing and natural mortality have grown. The advantage of this model is that all processes are based on size, regardless of age (Punt et al., 2013). The model includes spatial considerations (e.g., Haist et al., 2009; McGarvey et al., 2010; Lestang et al., 2012), and their main formulation is expressed by zone ($z = n, s$) as:

$$N_{y,z} = T_z \left(S_{y-1,z} N_{y-1,z}\right) + R_{y,z} \quad (1)$$

$$R_{y,z} = r_{y,z}\, \varphi_z \quad (2)$$

$$r_{y,z} = \begin{cases} \hat{r}_{y,z} + \pi \hat{r}_{y,z=2}\,, & z = n \\ \hat{r}_{y,z}(1-\pi)\,, & z = s \end{cases} \quad (3)$$

$$0 \leq \pi \leq 1 \quad (4)$$

$$\hat{r}_{y,z} = \frac{\alpha_z\, SSB_{y-\tau,z}}{\beta_z + SSB_{y-\tau,z}} e^{\varepsilon_{y,z}} \quad (5)$$

where $N_{y,z}$ is a column vector containing the number of individuals per size interval at the start of year y; n and s are related respectively the north and south zones; T_z is the transition matrix that determines the annual growth between the size classes, based on a normal probability distribution (e.g., Luke et al., 2014; Haddon, 2011; Punt and Kennedy, 1997; Punt et al., 2010); $S_{y-1,z}$ is a diagonal matrix with the proportion of survivors (of fishing and natural mortality) by length interval and zone in year y-1; and $R_{y,z}$ is a vector that represents the annual distribution of recruits by size and zone (z). The size-specific selectivity and catchability coefficients of both

the commercial fleet and scientific surveys are assumed to vary by zone but not over time. Selectivity is modeled logistically in both cases (see Appendix, B.2).

The annual distribution of recruits by size and zone ($R_{y,z}$) defined in Eq.2 comprises an annual number of recruits in each zone ($r_{y,z}$) and a column vector (φ_z) that describes the relative proportion of the $r_{y,z}$ in each class interval following a normal distribution with mean L_0 and standard deviation S_r (~$N(L_0, S_r)$) for each zone. Eq.3 defines the spatial connectivity between zones and is a function of the theoretical recruits ($\hat{r}_{y,z}$) for each zone and the parameter π, whose domain is defined in Eq.4. Depending on the hypothesis, this parameter determines the fraction of the recruits generated in the south zone (z = s) that move (through larval advection) to the north zone (z = n), or the proportion of allocated recruits to the north zone under a single-stock scenario (Fig. 2). The expected umber of recruits per year and zone $\hat{r}_{y,z}$ is modeled by the Beverton and Holt stock-recruitment relationship (Eq. 5), where SSB is the spawning stock biomass, τ is the time lag (assumed to be 2 years) (Canales et al., 2016a) between recruitment and spawning, and $\varepsilon_{y,z}$ is an annual deviation on the logarithmic scale (~$N(0,\sigma_R)$). The parameters α and β are calculated in terms of steepness (h = 0.75), virgin recruitment estimated by the model ($R_{0,z}$), and the spawning stock biomass ($SSB_{0,z}$) calculated in each zone (Francis, 1992). The model assumes that the stock was in an unfished state in 1945 and SSB_0 is calculated by projecting the survival (only from natural causes) of the distribution of annual recruits for as many years as necessary to reach a stable biomass value (Fig. 3).

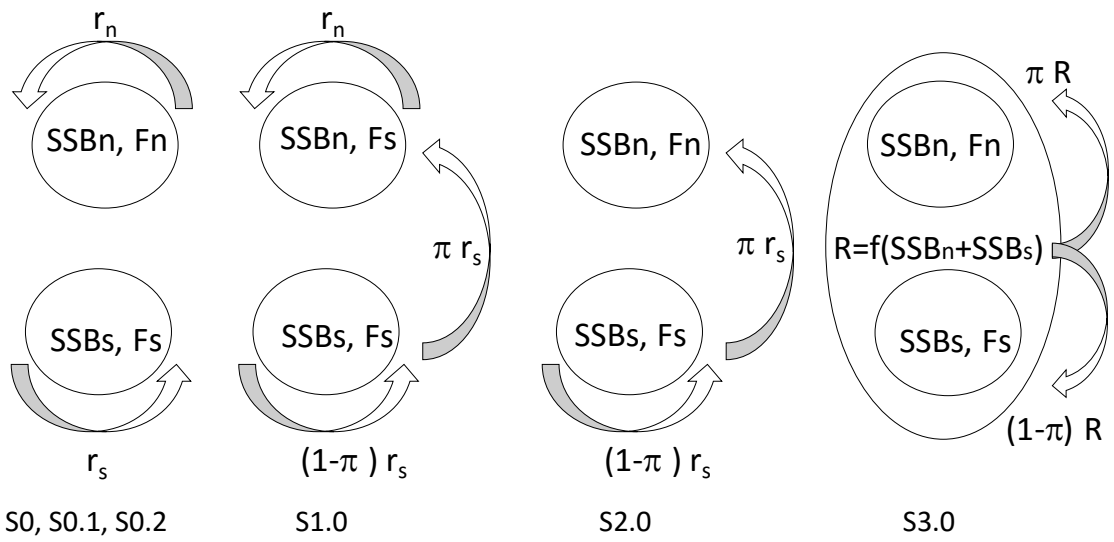

Fig. 2. Illustration of four hypotheses of nylon shrimp population structure. SSB represents the population spawning biomass, n and s are sub-indexes for 'north' and 'south', respectively, r is recruitment, F is the zone-specific fishing mortality and π is the proportion of south recruitment that migrated to the north (S0, S1.0, S2.0) or an allocation coefficient (S3.0). Recruitment occurs in scenarios S0, S0.1, S0.2 and S1.0 in each zone while in scenario S2.0 all recruitment to the north zone comes from south zone. S3.0 is the representation of a single stock where recruitment to each zone is a proportion of a total recruitment as a function of a combined biomass.

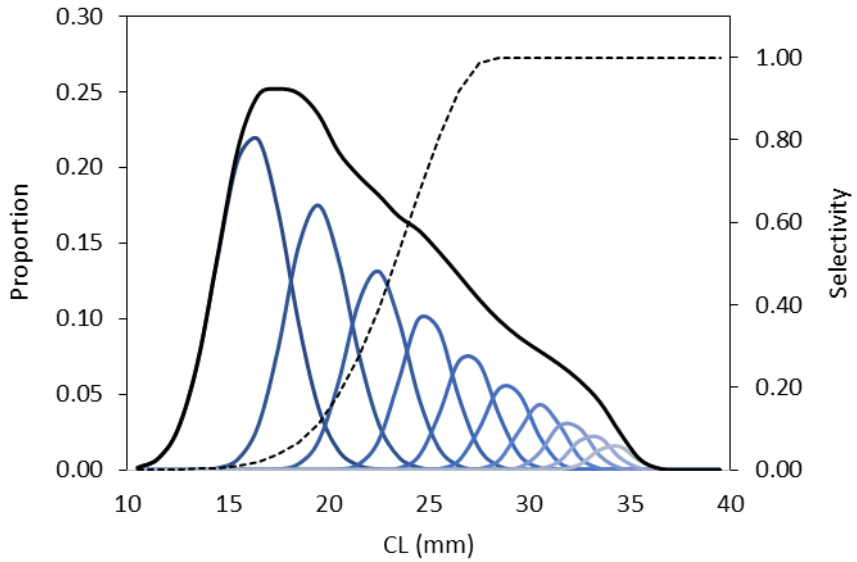

Fig. 3. Example of modal groups present in virgin length composition of nylon shrimp together to fleet selectivity (scenario S0, north). Bold line represents total population, blue lines represent each modal group and the dashed line corresponds to selectivity. Recruitment at length is represented by the first modal group.

2.4 Error model

Different log-likelihood functions are considered to capture the data, penalties, and *a priori* distributions of the parameters of interest (Appendix C). The size proportions of the commercial landings and scientific surveys are represented using a multinomial distribution with an effective sample size of n=30, which was calculated using the estimator of Gavaris and Ianelli (2002). The log likelihood of both abundance indices and landings assumes normality of the log-transformed variable. The standard deviation of the abundance indices is assumed not to vary between years and zones, and the values (σ=0.3 for CPUE; σ=0.15 for surveys) are verified *a posteriori* by calculating the standard deviation of the log-deviations. For catches, this standard deviation is assumed to be σ=0.05 (see Appendix C.2.).

The objective function further includes three penalty terms related to: (1) the recruitment deviations on a logarithmic scale ($\varepsilon_{y,z}$); (2) the deviations in the catchability coefficients of the scientific surveys between zones; and (3) the deviations in the random errors of annual recruitment on a logarithmic scale between zones (Appendix C.3.). The deviation in catchability of the surveys between zones is assumed to be normally distributed on the log-transformed scale subject to a low coefficient of variation (cv=0.05), which is justified because it allows the biomass estimates for each zone to be represented by the scale of local densities. The deviations in the random errors of the recruitment defined in (3) allow us to evaluate different levels of correlation for recruitment between zones, with values of cv equal to 1.0, 0.5, and 0.2, given low, medium, and high cross-correlation scenarios (Appendix, C.3.2.)

The values of the parameters are estimated by minimizing the objective function consisting of the sum of the marginal components of the negative log-likelihood, the penalties mentioned above, and an *a prior* distribution of the log_L_0 parameter assumed to be normal with a mean

log_L_r (baseline information) and a standard error of 0.1 (Table 2). In this sense and considering the nonlinearity of the model, a set of start parameters was selected given the predicted variables by the model compared to the observations, as a function of some key parameters, as the selectivity coefficients, distribution of recruitment at length, migration/allocation coefficient, and the average of fishing mortality by zone.

Table 2. Configuration of key model parameters for different hypotheses of shrimp population structure. σ_x represents deviates the standard error (log scale) of recruitments between zones (z), π is the proportion of migrant recruits from southern zone, R_0 is the virginal recruitment, and $\varepsilon_{y,z}$ is the annual deviate of recruitment (in log-scale). Letters F and E indicate if the parameter was fixed or estimated, respectively.

Population structure	Scenario	σ_x	π	$R_{0,z=n}$	$R_{0,z=s}$	R_0	$\varepsilon_{y,z=n}$	$\varepsilon_{y,z=s}$	ε_y	Number of parameter
Cross-correlated recruitments	S0.0	1.0	0 (F)	E	E	-	E	E	-	303
	S0.1	0.5	0 (F)	E	E	-	E	E	-	303
	S0.2	0.2	0 (F)	E	E	-	E	E	-	303
Metapopulation	S1.0	1.0	E	E	E	-	0 (F)	E	-	233
	S2.0	1.0	E	0 (F)	E	-	0 (F)	E	-	232
Single stock	S3.0	-	E	-	-	E	-	-	E	231

2.5 Evaluation of different population structures

Six different model configurations were used to represent alternative hypotheses for the dynamics of *H. reedi* recruitment and population structure. Three models involve independent populations (S0) with three magnitudes of cross-correlation (low, medium and high) in recruit recruitment (S0.1, S0.2, S0.3); the fourth is a metapopulation with a population/habitat pseudo-sink (Fig. 2); the fifth is a typical source-and-sink metapopulation (Fogarty and Botsford, 2006); and the sixth is a single-stock. Specifically, there is a cross-correlation of recruitments among zones in scenarios S0, represented by assuming that deviations in recruitment between zones follow a normal distribution (mean zero) with different variance

assumption (see Appendix, C.3.2). Scenarios S1.0 and S2.0 represent a metapopulation with different magnitudes of connectivity. In S1.0, the north zone is a pseudo-sink where, although the scale of local recruitment is determined by the zone's spawning biomass through Eq.5, its variability depends only on the recruits generated in the south zone (source population). In scenario S2.0, the northern population is a sink (no local generation of recruits, $R_{0,z=1}$= 0) and recruitment depends on a proportion of annual recruits generated by the south zone. In the last two cases, the number of model parameters are reduced by approximately 23% since deviations of annual recruitment in the north are not estimated (Table 2).

Particular considerations were taken account when the hypothesis of a single-stock (S3.0) in nylon shrimp was implemented, given its widespread distribution (25°-37°S) and its low level of latitudinal migrations. The main assumption was to consider that there a single theorical annual recruitment (with process error) as function (S/R) of a combined spawning biomass (both zones), while recruitments by zone are determined by applying a spatial allocation factor (π) assumed to be time invariant (north: $\pi\,\hat{r}_y$; south: $(1-\pi)\,\hat{r}_y$). After the recruitments to each zone, the exploitation levels depend on local fishing mortality.

Models are compared statistically using Akaike's Information Criterion (AIC) (Akaike, 1974) and Schwartz's Bayesian Information Criterion (BIC) (Schwartz, 1978). Both metrics satisfy the fundamental criteria for model selection: goodness of fit, parsimony, and objectivity (Langitoto et al., 2000).

$$AIC = 2\mathrm{L}_{max} + 2p \tag{6}$$

$$BIC = 2\mathrm{L}_{max} + p\log(n) \tag{7}$$

where L_{max} is the minimum of the negative of the total log-likelihood function of the data (not considering penalties or *a priori* distributions), *p* is the number of parameters, and *n* is the number of observations.

3. Results

3.1 Overall model fit

In all considered cases the model converges on a feasible solution with maximum gradient values that are lower than $2.58*10^{-4}$ for all scenarios (Table 3). The fit of the model to the data is adequate, and the model appears to reproduce the abundance index of the commercial fleet (CPUE) and research surveys well, as well as the average carapace length (CL) for these two data sources per year and zone (Fig. 4). The 95% confidence intervals suggest that the assumed observation errors of the abundance indices are adequate given that these contain most of the predictions. The consistency between the pieces of information (abundance indices, landings, size compositions), particularly for the growing trend of the indicators beginning in 2000, is also worthy of note. Similarly and as an example, the fit of the length compositions under the hypothesis of independent populations (S0) is notable, first, for the slight tendency of the model to over-estimate the frequency of individuals greater than 30.5 mm CL and, second, because the *H. reedi* recruits are distributed around 16 mm CL (Fig. 5). Also and without large impact in results, the residual pattern observed in model fit to abundance indexes for the south (Fig. 4 b and d) would represent hyper-stability effects in CPUE, which could be modelling under appropriate justifications.

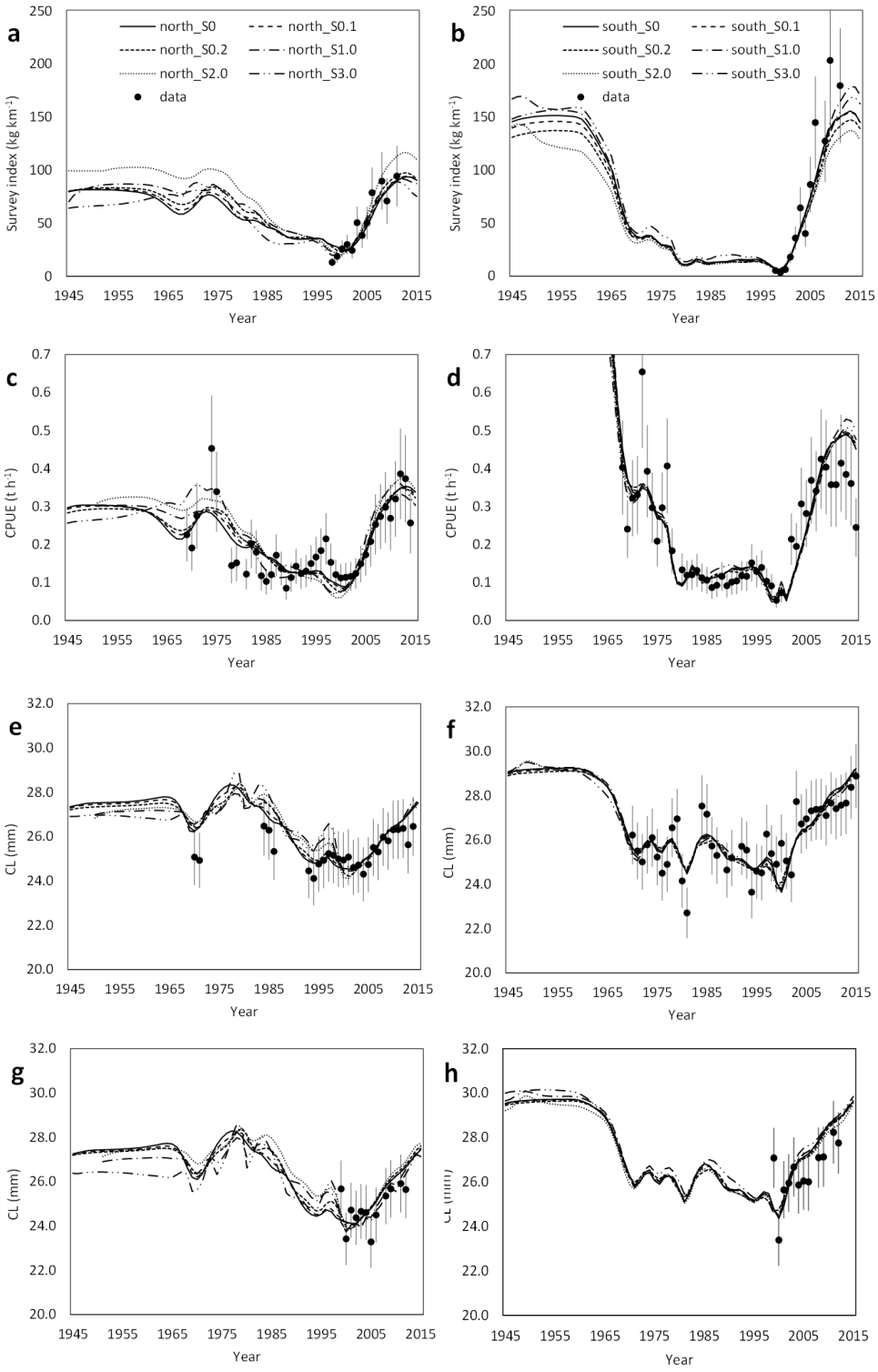

Fig. 4. Fit of the model to nylon shrimp information. Dots represent the information and lines the expected values (model) related to the different hypothesis. The lengths compositions in this figure are represented by the mean carapace length (*e* and *f* for catches, *g* and *h* for surveys). Right and left panels correspond to north and south zones, respectively. Vertical lines represent 95% confidence interval.

Table 3. Estimates of key parameters (log scale) model, marginal likelihood components and indexes of information criterion (AIC & BIC) for each scenario. The parameter standard error are given in parenthesis. The lowest scores are indicated in bold.

				Hypothesis (scenario)					
Parameter	*Source*	*name*	*stock*	*S0*	*S0.1*	*S0.2*	*S1.0*	*S2.0*	*S3.0*
Selectivity	fleet	log(μ)	north	3.28 (0.01)	3.28 (0.02)	3.27 (0.02)	3.31 (0.02)	3.27 (0.02)	3.29 (0.03)
		log(θ_1)		1.14 (0.06)	1.14 (0.06)	1.12 (0.06)	1.52 (0.19)	1.15 (0.08)	1.67 (0.21)
		log(μ)	south	3.41 (0.02)	3.41 (0.02)	3.41 (0.02)	3.41 (0.02)	3.42 (0.02)	3.42 (0.02)
		log(θ_1)		1.47 (0.04)	1.47 (0.04)	1.48 (0.04)	1.47 (0.04)	1.47 (0.04)	1.50 (0.05)
	survey	log(μ)	north	3.34 (0.03)	3.34 (0.03)	3.34 (0.03)	4.09 (0.52)	3.37 (0.04)	5.26 (1.18)
		log(θ_1)		1.43 (0.09)	1.43 (0.09)	1.43 (0.09)	3.19 (0.79)	1.55 (0.13)	4.53 (1.36)
		log(μ)	south	3.41 (0.02)	3.41 (0.02)	3.41 (0.02)	3.42 (0.03)	3.39 (0.02)	3.46 (0.03)
		log(θ_1)		1.37 (0.07)	1.38 (0.07)	1.39 (0.07)	1.41 (0.07)	1.34 (0.06)	1.48 (0.08)
Virginal recruitment		log(R_0)	north	7.75 (0.11)	7.78 (0.11)	7.85 (0.11)	6.94 (0.18)	-	-
			south	8.23 (0.08)	8.28 (0.08)	8.32 (0.09)	8.61 (0.07)	8.77 (0.08)	-
			single	-	-	-	-	-	8.60 (0.06)
Migrant rate/allocation		log(π)		-	-	-	-1.24 (0.16)	-0.97 (0.11)	-0.71 (0.05)
Catchability	fleet	log(q_f)	north	-11.16 (0.11)	-11.24 (0.13)	-11.44 (0.09)	-11.88 (0.12)	-11.74 (0.08)	-12.12 (0.11)
			south	-10.34 (0.13)	-10.39 (0.12)	-10.44 (0.12)	-10.32 (0.13)	-10.45 (0.12)	-10.34 (0.13)
	survey	log(q_s)	north	-5.57 (0.13)	-5.64 (0.12)	-5.75 (0.11)	-5.54 (0.19)	-5.94 (0.11)	-5.18 (0.16)
			south	-5.55 (0.13)	-5.61 (0.12)	-5.7 (0.11)	-5.53 (0.18)	-5.86 (0.11)	-5.18 (0.16)
Recruitments		log(l_r)	north	2.79 (0.05)	2.8 (0.05)	2.83 (0.05)	3.04 (0.03)	2.91 (0.04)	3.07 (0.02)
			south	2.79 (0.04)	2.78 (0.05)	2.77 (0.06)	2.81 (0.04)	2.78 (0.05)	2.82 (0.04)
Transition matrix		log(ω)	north	-2.31 (0.21)	-2.33 (0.22)	-2.36 (0.21)	-2.63 (0.17)	-2.48 (0.22)	-2.59 (0.18)
			south	-1.33 (0.19)	-1.45 (0.23)	-1.64 (0.29)	-1.35 (0.19)	-1.59 (0.26)	-1.44 (0.22)
Maximum gradient component				7.16e-04	1.82e-05	5.67e-05	2.58e-04	8.048e-05	3.91e-05
Log-likelihood components									
	cpue			30.77	32.16	35.62	42.32	45.78	41.94
	survey			52.14	53.91	61.16	40.08	59.70	41.93
	catch			0.73	0.90	1.52	0.63	2.27	2.70
	prop_catch			5,432.65	5,438.14	5,449.73	5,472.23	5,461.33	5,487.90
	prop_survey			1,930.41	1,930.82	1,933.58	1,950.42	1,937.24	1,958.35
	Total likelihood			7,446.7	7,455.9	7,481.6	7,505.7	7,506.3	7,532.8
Number of parameters				303	303	303	233	232	231
Index of information criterion									
	AIC			15,499.4	15,517.9	15,569.2	15,477.4	**15,476.6**	15,527.6
	BIC(*)			17,912.4	17,930.8	17,982.2	17,332.9	**17,324.2**	17,367.2

(*) based on 2,406 observations

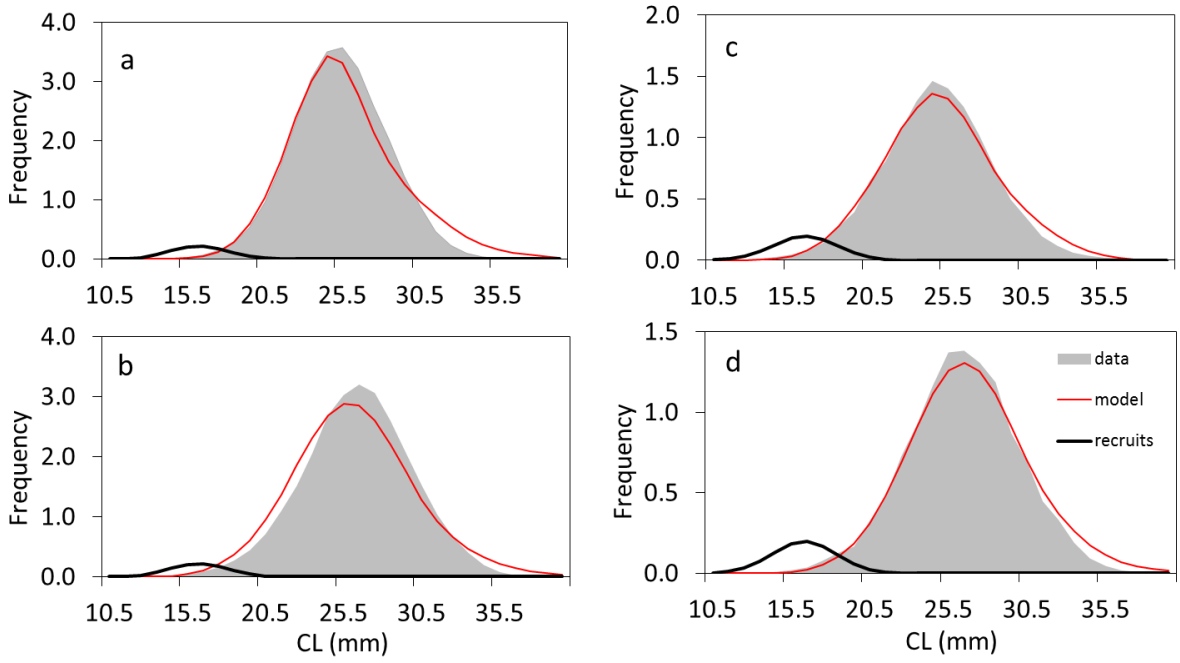

Fig. 5. Summary of model fit (S0) to the length compositions of nylon shrimp for all years combined (marginal compositions). The shading represents the data and red lines represent the predicted values by the model. The black lines represents the recruitment distribution by size. The left panels show results for the catches and the right panels the results for the trawl surveys. The upper panel corresponds to north zone while the lower one the south zone.

3.2 *Population parameters*

H. reedi is characterized by reduced biomass in both zones until the mid-1990s and a subsequent population increase and expansion from 2000 onwards (Fig. 6a, 6b). As expected, the hypotheses of population structure appear to have a greater impact for the north zone, with S1.0 and S2.0 (metapopulation) presenting the greatest sensitivity on the biomass scale, differing by more than 30% from the hypothesis of independent populations (S0) (Fig. 6a). Average biomass estimates in the south zone are around 50,000 tons, which is 24% higher than in the north zone. The results also show that the main changes in biomass are explained by large pulses of recruits recorded throughout the decade of the 2000s in both zones, even when

(and depending on the hypothesis), recruits in the north are influenced by recruits in the south (S1.0 and S2.0) (Fig. 6c, 6d).

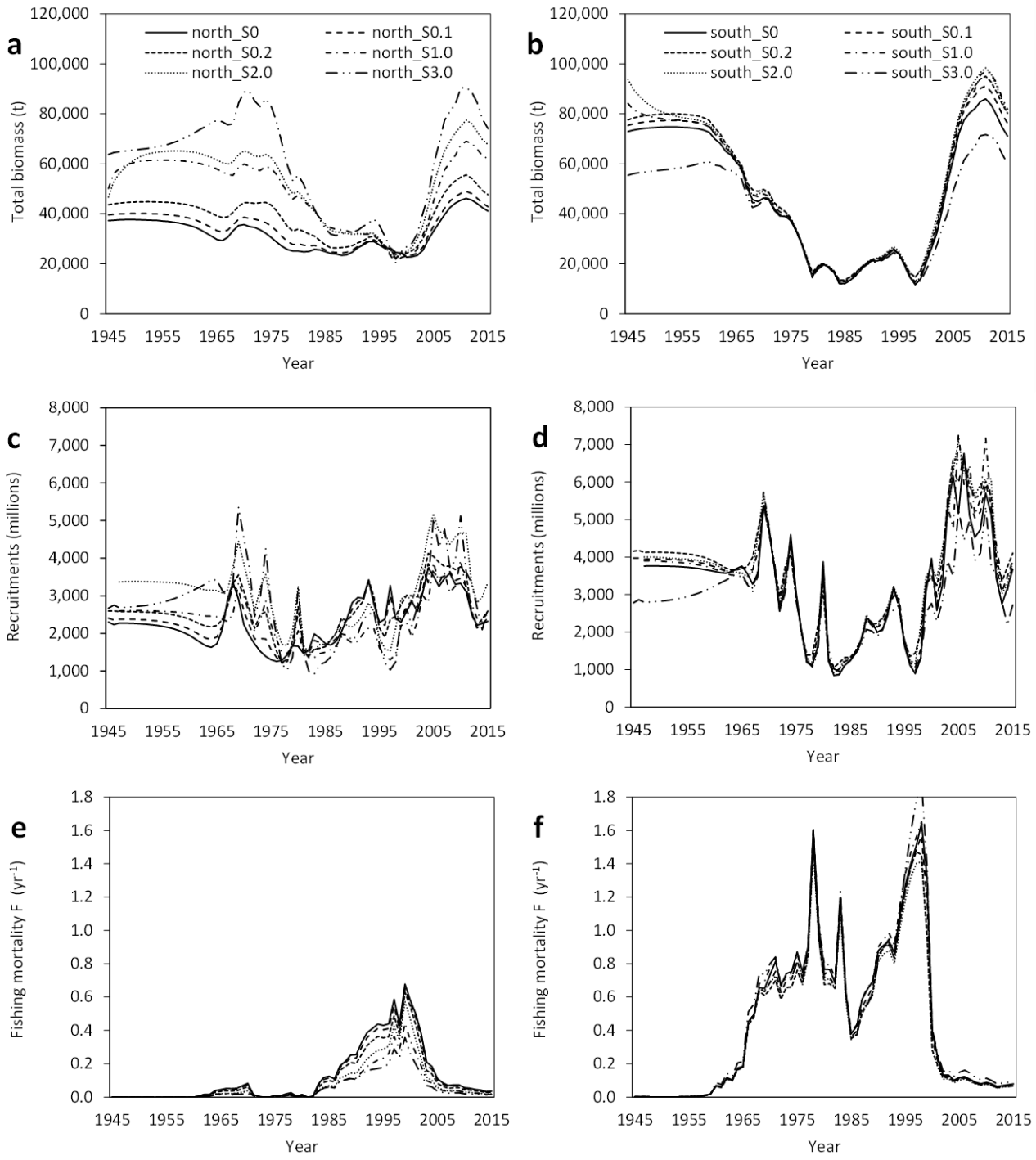

Fig. 6. Total biomass, recruitments and fishing mortality of nylon shrimp by zone and year for each scenario. The right and left panels correspond to north and south zones, respectively.

The estimates of selectivity, catchability, and virgin recruitment are robust to the scenarios analyzed. In the south zone, size at 50% of selectivity of the commercial fleet (30.1 mm average CL) is estimated to be 14% higher than in the north zone, whereas the research surveys report a difference of only 6% (Table 3). In this sense, while in the recent years the catches between zones have had similar levels, the fishing mortality at south zone is the larger in each scenario (Fig. 6e, 6f) and this is to due to selectivity in this zone being focused on larger shrimps (see the estimates of log(μ) in Table 3). The average virgin recruitment (R_0) in the south zone is estimated to be more than twice that of the north (Table 3), partly explaining the different biomass estimates for these two zones (Fig. 6a, 6b). Considering all the scenarios, the average CL that determines recruitment (L_r) is estimated to be slightly higher in the north zone (near 17.7 mm) than in the south (16.2 mm). In both cases, the estimates of this parameter (*a posteri*) are lower than the *a priori* assumptions (Table 2). The low standard error of L_r (<0.06) (Table 3) suggests that the data contain relevant information with respect to the size range covered in nylon shrimp recruitment. In the same sense, the results also show that, regardless of the zone and scenario, the size composition of the exploitable population of *H. reedi* could be sustained in up to 10 modal groups (or states of average annual molt) (Fig. 3).

As for the hypothesis of spatial connectivity, the value of the parameter that measures the proportion of migrant recruits (π) in the two metapopulation scenarios (in natural scale) is estimated to be 0.28 (S1.0) and 0.37 (S2.0) (Table 3). This means that, under the hypothesis of a metapopulation with a pseudo-sink (S1.0), the average proportion of recruits moving from the south to the north zone (which would explain the increased recruits in this area) is 28%, $CI_{95\%}$ = [21%-39%]. In the case of a metapopulation with a sink zone (i.e., no generation of recruits) in the north, the contribution from the south reaches 37%, $CI_{95\%}$ = [30%-47%].

Nonetheless, and in agreement with the amplitude of the intervals determined by the standard error of these parameters, these measures seems to be not statistically different. In the same sense but in the single-stock hypothesis (S3.0), the spatial allocation coefficient was estimated in 49% and whose $CI_{95\%}$ = [44%-54%] indicates that recruitments would have equal allocation among zones.

3.3 Statistical discrimination

The value of the functions of log-likelihood and its marginal components (log-l), referring only to the fit of the model to the data, indicates that the hypothesis of population independence (S0) fits the data best (Table 3). When including recruits correlated between zones (S0.1 and S0.2), the model fit (Δ *log-l* > 2) is significantly poorer for the same hypothesis, with estimated correlation coefficients of 27% (S0), 53% (S0.1), and 86% (S0.2). Furthermore, and although the metapopulation scenarios (S1.0 and S2.0) have larger *log-l* values, probably due to the smaller number of parameters estimated, the best fit of the abundance index of the surveys is obtained under the hypothesis of a pseudo-sink metapopulation (S1.0). This log-likelihood value (*log-l*=40.1) is more than two points lower than the rest of the scenarios considered (Table 3). The results also show that goodness fit (negative log likelihood) of the model to length compositions in S2.0 is better than S1.0, this because the model in S2.0 have larger value of R_0 (in log scale, Table 3) and larger annual variation of recruitment, which leads to more flexibility in the model to fit the length comps. Also, the results show that single-stock hypothesis (S3.0) has a poor fit to abundance indexes due to the assumption that a time-invariant spatial distribution applied on a single recruitments series can explain the data in two zones at same time.

Notwithstanding the above and considering the criteria for model selection, the hypothesis of metapopulation defined in scenarios S1.0 and S2.0 is the most likely with regard to the hypothesis of population independence (S0), since the values of the AIC and BIC are both significantly lower. The result is expressed in terms of a balance between the number of parameters in each model (303 vs. 233), the number of observations (2,406 recorded), and the goodness of fit of the model to the data (log likelihood). The AIC values are identical (AIC=15,477) for both metapopulation cases, whether pseudo-sink (S1.0) or sink (S2.0), but 23 points lower than that of the null hypothesis (two units of independent stock, S0) and 51 point lower than the single-stock scenario (S3.0) . In this same context, the difference in the BIC between scenarios is noticeably higher, as reflected in the 617.6 points (on average) below S0 and in favor of the metapopulation hypothesis (S1.0, S2.0). Thus, S2.0 (metapopulation-sink) seems the most likely alternative since it has the lowest score (BIC = 17,324) (Table 3).

4. Discussion

The model-based analysis of the data from the commercial fishery and research surveys for *H. reedi* caught off central Chile reveals that, in general, the historical record can be explained by alternative hypotheses as to population structure and spatial connectivity between zones, with the metapopulation hypothesis being the most likely in statistical terms. The model used allows us to investigate the spatial distribution of recruits, obtain more details about the population structure, and learn about the biological processes based on length regardless of the age structure (Punt et al., 2013). In general, the model performs well for all of the scenarios, although the fit of the compositions of lengths improves when considering, for example, changes in functional types and/or temporal variations in selectivity (Lee et al., 2014; Wang et

al., 2014) at the expense of a greater number of parameters. Nonetheless, in this work, we favor the use of a model with the greatest possible parsimony and the best goodness of fit to the data.

Our analysis shows that the subpopulations to the north and south of 32°S experience important variation caused by pulses of recruits, with the south acting as a source population. Although the abstraction of a model generates results that can only be considered in a relative or referential way, it gives an idea of the probable theoretical contribution of the larvae that could be drifting northward, estimating this to be, on average, between 28 and 37%, depending on the type of metapopulation. For the hypothesis of population independence (S0), the likely synchrony of recruitment between zones is rejected given the lower goodness of fit of the model under the scenarios of forced correlations of recruitment (S0, S0.1, and S0.2). In this sense, while we cannot rule out that large scale environmental variation could be equally responsible for temporal synchrony recruitment spatially. The metapopulation hypothesis is further supported by local oceanographic characteristics, where the orientation of advective flow would influence larval transport and hence connectivity between both zones. Likewise, environmental changes probably would determine annual variation in the migrant proportions that in this work were assumed to be time-invariant, being necessary to develop further empirical researches to respond this scientific interrogant.

Although the hypothesis of an *H. reedi* metapopulation proposed by Canales et al. (2016b) requires more empirical evidence, it is based on observations that coincide with proposals made by Orensanz et al. (2006) and Defeo and Cansado (2015) as to the type of characteristics that can be expected in populations with spatial connectivity patterns. For nylon shrimp, the gradual expansion of the population towards the north from 1995 to 2005 as a result of greater

recruitment is of particular interest and is reflected in the increased presence of juveniles in this zone, as a response the region's predominantly northward surface flow determined by the Humboldt Current (Fuenzalida et al., 2008), and the association of zones with greater abundances located south of 32°S (source population) with areas of improved environmental conditions in terms of chlorophyll-a and dissolved organic material (Canales et al., 2016b). Lipcius et al. (1997) reports the importance of source populations in the process of population expansion of *Panulirus argus* from the perspective of a metapopulation, and Caddy and Defeo (2003) use this concept to explain the increased biomass of *Homarus americanus* and its expansion to previously less abundant areas.

Considering the region south of 32°S to be a reproductive refuge or a source population of larvae and post-larvae that partially or totally supplies the area north of 32°S (sink or pseudo-sink population) generates important challenges for the future management of the fishery. Priority should be given to management mechanisms such as increased caution in exploitation and continuous monitoring of the reproductive refuge (e.g., Campbell, 1986; McGarvey et al., 1992; McGarvey and Willison, 1995; Kjelland et al., 2015). Proposals such as those of Gutierrez and Defeo (2003), for example, regarding the rotation and closure of areas, should be considered. Yakubu and Fogarty (2006) demonstrate, theoretically and mathematically, that the conservative management of larval source populations can contribute to the resilience of exploited species. Other extensions of this idea can be found in Kough et al. (2013), who explored the relevance of considering larval drift when managing resources of economic importance such as the Caribbean spiny lobster (*Panulirus argus*). Likewise, the works of Goethel et al. (2011) and Guan et al. (2013) explore how considering the spatial structure in stock assessment and management impacts a population and fishery. Finally, these findings

should be considered to extend the research on other demersal crustaceans of commercial relevance, such as the red squat lobster (*Pleuroncodes monodon*) and yellow squat lobster (*Cervimunida johni*) among others, those who inhabit similar bottom conditions than nylon shrimp.

5. Conclusion

This research generates statistical evidence supporting the proposal by Canales et al. (2016b) that the area south of 32°S could be considered a source population or reproductive refuge. The biological and fishery data available for nylon shrimp since 1945 are evaluated in terms of two population structure hypotheses. Of these, the metapopulation hypothesis is better supported statistically. Although further empirical evidence is necessary to sustain the proposal of Canales et al. (2016b), the ecological grounds given in the literature along with our results and observations suggest that the hypothesis of a reproductive refuge area for *H. reedi* south of 32°S should not be discarded. Therefore, fisheries management should focus on this area in order to ensure the generation of recruits across the resource's distribution, thereby endowing the fishery with resilience and sustainability.

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Appendix A

Table A1. Parameter of the size-based model applied to nylon shrimp data exploited off Chile. The letter F indicates if the parameter was fixed.

Parameter	Nomenclature	Parameters	Initial values	Distribution
Selectivity (fleet and survey by zone)	μ	4	25.0	U[-∞,+∞]
	ϑ_1	4	4.0	U[-∞,+∞]
	ϑ_2	4	1000 (F)	
Fishing mortality by year and zone	$F_{cr,y,z}$	142	0.2	U[-∞,+∞]
Virgin recruitment by zone	$R_{0,z}$	2	5000	U[-∞,+∞]
Recruitment annual deviates by	$\varepsilon_{y,z}$	142	0.0	U[-∞,+∞]
Steepness	h	1	0.75 (F)	
Migrant proportion	π	1	0.0	U[-∞,0]
CPUE catchability by zone (z)	qf_z	2	0.01	U[-∞,+∞]
Survey catchability by zone (z)	qs_z	2	0.01	U[-∞,+∞]
Recruitment length distribution by	L_0(3)	2	[20.1; 18.2]	N(log_$L_{0,}$
	S_r(4)	2	[2.00; 1.80]	
Transition matrix (growth) by zone(2)	l_{oo}	2	[41.1; 42.3]	
	K	2	[0.14; 0.15]	
	ω	2	0.5	U[-∞,+∞]
Natural mortality	M	1	0.35 (F)	

(1) based on S0; (2) [north; south]; (3) Mean carapace size of the first modal-group; (4) standard error of the first modal-group.

Appendix B . Observation model

B.1. Predicted catches in number at-size (*l*), by year (*y*) and zone(*z*).

$$\hat{c}^f_{l,y,z} = N_{l,y,z}F_{l,y,z}(1 - e^{-F_{l,y,z}-M})/(F_{l,y,z} + M) \quad (8)$$

N is the population abundance at the start of the year, *F* is fishing mortality rate and *M* is natural mortality rate. The fishing mortality at-size, by year (y) and zone (z) is modelled as

$$F_{l,y,z} = F_{cr,y,z}\, O^f_{l,z} \quad (9)$$

F_{cr} is the fully recruited fishing mortality and $O_{l,z}^{f}$ the selectivity of the fleet (*f*) by size and zone.

B.2. The selectivity at-size, by year (y), zone (z) and source type (fleet (f) or survey(s)) is formulated as double normal function

$$O_{l,z}^{f,s} = \begin{cases} \exp\left(-0.5\frac{\left(l-\mu_z^{f,s}\right)^2}{\theta_{1,z}^{f,s}}\right) & l \le \mu_z^{f,s} \\ \exp\left(-0.5\frac{\left(l-\mu_z^{f,s}\right)^2}{\theta_{2,z}^{f,s}}\right) & l > \mu_z^{f,s} \end{cases} \quad (10)$$

μ is the fully recruited size and θ is the dispersion parameter for each normal distribution. $\theta_{2,z}^{f,s}$=1000 (fixed to produce a logistic model).

B.3. Available abundance for surveys in number at-size, by year (y) and zone (z).

$$\hat{c}_{l,y,z}^{s} = N_{l,y,z} O_{l,z}^{s} e^{-0.5(F_{l,t,z}+M)} \quad (11)$$

B.4. Predicted catches of the fleet in weight by year (y) and zone (z).

$$\hat{Y}_{y,z} = \sum_{l} \hat{c}_{l,y,z}^{f} w_{l,z} \quad (12)$$

$w_{l,z}$ is the expected weight at-size by zone.

B.5. Predicted proportions at-size, by year (y), zone (z) and source (fleet (f) or survey(s))

$$\hat{p}_{l,y,z}^{f,s} = \hat{c}_{l,y,z}^{f,s} / \sum_{l} \hat{c}_{l,y,z}^{f,s} \quad (13)$$

B.6. Abundance indices (CPUE or density of shrimp in surveys) by year (y), zone(z) and source (fleet (f) or survey(s))

$$\hat{I}_{y,z}^{f,s} = q_z^{f,s} \sum_{l} N_{l,y,z} e^{-0.5(F_{l,t,z}+M)} w_{l,z} O_{l,z}^{f,s} \quad (14)$$

$q_z^{f,s}$ is catchability coefficient by zone and source (fleet (f) or survey(s)).

B.7. Spawning biomass by zone

$$SSB_{y,z} = \sum_{l} N_{l,y,z} e^{-0.67(F_{l,y,z}+M)} w_{l,z} m_{l,z} \tag{15}$$

$m_{l,z}$ is maturity at size. 0.67 indicates the fraction of the year when the spawning occurs

B.8. Transition matrix

The individual growth is driven by a transition matrix *T* defined by zone as:

$$\mathrm{T_z} = \int_{l(i)}^{l(i+1)} \frac{1}{\sqrt{2\pi\delta_l}} \exp\left(-\frac{[l-(l+\Delta(l))]^2}{{\delta_l}^2}\right) dl \tag{16}$$

where $\Delta(l) = (l_{oo} - l)(1 - e^{-k})$ which reflecst the marginal increment in a year of individuals with size *l*. The variance of this increment is given by $\delta_l = \omega\, \Delta(l)$, ω being a scale factor to be estimated, while l_{oo} and *k* are parameters of Von Bertalanffy growth model.

Appendix C. Error model (negative log-likelihood functions)

C.1. Catch at-size proportions

$$L_p^{f,s} = -n \sum_l \sum_y \sum_z p^{f,s}{}_{l,t,z} \log\left(\hat{p}^{f,s}{}_{l,y,z}\right) \tag{17}$$

n=30.

C.2. Abundance indices and annual catches (y) by zone

$$L_I^{f,s} = \frac{0.5}{(\sigma^{f,s,y})^2} \sum_y \sum_z \left(\frac{\log\{\hat{I}_{y,z}^{f,s}\}}{\log\{I_{y,z}^{f,s}\}}\right)^2 \tag{18}$$

σ^f=0.3, σ^s=0.15, σ^y=0.05.

C.3. Penalties & priors:

C.3.1. Annual deviates of stock-recruitment relationship

$$p_1 = \frac{0.5}{{\sigma_R}^2} \sum_y \sum_z {\varepsilon_{y,z}}^2 \tag{19}$$

σ_R=0.6

C.3.2. Annual recruitment deviates between zones (cross-correlation)

$$p_2 = \frac{0.5}{{\sigma_x}^2} \sum_y \left(\varepsilon_{y,z=n} - \varepsilon_{y,z=s}\right)^2$$

(20)

σ_x = [1.0; 0.5; 0.2]

C.3.3. Surveys catchability deviates between zones

$$p_3 = \frac{0.5}{{\sigma_q}^2} (\log(q^s_{z=n}) - \log(q^s_{z=s}))^2$$

(21)

σ_q=0.05

C.3.4. Size of recruitment deviates by zone

$$p_4^z = \frac{0.5}{{\sigma_{Lo}}^2} \left(\log(Lr_z) - \log(Lo_z)\right)^2$$

(22)

σ_{Lo}=0.10

II.4. Summary of results

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Chapter II.1. Population structure of nylon shrimp *Heterocarpus reedi* (Crustacea: Caridea) and its relationship with environmental variables off Chile

The surface distribution of organic matter and dissolved detritus (OMD) and Chl-*a* between 1997-2011 showed concentration zones near the affluent of the main rivers and at coastal upwelling areas, and as a result of this, a higher number of OMD and Chl-*a* concentration areas were registered southward of 32°S. In terms of *H. reedi* depth distribution, the bathymetric information shows that the highest *H. reedi* abundance is located in depths of 200-400 m, showing a pattern in which, at a lower latitude, the foci of highest abundance are obtained at deeper depths. The temporal variations in the bathymetric range indicate that since 2004 the abundance has gradually expanded towards higher depths, reaching a peak in 2008. In addition, an important discontinuity is observed in the abundance of *H. reedi*, whose reference points are around parallel 32°S. The increase in abundance reported southward 32°S was the most important, where the displacement of the isopleth of 120 kg km-linear^{-1} registered a gradual northward movement according to the increase of abundance.

In general, larger individuals have been found south 32°S reaching over 27 mm caparace length (CL) as average, while in the north zone, size of *H. reedi* has varied almost always below the 25 mm CL. The spatial-temporal dynamic in this variable southward 32°S shows that isopleths of 25 and 26 mm CL had a displacement in the south-to-north axis since 2001, similar to the behaviour of the isopleth of relative abundance of 120 kg km-linear^{-1} mentioned above. This situation coincides with the increase of population abundance and is explained by the

individual somatic growth alongside the contribution of juveniles located towards the borders of the population expansion. An example of this, is the gradual increase that shows the average CL through years at the 34°-36°S latitudinal range.

Since 2006 and particularly southward 32°S, both the relative abundance as the environmental variables (OMD and Chl-*a*) have registered positive anomalies. In spatial-temporal terms, the environmental and population abundance distribution suggest a spatial correlation, showing coherence both in the concentration nuclei as episodes where favourable environmental conditions are followed by high abundances of *H. reedi*. The partial correlation analysis shows that the highest level of linear relationship (0.43-0.67) between the environmental variables and the population abundance southward 32°S are obtained when a 2-year lag is considered.

Chapter II.2. Spatio-temporal modelling of the maturity, sex ratio, and physical condition of nylon shrimp *Heterocarpus reedi* (Decapoda, Caridea), off Central Chile

The results sowed, in general, the *H. reedi* carapace length (CL) measured between 10 and 40 mm CL, averaging nearly 25 mm CL and 7.25 g. Females were more prevalent in catches over 26 mm CL and were, on average, larger than males (up to 38 mm CL vs. about 33 mm CL). The prevalence of ovigerous females was greater during the third quarter, with mature individuals starting at 22 mm CL and reaching a maximum incidence of 80% at lengths >30 mm CL.

According to the General Linear Models (GLM) fitted to caparace length and individual weight, all the factors considered were significant (zone, year, sex, length). The main factors determining the variability of *H. reedi* carapace length (CL) and body weight were sex and zone, and CL was the co-variable in the GLM for body weight. The model coefficients showed that

the average length and weight increased significantly from north to south. The individuals at the southernmost zone were, on average, 12% longer and heavier than those from the northernmost zone. Also, females were 4% longer and heavier than males and irrespective of the CL, berried (mature) females weighed 16% more than resting females. Seasonally, the model's coefficient indicate both CL and body weight decreased significantly towards the second and third quarters of each year, coinciding with the period of greatest reproductive activity. Annually, CL growth was found to follow a linear trend particularly from 2007 to 2013.

On the other hand, the used model to describe both the variability of maturity and the proportion of females, shows that CL and quarters were the most relevant and significant variables. The proportion of mature females decreased significantly from north to south. Taking the third quarter to be the period when reproductive activity peaked for *H. reedi*, estimates of size at 50% maturity ($CL_{50\%}$) were significantly different between zones. North of 32°S, $CL_{50\%}$ ranged from 20.9 mm to 24.1 mm CL, whereas south of 32°S, $CL_{50\%}$ was significantly higher, ranging from 26.1 mm to 28.6 mm. Combining all years and zones, the model of proportion of maturity at size during the third quarter was P(CL)=exp(-6.53 + 0.26 CL)/(1+exp(-6.53 + 0.26 CL)). $CL_{50\%}$ was estimated to be 24.9 mm CL, and annually the results suggested a negative trend for this parameter. With respect to the sex ratio (female), CL was the most important variable and a lower proportion of *H. reedi* females were estimated south of 32°S. The results showed that females were dominant in the population (>50%) beginning at 25 mm CL.

Chapter II.3. Using a length-based stock assessment model to evaluate population structure hypotheses of nylon shrimp *Heterocarpus reedi* (Decapoda, Caridea) exploited off central Chile

The fit of the model to the historical data was adequate and reproduced the variations in the abundance index of the commercial fleet (CPUE) and research surveys, as well as the average carapace length (CL) for these two data sources per year and zone (north and south 32°S). The consistency between the pieces of information (abundance indices, landings, size compositions), particularly for the growing trend of the indicators beginning in 2000, is also worthy of note.

The results show important annual variations in the sub-populations (zones) of *H. reedi*, characterized by reduced biomass in both zones until the mid-1990s and a subsequent population increase and expansion from 2000 on. The metapopulation hypothesis showed the greatest sensitivity on the biomass scale, differing by more than 30% from the hypothesis of independent populations (north and south 32°S). Average biomass estimates in the south zone (south 32°S) are around 50,000 tons, which is 24% higher than in the north zone. The results also show that the main changes in biomass are explained by large pulses of recruits recorded throughout the decade of the 2000s in both zones. The model's parameters show that size at 50% of selectivity of the commercial fleet (30.1 mm average CL) is estimated to be 14% higher than in the north zone. The average virgin recruits in the south zone are estimated to be more than twice those of the north and explaining the different biomass estimates for these two zones. The average CL that would determines recruitment is estimated to be slightly higher in the north zone (near 17.7 mm) than in the south (16.2 mm). In the same sense, the results also

show that, regardless of the zone, the size composition of the exploitable population of *H. reedi* could be sustained in up to 10 modal groups (or states of average annual molt).

As for the hypothesis of spatial connectivity, under the scenario of a metapopulation with a pseudo-sink, the average proportion of recruits moving from the south to the north zone (which would explain the increased recruits in this area) is 28%. In the case of a metapopulation with a sink zone (i.e., no generation of recruits) in the north, the contribution from the south would reaches 37%. Considering the criteria for model selection, the hypothesis of metapopulation is the most likely with regard to the hypothesis of population independence, since the values of the AIC and BIC (statistical discrimination indexes) are both significantly lower. The results are expressed in terms of a balance between the number of resolved parameters in each model, the number of observations, and the goodness of fit of the model to the data (log likelihood), whereby the hypothesis of a metapopulation-sink seems the most likely alternative.

III. GENERAL DISCUSSION

III. GENERAL DISCUSSION

Through the historic information analysis recorded in scientific trawling surveys carried out off central Chile, we could determine that *H. reedi* distribution along the Chilean coast have not changed in the time and that population changes has been located mainly southward 32°S. The population increase recorded since 2006 was accompanied by south-to-north geographic expansion through a colonization process of less dense areas and the expanding the range of its bathymetric distribution (Fig 1a). The colonization of areas as expansion mechanism of populations has been extensively discussed on the scientific literature (e.g., Rockwood, 2006), and particularly on crustaceans decapods by authors such as Fogarty & Botsford (2006), Fëlix-Hackradt et al. (2010) and Lavesque et al. (2010).

The main nuclei of aggregations of the *H. reedi* were located nearby the mouths of rivers and upwelling zones (Fig. 2), which is an observed characteristics in other coastal decapods (e.g. Haas et al., 2001; Medina-Reyna, 2001; Ramírez-Rodríguez et al., 2003; Carvalho et al., 2011). In this context, at the southern area of the distribution of *H. reedi* (southward 32°S), a significant correlation between abundance and concentrations of organic matter dissolved (OMD) and surface chlorophyll (Chl-a) was found. This correlation was maximum (r = 0.78-0.86) when a two-year lag was considered among the variables, coinciding also with the recruitment age at which the shrimp reach around 11.5 mm CL size (e.g., Ziller, 1993; Roa & Ernst, 1996; Canales et al., 1999).

This relationships could find its explanation if we think on the idea that, when there are good surface environmental conditions of OMD and Chl-a, derived probably from the discharge of rivers and the coastal upwelling, the conditions would be favourable for feeding and spawning of adults and for the survival of larvae and post-larvae. Later, these would settle

following the course of the larval drift and would recruit to the fishing gear or zone as juveniles of two years old. Also and as a consequence of speed and the south-to-north direction of the Humboldt Current System (Glantz, 1998; Lorca et al., 2004; Fuenzalida et al., 2008; Silva, 2012), larvae could be transported more than one thousand km in three months, which would explain the direction and orientation of the spatial expansion of the *H. reedi* population indicated above.

Important to note that these relationships were not necessarily associated to “El Niño” events. For example, considering the strong event recorded in 1997-1998, no significant relationship was found with shrimp density in posterior years. This lack of correlation between both events might be due to the fact that our sampling period was conducted during spring months, when rains as main predictor of river discharges begins its decline.

Important differences in the spatial characteristics of the population were observed, for example, the predominance of adults (>25 mm de CL) southwards 32°S, where the biomass increase is explained by somatic growth and where the bulk of the parental population inhabits (Fig. 1b). Following the idea of Pulliam (1988), Hanski & Gilpin (1997), and Hanski (1998), this area would act as “source habitat” or "reproductive refuge", and could be providing a larval fraction to the zone located northward 32°S. This last would represent a “pseudo-draining" habitat where the population biomass is smaller and there is a majority presence of juveniles. Thereby, considering also that an heterogeneous quality of the habitat can generate larger populations as a source of migrants (Rockwood , 2006), and that colonization in decapods occurs by larval dispersion (Fogarty & Botsford, 2006; 2007), we have suggested that *H. reedi* could constitute a metapopulation with at least two sub-populations, located northward and southward of 32°S. This proposal is reinforced by Acuña et al. (1997), who found out significant differences in morphometric aspects in the samples coming from these two areas. The authors

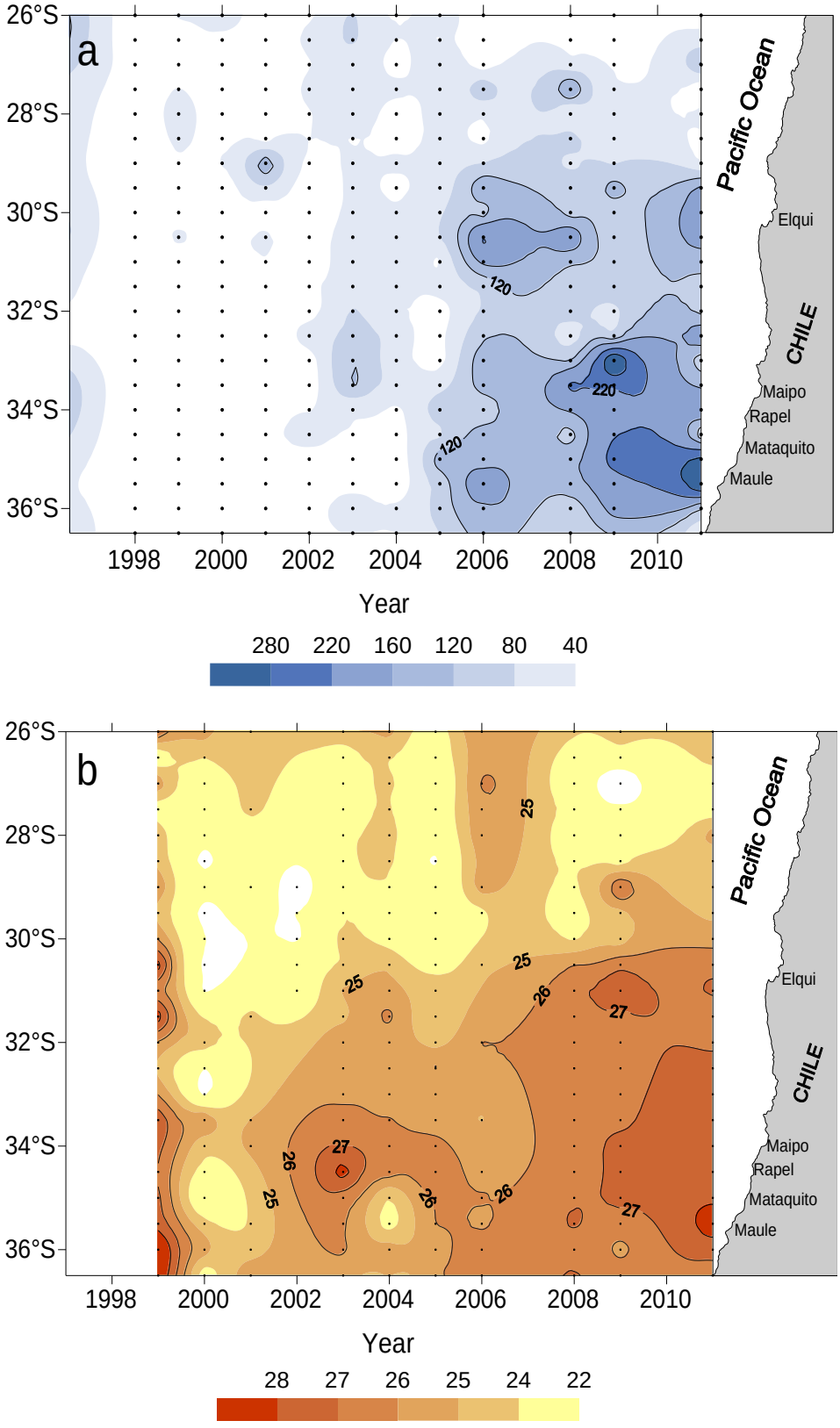

Fig. 1. a) Isopleths of abundance (kg km-lineal^{-1}), and b) mean carapace length (mm) (both genders) of *Heterocarpus reedi* estimated in surveys using swept area method by latitude and year. Dots represent the information nodes (Source: Canales et al., 2016a)

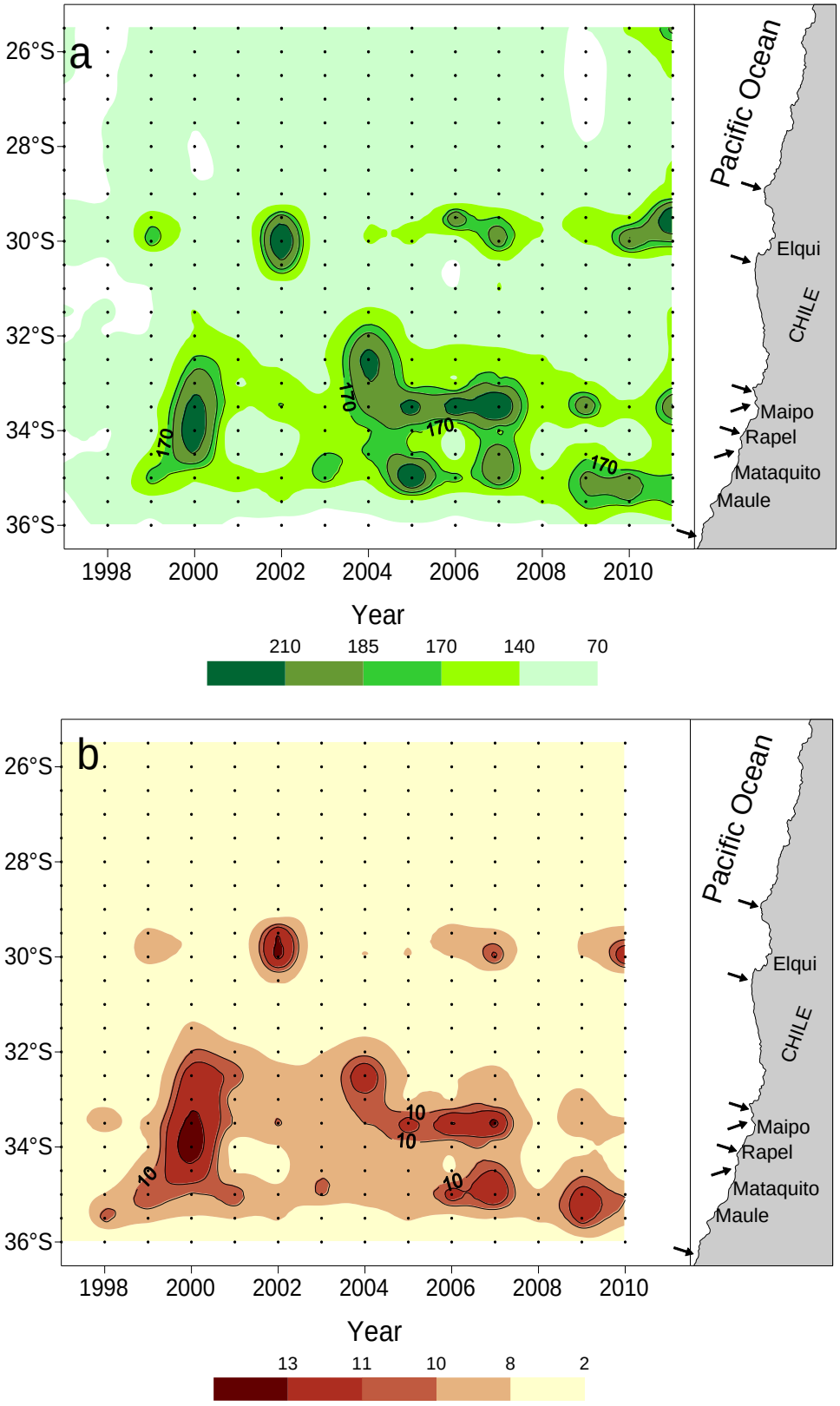

Fig. 2. a) Isopleths of absorption coefficient of chlorophyll-a concentration (mg m^{-3}) and b) organic matter and dissolved detritus (m^{-1}). Dots represent the information nodes. Over the map the main river names are displayed. The black arrows correspond to main upwelling zones (Source: Canales et al., 2016a).

complemented their results with a genetic analysis, determining that population heterogeneity would be explained by a migratory process along the spatial distribution.

On the base of the main findings of Chapter II.1, and considering the spatial and temporal analysis of biological samples collected in 17 years of nylon shrimp fishery through a General Linear Model (GLM; McCullagh and Nelder, 1989), it was determined that main biological attributes, particularly those related to physical condition and maturity, have a significant spatial and temporal heterogeneity.

The spatial pattern for the physical conditions of *H. reedi* were associated to environmental heterogeneity observed along its distribution as was mentioned before, this as determinant in food availability as detritus and other organic materials. Similar findings have been reported in other marine decapods, where bottom conditions seem explain seasonal and spatial differences in some biological parameters (e.g., Company et al., 2001, 2004; Encarnaçaô et al., 2013; Sancinetti et al., 2014). In our analysis area, north of 32°S there is a semi-desertic weather, low precipitations and a narrow continental shelf, while south, several tributary rivers and coastal upwelling zones contribute with important amounts of organic matter and detritus (Fig 3), and probably determining an important food source (Canales et al., 2016a). Both individual CL and weight differed significantly on spatial and seasonal scales, and as was mentioned by Canales et al (2016a) in Chapter II.1, the individuals of both sexes are longer and in better physical condition south of 32°S. Also and consequently with reproductive process, a significant weight loss was observed at third quarter, aspect that also has been documented for decapods in regards to energy transference destined the reproductive aspects. (Bauer, 2004).

The modelling did not provide evidences about seasonality in the proportion of females in the samples and it could not be established connection with the reproductive

process. Instead, a weak geographic pattern was observed where the relative predominance of females decreased gradually from north to south, and was heavily dependent on caparace length (CL). Also, our results confirmed the findings provided by Gaete and Arana (1986) related to sex ratio of *H. reedi*, where females are the dominant gender in the size ranges over 25 mm CL and with no significant differences between months

The nylon shrimp maturity was also characterized by a size that at 50% of mature females ($CL_{50\%}$) is 24.9 mm CL, measure similar to those found in previous works: 25.5 mm CL (Arana and Tiffou, 1970), 24.3 mm CL (Canales et al., 1998), and 25.1 mm CL (Arana et al., 1976). Also and with less relevance, the results confirmed the spatial pattern suggested by Bahamonde and Henríquez (1970), where length at maturity $CL_{50\%}$ increased significantly from north to south. In this sense, several authors have described changes of this parameter in decapods (e.g. Tuck et al., 1997; Hill et al., 1997; Kuhulmann and Walker, 1999; Queiroz et al., 2013), relating it for example, with the reduction in average length at age due to overexploitation, or habitat characteristics (food availability) in determining life parameters in discrete population units. In the case of *H. reedi*, the latter may be the more likely scenario since fishery exploitation does not seem to have generated significant changes in the population structure (Montenegro et al., 2014).

According to Canales et al. (2016a), *H. reedi* has a heterogeneous population structure, where greatest densities and largest individuals are located south of 32°S, probably as response of better food supply and sediment quality, thereby determining the larger sizes of $CL_{50\%}$. Our interpretation is that better quality of the habitat may lead to delayed maturity, allowing individuals to allocate more of their energy consumption to growth and, thereby, explaining why few large individuals were found north of 32°S and why females in that area were smaller at maturity. As indicated by Kuhlmann and Walker (1999), latitudinal differences

in $CL_{50\%}$ result in implicit changes in the growth patterns and could have important implications for management of *H. reedi* fishery.

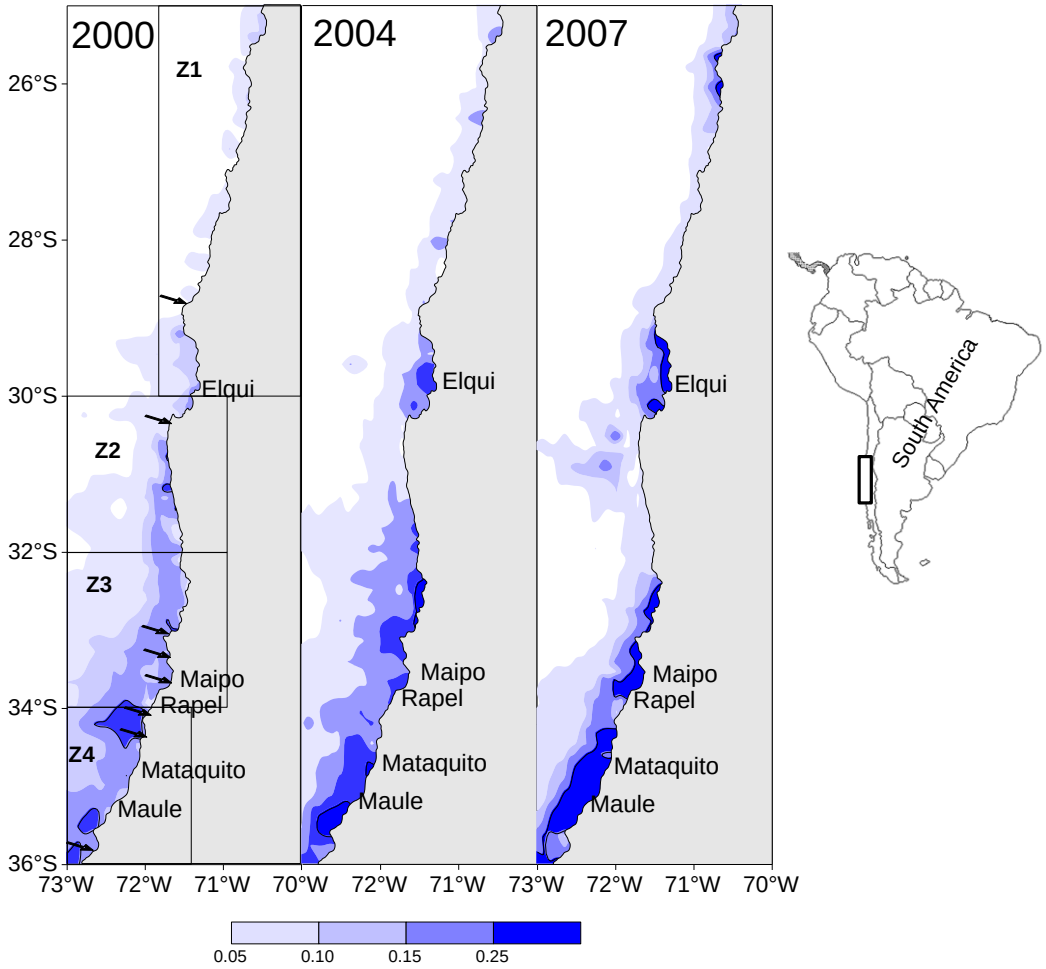

Fig. 3. Study zone and distribution of cumulative organic matter and dissolved detritus between September and December in three years, with the main river names are displayed. The black arrows indicate the main upwelling zones. The rectangles make reference to subzones of analysis (Source: Canales et al., 2016b).

The results also showed annual trends in key biological attributes, as the increase in proportion of mature females together to a decline in $CL_{50\%}$ (Fig 4), changes that have often been related with variations in bottom characteristics, environmental stress factors and

exploitation (e.g. Phillip, 2013; Zheng, 2008; Castilho et al., 2007). Several of revised works indicate that food availability seems to be related environmental conditions, thereby being a key factor for the larval survival in decapods. In this sense, for *H. reedi*, Canales et al. (2016a) provided environmental indicators associated with the area south of 32°S, showing a suggested decrease in the anomalies of chlorophyll-a and organic matter dissolved in last years, which could explain in some way the decline in $CL_{50\%}$ mentioned above.

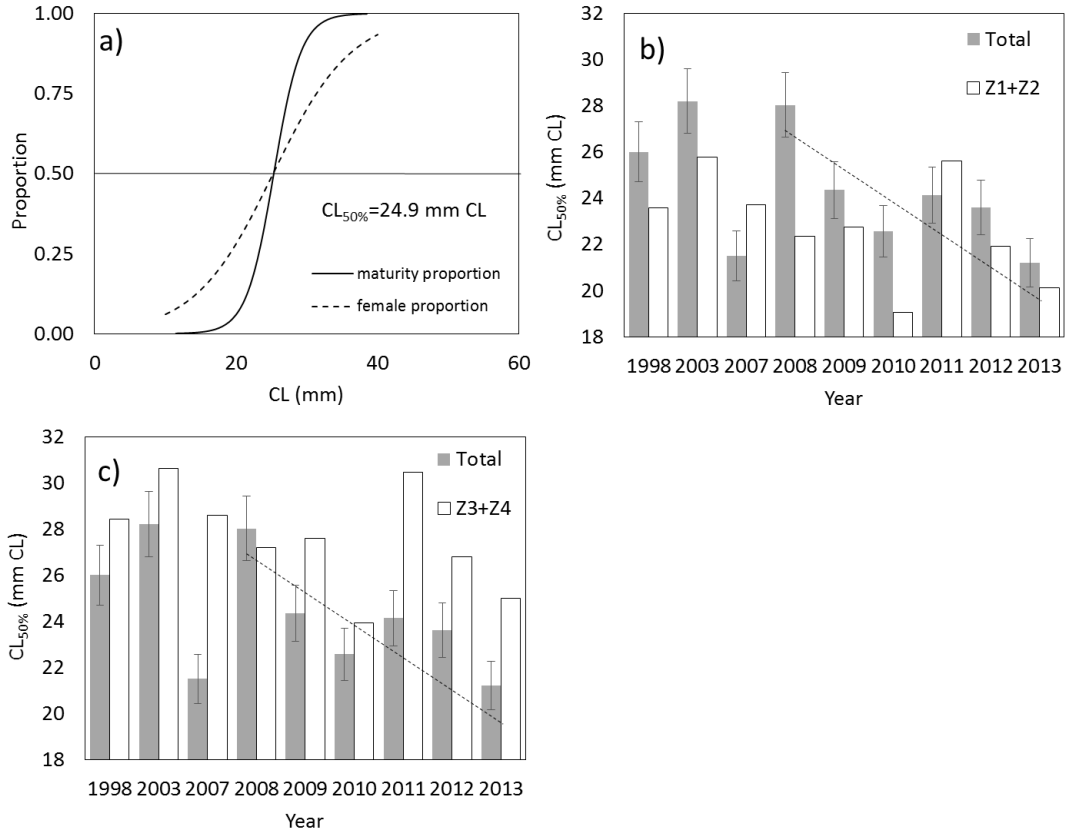

Fig. 4. (a) Proportion of mature females by size of *H. reedi* in the third quarter, for all years and combined zones, plus the proportion of females by size. In panels b) and c), comparative annual changes in maturity size (CL50%) by zones: total vs Z1+Z2 combined (b), total vs Z3+Z4 combined (c). The dotted line represents the annual trend, and error bars show the 95% confidence interval (Source: Canales et al., 2016b).

Considering the results found in the work on population structure of *H. reedi* (Cap. II.1) and spatial and temporal heterogeneity in its biological attributes (Cap. II.2), a spatially explicit model of its population dynamic was developed in order to verify the information's reproductibility according to alternatives of population structure hypotheses. The statistic model of large scale was coded in Automatic Differentiation Model Builder (ADMB) (Fournier et al., 2012), a contemporary computer language used for stock assessment at important fisheries of the world.

The model-based analysis of the data from the commercial fishery and research surveys for *H. reedi* caught off central Chile reveals that, in general, the historical record can be explained by alternative hypotheses as to population structure and spatial connectivity between zones, with the metapopulation hypothesis being the most likely in statistical terms (Fig 5).

The data analysis based on a population model allowed us to investigate the spatial distribution of recruits, obtain more details about the population structure, and learn about the biological processes regardless of the age structure (Punt et al., 2013). We determined that the subpopulations to the north and south of 32°S experience important variations caused by pulses of recruits (Fig. 6)(Montenegro et al., 2015), with the south acting as a source population. In this sense, average biomass estimates in the south zone was around 50,000 tons, which is 24% higher than in the north zone (sink population) (Fig. 6).

Although the abstraction of a model generates results that can only be considered in a relative or referential way, it gives an idea of the probable theoretical contribution of the larvae that could be drifting northward, estimating this to be, on average, between 28% and 37%, depending on the type of metapopulation (“sink” or “pseudo-sink”).

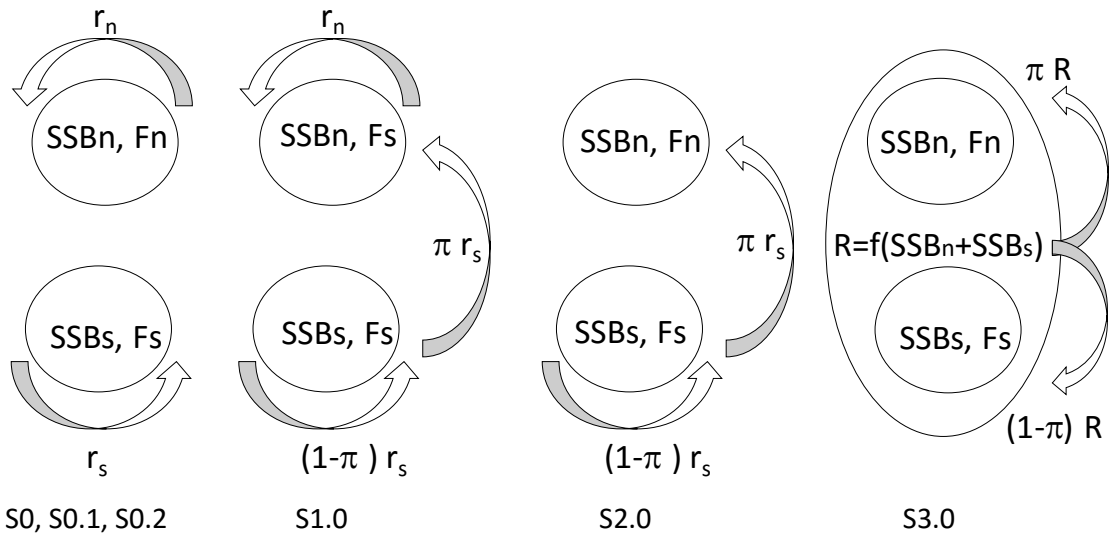

Fig. 5. Illustration of four hypotheses of nylon shrimp population structure. SSB represents the population spawning biomass, n and s are sub-indexes for 'north' and 'south', respectively, r is recruitment, F is the zone-specific fishing mortality and □ is the proportion of south recruitment that migrated to the north (S0, S1.0, S2.0) or an allocation coefficient (S3.0). Recruitment occurs in scenarios S0, S0.1, S0.2 and S1.0 in each zone while in scenario S2.0 all recruitment to the north zone comes from south zone. S3.0 is the representation of a single stock where recruitment to each zone is a proportion of a total recruitment as a function of a combined biomass. (Source: Chapter II.3).

We propose to considering the region south of 32°S as a reproductive refuge or a source population of larvae and post-larvae that partially or totally supplies the area north of 32°S (sink or pseudo-sink population), which generates important challenges for the future management of the fishery. Priority should be given to management mechanisms such as increased caution in exploitation and continuous monitoring of the reproductive refuge (e.g., Campbell, 1986; McGarvey et al., 1992; McGarvey & Willison, 1995; Kjelland et al., 2015). Finally, the proposed population model could be useful not only to assess the stock size annually and as reference for fishery management, but also for evaluate the hypotheses about the population structure as far new information pieces be generated.

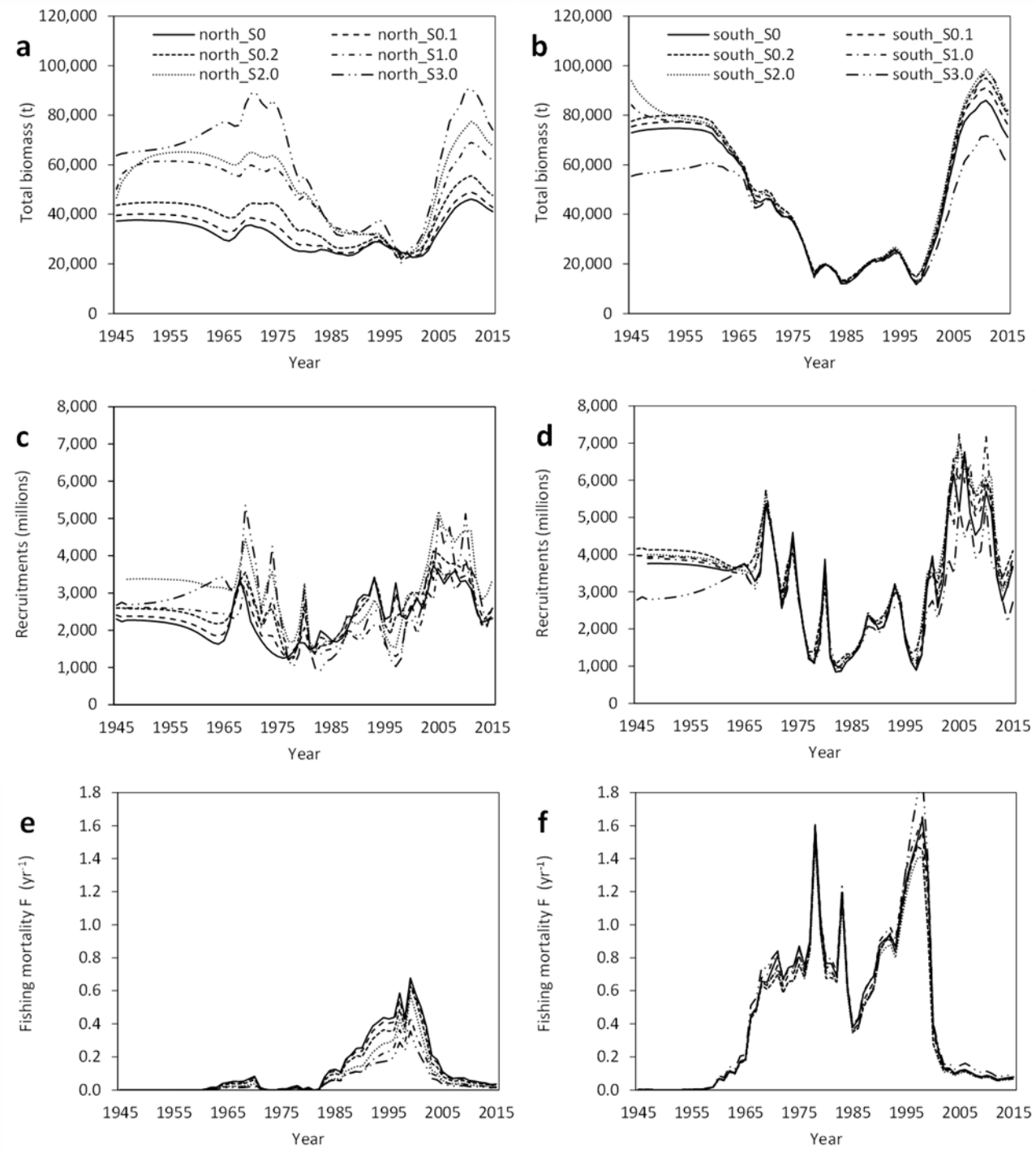

Fig. 6. Total biomass and recruitments of nylon shrimp by zone and year under different hypothesis. Right and left panels correspond to northern and southern zone, respectively. Scenarios S0, S1 and S2 correspond to hypotheses of population structure (Source: Chapter II.3).

IV. CONCLUSIONS

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Noticeable patterns in environmental conditions along nylon shrimp distribution were identified, mainly in those areas close to rivers mouth and upwelling zones southward 32°S, which would be related with fluctuations in abundance and distribution of *H. reedi*. This evidence was supported by positive correlation levels between abundance and concentration of environmental variables as organic dissolved matter and Chlorophyll-α with lag of two years, and whose explanation would be given by the relationship between good environmental conditions, larval survival success and its later settlement before to reach the recruitment size at two years old.

The results permit conclude that biomass increment of *H. reedi* is explained both somatic growth of individuals that remained within its abundance nuclei as the expansion process in north direction determined probably by the larvae drift. This population expansion is also related with an important amplitude of all its bathymetric range. In this sense, the shrimp population is likely to be constituted by a metapopulation structure with at least two subunits located north and south 32°S, and whose connectivity would be explained by larvae drift through Humboldt Current System in south-north direction, situation very relevant for fishery management when conversely, them are considered as independent stock units.

Thereby, given the level of relationship found between the environmental variables and the abundance of the *H. reedi*, including the population structure, it is concluded that is need to further investigate and strengthen this evidence, since this could become as a forecasting tool in the management of this fishery when poor environmental anomalies be detected. To reinforce that, it is suggested to develop a more detailed research on the river tributaries related to nylon shrimp distribution, and the early development stages of this crustacean

related to its larval drift along the coast of Chile and its dependence with environmental factors.

In regards to spatio-temporal variations in biologic attributes of nylon shrimp *Heterocarpus reedi*, the analyses allow conclude that there is a noticeable spatial pattern from north to south in biologic attributes of *H. reedi* characterized by: increasing of weight and individual size, a larger maturity size, and a lower female proportion. In general, nylon shrimp females are dominant in the population beginning 25 mm CL and the spawning activity is more prevalent at third quarter, coinciding with the spring start at southern hemisphere where the south wind is predominant, more upwelling events are recorded, and increase discharges of rivers by thaws of mountain range.

In addition, it can conclude that better environmental conditions in the southern portion of the nylon shrimp distribution (southward 32°S), this is defined by an increase of organic dissolved material and Chlorophyll-α as indicators of food availability, would explain its better physical conditions, and summarized as bigger individuals with higher maturity size. This better quality of the habitat would lead to delayed maturity, allowing individuals to allocate more of their energy consumption to growth. In same sense, it is concluded that the average maturity size in nylon shrimp is larger in the south, and its time variations would be related directly with environmental conditions as reproductive adaptative strategy of the population. The decrease in the anomalies of chlorophyll-α and organic matter dissolved since 2008 would explain the increase of proportion of mature females as response to a decline in size at first maturity.

Notwithstanding the foregoing, further investigations are necessary to evaluate the apparent relationship between maturity, zone and quarter. This reason is particularly relevant for fishery management purposes when the close of fishing seasons is conducted by zone and

based on local reproductive processes. In this sense, a particular monitoring design should be implemented to collect the relevant information

In regards to the modelling to evaluate the population structure of nylon shrimp *Heterocarpus reedi* and however the historical information of nylon shrimp fishery can be explained by alternative hypotheses regarding its population structure, statistically, it is concluded that a metapopulation with two subpopulations located north and south of 32 ° S turns out to be the most likely hypothesis, being the southern subpopulation considered as source population or reproductive refuge. In this sense, the scale of virgin recruitment in the south would be more than twice the scale of the north, while the proportion of migrants recruits from south to north is estimated between 28% and 37% depending on the type of metapopulation (pseudo-sink or sink). With all this, the population biomass in the south is estimated varying around 50 thousand tons, 24% higher than the subpopulation located in the north.

Although further empirical evidence is necessary to support the population structure hypothesis, it is concluded that ecological grounds given in the literature along with our results and observations suggest that a reproductive refuge area for *H. reedi* south of 32°S should not be discarded. Therefore, priority should be given to management mechanisms such as increased caution in exploitation and continuous monitoring of both the fishery as indexes of scientific surveys in this zone, in order to ensure the generation of recruits along the shrimp distribution, thereby endowing the fishery with resilience and sustainability.

Finally, it is recommended to extend these findings to develop similar researches in other crustacean decapods and consider the model of population dynamic developed in this thesis, as an alternative tool for stock assessments in crustaceans and its use for fishery management.

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APPENDICES

Appendix I. Details of trawl surveys and environmental variables used to analyzing of population structure of *Heterocarpus reedi* (Chapter II.1)

Table 1

Nylon shrimp (*Heterocarpus reedi*) biomass (tons) in trawl surveys by year and zone. (Source: Fondo de Investigación Pesquera, Chile).

Year	24°00'-32°10'S	32°10'-37°00'S	Total
1996	24,557	10,873	35,430
1998	2,593	2,593	5,186
1999	876	20,872	21,748
2000	725	21,086	21,811
2001	3,224	19,575	22,799
2002	8,348	18,256	26,604
2003	7,465	18,079	25,544
2004	8,281	21,545	29,826
2005	14,382	27,561	41,943
2006	19,486	37,111	56,597
2007	-	-	-
2008	15,809	28,772	44,581
2009	27,718	38,058	65,776
2010	-	-	-
2011	23,515	35,048	58,563
2012	16,205	26,367	42,572

Table 2

Catches of nylon shrimp (*Heterocarpus reedi*) and general sampling details of surveys carried out off Chile between 1996 and 2011. In years, 1997, 2007 and 2010 surveys were not carried out.

Year	Catch (kg)	Hauls (n)	Effort (km)	Biological samples (n)	(fp)*	Depth (m) (min)	(max)	Latitude (°S) (min)	(max)	Period
1996	32271	297	400	74587	45%	170	440	25.9	38.5	May - Ago
1998	4552	274	456	36415	70%	46	649	21.6	38.2	Ago - Dic
1999	5362	248	439	18449	67%	122	505	21.7	38.5	Jul - Jul
2000	23181	780	1427	152816	65%	74	604	23.0	37.0	Jun - Oct
2001	13090	348	740	23989	58%	84	617	21.7	38.3	Jun - Jul
2002	55793	1156	2308	97860	66%	51	584	23.0	37.0	Ago - Oct
2003	44588	442	805	266416	63%	148	497	23.0	36.7	Ago - Sep
2004	32175	502	855	151041	60%	120	562	23.0	36.9	Jul - Sep
2005	64685	562	1235	208964	57%	110	640	25.2	37.0	Jul - Ago
2006	42068	407	376	19045	50%	118	648	24.2	36.7	Oct - Dic
2008	55225	515	531	54991	51%	125	518	25.3	36.7	Jun - Dic
2009	69324	490	513	49567	56%	108	575	25.1	36.7	Ago - Nov
2011	54626	379	538	39662	56%	131	652	25.2	36.7	Oct - Dic

* fp: female proportion

Table 3.

Hauls fishing number carried out in swept area surveys by year and latitudinal range.

	Year													
Latitude (°S)	1996	1998	1999	2000	2001	2002	2003	2004	2005	2006	2008	2009	2011	Total
21-5-23.5	0	26	21	9	21	8	2	3	0	0	0	0	0	90
23.5-25.5	0	22	22	96	28	139	37	30	2	18	0	3	2	399
25.5-27.5	38	47	31	96	41	164	50	62	106	50	59	53	34	831
27.5-29.5	27	30	24	93	22	165	55	65	70	33	59	44	33	720
29.5-31.5	61	46	24	103	42	138	75	85	100	86	135	85	71	1051
31.5-33.5	47	34	31	120	53	186	83	89	104	98	106	82	81	1114
33.5-35.5	59	32	37	119	66	129	76	94	92	74	77	125	83	1063
35.5-37.5	56	23	32	144	54	227	64	74	88	48	79	98	75	1062
37.5-39.0	9	14	26	0	21	0	0	0	0	0	0	0	0	70
Total	297	274	248	780	348	1156	442	502	562	407	515	490	379	6400

Table 4

Hauls fishing number carried out in swept area surveys by year and depth.

	Depth (m)					
Year	100-200	200-300	300-400	400-500	>500	Total
1996	5	88	191	13	0	297
1998	91	67	61	43	12	274
1999	52	65	70	60	1	248
2000	145	274	244	84	33	780
2001	94	118	61	60	15	348
2002	278	397	288	155	38	1156
2003	17	152	203	70	0	442
2004	41	154	191	105	11	502
2005	22	136	178	95	131	562
2006	56	129	140	61	21	407
2008	51	216	209	34	5	515
2009	47	219	171	50	3	490
2011	30	160	164	24	1	379
Total	929	2175	2171	854	271	6400

Table 5

Summary of georeferenced information of absorption coefficients of organic matter and dissolved detritus (OMD) (m^{-1}) and Chlorophyll-α (Chlo-*a*) (mg m^{-3}) obtained by satelital telemetry (NASA- Giovanni Web) Cuadrant 26°-36°S ; 70°-73°W.

	OMD				Chlo-*a*			
Año	Records	Mín	Máx	Mean	Records	Min	Max	Mean
1997	3331	0.014	0.291	0.038	3224	0.193	6.474	0.594
1998	3319	0.012	0.452	0.041	3207	0.125	28.681	0.655
1999	3303	0.013	0.545	0.050	3206	0.176	10.298	0.849
2000	3305	0.014	0.482	0.059	3211	0.189	20.713	0.987
2001	3297	0.015	0.424	0.051	3191	0.213	7.832	0.854
2002	3306	0.016	0.911	0.058	3205	0.223	38.816	1.031
2003	3302	0.013	0.433	0.049	3189	0.160	10.485	0.895
2004	3297	0.011	1.322	0.052	3191	0.200	17.382	1.020
2005	3328	0.016	0.614	0.051	3228	0.227	33.489	0.999
2006	3317	0.015	1.469	0.051	3217	0.235	22.368	0.921
2007	3322	0.018	1.582	0.058	3216	0.278	20.398	1.088
2008	3330	0.014	0.512	0.046	3223	0.153	17.149	0.885
2009	2962	0.010	1.155	0.054	2777	0.116	36.926	1.050
2010	3281	0.015	1.380	0.052	3192	0.228	20.957	0.940
2011	-	-	-	-	3325	0.240	30.398	1.203

Appendix II. Data summary used to modelling the biological attributes of *H. reedi* through a Generalized Linear Model (GLM) (Chapter II.2)

Table 1.

Main data set attributes of biological sampling of *Heterocarpus reedi* in Chile.

Year	Latitude range (°S)	Sample size	Females		mature females		CL range (mm)	mean-CL (mm)	mean-W (g)
1997	25.5 - 36.5	11,357	6,472	(57%)	2,166	(33%)	30.00 - 41.50	25.05	7.47
1998	27.1 - 36.7	12,149	6,792	(56%)	1,788	(26%)	12.70 - 37.40	25.13	7.05
1999	25.3 - 36.7	18,808	10,379	(55%)	2,184	(21%)	12.10 - 39.10	24.17	6.19
2000	25.6 - 36.7	11,120	5,147	(46%)	450	(9%)	11.60 - 34.80	23.94	5.98
2001	26.5 - 32.8	19,341	9,232	(48%)	57	(1%)	10.00 - 38.20	23.83	5.83
2002	26.4 - 32.8	22,927	11,373	(50%)	21	(0%)	10.30 - 39.00	22.85	4.96
2003	26.4 - 34.5	23,650	11,452	(48%)	1,466	(13%)	13.30 - 37.10	24.48	6.35
2004	25.3 - 35.9	16,867	9,065	(54%)	1,984	(22%)	10.00 - 35.70	24.87	6.49
2005	26.8 - 36.7	12,468	6,403	(51%)	1,422	(22%)	14.70 - 35.70	24.99	6.30
2006	29.2 - 36.4	7,871	3,979	(51%)	689	(17%)	10.00 - 35.10	25.39	6.40
2007	28.2 - 36.7	19,485	11,149	(57%)	4,483	(40%)	10.00 - 40.70	27.14	9.03
2008	27.2 - 36.6	15,756	8,521	(54%)	1,007	(12%)	11.30 - 39.50	26.34	8.14
2009	28.0 - 36.7	23,491	11,820	(50%)	2,761	(23%)	11.80 - 39.40	26.11	7.60
2010	29.2 - 36.6	21,756	11,784	(54%)	3,926	(33%)	10.80 - 39.20	26.83	9.20
2011	28.8 - 36.6	26,705	14,214	(53%)	4,161	(29%)	11.40 - 39.10	26.83	9.07
2012	29.4 - 36.6	20,038	9,349	(47%)	2,255	(24%)	12.20 - 41.10	26.99	8.92
2013	29.3 - 36.2	11,143	4,874	(44%)	1,310	(27%)	11.20 - 37.80	26.77	8.21

Table 2.

Number of individuals of *Heterocarpus reedi* measured by year, quarter and zone.

	Quarter				Zone			
Year	1th	2th	3th	4th	25°- 30°S	30°- 32°S	32°- 34°S	34°- 36°S
1997	334	2,653	6,351	2,019	1,512	1,248	4,086	4,511
1998	2,667	3,349	1,414	4,719	5,882	1,462	1,541	3,264
1999	6,390	5,327	1,706	5,385	14,440	478	1,756	2,134
2000	5,859	2,422	1,888	951	8,582	227	1,076	1,235
2001	3,623	4,598	3,437	7,683	12,500	2,976	3,865	0
2002	4,642	6,501	3,891	7,893	18,227	2,184	2,516	0
2003	8,064	6,866	2,236	6,484	15,981	1,334	4,662	1,673
2004	6,307	4,333	2,096	4,131	9,921	2,200	3,808	938
2005	4,317	4,775	328	3,048	5,785	1,616	3,455	1,612
2006	3,257	1,552	832	2,230	1,982	565	2,125	3,199
2007	6,588	5,491	2,385	5,021	2,225	840	1,550	14,870
2008	8,639	2,055	1,942	3,120	4,687	1,162	4,041	5,866
2009	11,214	8,735	1,810	1,732	6,846	3,277	8,344	5,024
2010	7,960	5,631	2,782	5,383	2,484	2,333	5,012	11,927
2011	11,381	5,006	6,280	4,038	1,460	4,522	7,727	12,996
2012	11,937	2,510	2,982	2,609	1,206	2,014	5,817	11,001
2013	6,350	1,749	1,835	1,209	761	1,202	4,660	4,520

Appendix III. Codes (in R) used to modelling the biological attributes of *H. reedi* through a Generalized Linear Model (GLM) (Chapter II.2)

1. Fit of GLM to individual weight data

```
rm(list=ls())

matriz=read.csv("base_biol_1997_2013.csv", header=T, sep=",")

matriz$Quarter=as.factor(matriz$trim)
matriz$Zone=as.factor(matriz$zona)
matriz$Year=as.factor(matriz$anho)
matriz$Sex=as.factor(matriz$sexo)


#-------modelo normal relacion talla peso
mod1<-glm(log(peso)~Quarter+Zone+Year+Sex+log(talla),data=matriz,family=gaussian(link = "identity"))


summary(mod1)
anova(mod1,test="Chisq")
drop1(mod1,test="F")

library(boot)
mod1.diag<-glm.diag(mod1)
glm.diag.plots(mod1,glmdiag=glm.diag(mod1),subset=NULL,iden=FALSE,labels=NULL,ret=FALSE)

library(MASS)
par(mfcol=c(2,2))
Residuals <- studres(mod1) #resid(mod0)
xfit<-seq(min(Residuals),max(Residuals),length=40)
yfit<-dnorm(xfit)
hist(Residuals, freq=FALSE, xlab="Std. residuals", ylab="Frequency")
lines(xfit, yfit)
qqnorm(Residuals,xlab="Theoric quantiles", ylab="Std. residuals")
lines(xfit, xfit)
plot(fitted(mod1),Residuals,xlab="Predicted values", ylab="Std. residuals")
```

2. Fit of GLM to mature females data

```
#-------modelo binomial para la proporcion de maduros
mod1<-glm(madurez~Quarter+Zone+Year+talla,data=matriz,family=binomial(link = "logit"),subset=aux)

summary(mod1)
anova(mod1,test="Chisq")
drop1(mod1,test="Chisq")
drop1(mod1,test="F")


#-------modelo binomial para la proporcion de maduros con interaccion trimestre@zona
```

```
mod2<-glm(madurez~Quarter+Zone+Year+talla+Quarter*Zone,data=matriz,family=binomial(link =
"logit"),subset=aux)
summary(mod2)
anova(mod2,test="Chisq")
drop1(mod2,test="Chisq")
drop1(mod2,test="F")
```

3. Fit of GLM to caparance length data

```
#-------modelo gaussiano para la talla promedio
aux3<-matriz$IDyear>0
mod5<-glm((talla)~Quarter+Zone+Year+Sex,data=matriz,family=gaussian(link = "log"))
summary(mod5)
anova(mod5,test="Chisq")
drop1(mod5,test="F")


#-------modelo gaussiano para la talla promedio + interacciones
mod5b<-glm((talla)~Quarter+Zone+Year+Sex+Quarter*Zone,data=matriz,family=gaussian(link = "log"))
summary(mod5b)
anova(mod5b,test="Chisq")
drop1(mod5b,test="F")
```

4. Fit of GLM to female proportion data

```
#-------modelo binomial para la proporcion de hembras
aux2<-matriz$IDyear>0
mod4<-glm(hembras~Quarter+Zone+Year+talla,data=matriz,family=binomial(link = "logit"))
write.table(mod4$fitted.values, "D:/DoctoradoUB/2do Articulo/datos/predproph.txt",
summary(mod4)
anova(mod4,test="Chisq")
drop1(mod4,test="F")

#----------modelo 4 pero con interacciones zona-quarter
mod4b<-glm(hembras~Quarter+Zone+Year+talla+Quarter*Zone,data=matriz,family=binomial(link = "logit"))
summary(mod4b)
anova(mod4b,test="Chisq")
drop1(mod4b,test="F")
```

Appendix IV. Codes (in ADMB) of MODMETAPOP.TPL file developed to modelling the population of *Heterocarpus reedi* (Chapter II.3).

```
GLOBALS_SECTION
 #include <admodel.h>
 #include <stdio.h>
 #include <time.h>
 time_t start,finish;
 long hour,minute,second;
 double elapsed_time;
 ofstream mcmc_report("mcmc.csv");

TOP_OF_MAIN_SECTION
 time(&start);
 arrmblsize = 90000000;
 gradient_structure::set_GRADSTACK_BUFFER_SIZE(1.e7);
 gradient_structure::set_CMPDIF_BUFFER_SIZE(1.e7);
 gradient_structure::set_MAX_NVAR_OFFSET(5000);
 gradient_structure::set_NUM_DEPENDENT_VARIABLES(5000);


DATA_SECTION


 init_int ntime
 init_int nedades
 init_int ntallas
 init_int nzonas


 init_matrix mdatos(1,ntime,1,17)

 init_vector Tallas(1,ntallas)

 init_3darray Ctot(1,nzonas,1,ntime,1,ntallas)
 init_3darray Ncru(1,nzonas,1,ntime,1,ntallas)
 init_matrix  msex(1,nzonas,1,ntallas)
 init_matrix  Wmed(1,nzonas,1,ntallas)

 init_number sigmaR
 init_number sigma2R// penaliza desvios entre zonas
 init_number cvq// penaliza desvios de q cruceros entre zonas

 init_matrix dt(1,nzonas,1,3) //fraccion del año del desova e indices
 init_matrix Par_bio(1,nzonas,1,7)
 init_matrix cv_Par_bio(1,nzonas,1,7)

 //------------------------------------------------------------------------
 vector log_Lr_prior(1,nzonas)
 vector log_sr_prior(1,nzonas)
 vector log_beta_prior(1,nzonas)

  !! log_Lr_prior(1) = log(Par_bio(1,3));
  !! log_sr_prior(1) = log(Par_bio(1,4));
  !! log_beta_prior(1)= log(Par_bio(1,5));
  !! log_Lr_prior(2) = log(Par_bio(2,3));
  !! log_sr_prior(2) = log(Par_bio(2,4));
  !! log_beta_prior(2)= log(Par_bio(2,5));
 //------------------------------------------------------------------------

 init_int    minedad
 init_number   p_prior // nivel de conectividad
 init_number   cv_p_prior

 number   log_p_prior
 !!log_p_prior = log(p_prior+1E-10);

 //------------------------------------------------------------------------
 init_number bprior //Hiperestabilidad
 number log_b_prior
  !! log_b_prior = log(bprior);

 //------------------------------------------------------------------------
```

```
 init_number L50prior
 init_number s1prior
 init_number s2prior
 init_int opt_sel2 // opcion domo en flota
 init_int opt_sel3 // opcion domo en crucero

 number log_L50prior
 number log_s1prior
 number log_s2prior

 !! log_L50prior = log(L50prior);
 !! log_s1prior = log(s1prior);
 !! log_s2prior = log(s2prior);
//-------------------------------------------------------
 // bloques de selectividad y q NORTE
 init_int    nbloques1n
 init_vector ybloques1n(1,nbloques1n)

 init_int    nbloques2n // cruceros
 init_vector ybloques2n(1,nbloques2n)

 init_int    nqbloquesn
 init_vector yqbloquesn(1,nqbloquesn)

 init_int    nqbloquescn
 init_vector yqbloquescn(1,nqbloquescn)

 // bloques de selectividad y q SUR
 init_int    nbloques1s
 init_vector ybloques1s(1,nbloques1s)

 init_int    nbloques2s
 init_vector ybloques2s(1,nbloques2s)

 init_int    nqbloquess
 init_vector yqbloquess(1,nqbloquess)

 init_int    nqbloquescs
 init_vector yqbloquescs(1,nqbloquescs)


//-------------------------------------------------------

 init_int    opt_qf
 init_int    opt_qc

 init_int    opt1_fase // selectividad flota
 init_int    opt2_fase // selectividad cruceros


 init_int    opt_Lr
 init_int    opt_sr
 init_int    opt_beta
 init_int    opt_F
 init_int    opt_R0n
 init_int    opt_R0s
 init_int    opt_devRn
 init_int    opt_devRs
 init_int    fase_propR
 init_int    opt_bpow //hiperestabilidad

 init_number  festim


INITIALIZATION_SECTION

  log_Lr            3.05527650665 //log_Lr_prior
  log_sr            0.182321556794 //log_sr_prior
  log_beta          -1.62782331781 //log_beta_prior

  log_L50n          log_L50prior
  log_L50cn         log_L50prior
  log_sigma1n       log_s1prior
  log_sigma2n       log_s2prior
  log_sigma1cn      log_s1prior
  log_sigma2cn      log_s2prior
```

```
  log_L50s          log_L50prior
  log_L50cs         log_L50prior
  log_sigma1s       log_s1prior
  log_sigma2s       log_s2prior
  log_sigma1cs      log_s1prior
  log_sigma2cs      log_s2prior

  log_b            log_b_prior
  log_prec         log_p_prior


PARAMETER_SECTION


// selectividad paramétrica FLOTA

 init_vector log_L50n(1,nbloques1n,opt1_fase)
 init_vector log_sigma1n(1,nbloques1n,opt1_fase)
 init_vector log_sigma2n(1,nbloques1n,opt_sel2)

 init_vector log_L50s(1,nbloques1s,opt1_fase)
 init_vector log_sigma1s(1,nbloques1s,opt1_fase)
 init_vector log_sigma2s(1,nbloques1s,opt_sel2)

// selectividad paramétrica CRUCERO
 init_vector log_L50cn(1,nbloques2n,opt2_fase)
 init_vector log_sigma1cn(1,nbloques2n,opt2_fase)
 init_vector log_sigma2cn(1,nbloques2n,opt_sel3)

 init_vector log_L50cs(1,nbloques2s,opt2_fase)
 init_vector log_sigma1cs(1,nbloques2s,opt2_fase)
 init_vector log_sigma2cs(1,nbloques2s,opt_sel3)

// parametros reclutamientos y mortalidades)
 init_number log_Rmedn(opt_R0n)
 init_number log_Rmeds(opt_R0s)

 init_bounded_number log_prec(-20,0,fase_propR) //// prop de reclutas de sur a norte

 init_bounded_dev_vector log_desv_Rn(1,ntime,-10,10,opt_devRn)
 init_bounded_dev_vector log_desv_Rs(1,ntime,-10,10,opt_devRs)

 init_bounded_matrix log_F(1,nzonas,1,ntime,-20,0.7,opt_F) // log  mortalidad por pesca por
flota

// capturabilidades
 init_vector log_qflon(1,nqbloquesn,opt_qf)
 init_vector log_qflos(1,nqbloquess,opt_qf)

 init_vector log_qcrun(1,nqbloquescn,opt_qc)
 init_vector log_qcrus(1,nqbloquescs,opt_qc)


 init_number log_b(opt_bpow)

// Crecimiento
 init_vector log_Lr(1,nzonas,opt_Lr)
 init_vector log_sr(1,nzonas,opt_sr)
 init_vector log_beta(1,nzonas,opt_beta)


//--------------------------------------------------------------------------------
//Defino las variables de estado
 matrix BD(1,nzonas,1,ntime)
 matrix BMflo(1,nzonas,1,ntime)
 matrix BMcru(1,nzonas,1,ntime)
 matrix BT(1,nzonas,1,ntime)
 matrix RPRlp(1,nzonas,1,ntime)
 matrix Reclutas(1,nzonas,1,ntime)
 matrix Rpred(1,nzonas,1,ntime)
 matrix S1(1,nbloques1n,1,ntallas)
 matrix S2(1,nbloques2n,1,ntallas)
 matrix S3(1,nbloques1s,1,ntallas)
 matrix S4(1,nbloques2s,1,ntallas)
 matrix T(1,ntallas,1,ntallas)
 matrix pred_CPUE(1,nzonas,1,ntime)
```

```
 matrix pred_Bcru(1,nzonas,1,ntime)
 matrix pred_Desemb(1,nzonas,1,ntime)
 matrix CPUE(1,nzonas,1,ntime)
 matrix Bcru(1,nzonas,1,ntime)
 matrix Desemb(1,nzonas,1,ntime)
 matrix nm(1,nzonas,1,ntime)
 matrix nmc(1,nzonas,1,ntime)
 matrix pre(1,nzonas,1,ntallas);
 matrix likeval(1,nzonas,1,10);
 matrix Lmed_pred(1,nzonas,1,ntime)
 matrix Lmed_obs(1,nzonas,1,ntime)
 matrix Lmed_predc(1,nzonas,1,ntime)
 matrix Lmed_obsc(1,nzonas,1,ntime)


 vector No(1,ntallas);
 vector Neq(1,ntallas);
 vector SSBo(1,nzonas);
 vector alfa_sr(1,nzonas);
 vector beta_sr(1,nzonas);
 vector delta(1,ntallas);
 vector Lesp(1,ntallas);
 vector sigmaL(1,ntallas);
 vector Lr(1,nzonas);
 vector sr(1,nzonas);
 vector Linf(1,nzonas);
 vector k(1,nzonas);
 vector M(1,nzonas);
 vector h(1,nzonas);
 vector beta(1,nzonas);
 vector Unos_tallas(1,ntallas);
 vector Unos_year(1,ntime);
 vector yrs(1,ntime);
 vector suma1(1,nzonas);
 vector suma2(1,nzonas);
 vector Migra(1,ntime)
 //vector suma3(1,nzonas);
 //vector suma4(1,nzonas);
 matrix suma3(1,nzonas,1,ntime);
 matrix suma4(1,nzonas,1,ntime);
 number penalty
 number propR;
 number Reqs
 number Reqn
 number penq

 3darray Sel(1,nzonas,1,ntime,1,ntallas)
 3darray Selc(1,nzonas,1,ntime,1,ntallas)

 3darray F(1,nzonas,1,ntime,1,ntallas)
 3darray Z(1,nzonas,1,ntime,1,ntallas)
 3darray S(1,nzonas,1,ntime,1,ntallas)

 3darray N(1,nzonas,1,ntime,1,ntallas)

 3darray NM(1,nzonas,1,ntime,1,ntallas)
 3darray NMD(1,nzonas,1,ntime,1,ntallas)
 3darray NVflo(1,nzonas,1,ntime,1,ntallas)
 3darray NVcru(1,nzonas,1,ntime,1,ntallas)

 3darray pred_Ctot(1,nzonas,1,ntime,1,ntallas)
 3darray pobs(1,nzonas,1,ntime,1,ntallas)
 3darray ppred(1,nzonas,1,ntime,1,ntallas)
 3darray pobsc(1,nzonas,1,ntime,1,ntallas)
 3darray ppredc(1,nzonas,1,ntime,1,ntallas)

 3darray Trans(1,nzonas,1,ntallas,1,ntallas)
 3darray cv_index(1,nzonas,1,3,1,ntime)


 objective_function_value f


PRELIMINARY_CALCS_SECTION

 yrs=column(mdatos,1);
 Desemb(1)=column(mdatos,2); // definir como matriz (zona, año)
```

```
 CPUE(1)=column(mdatos,4);
 Bcru(1)=column(mdatos,6);
 nm(1)=column(mdatos,8);
 nmc(1)=column(mdatos,9);

 Desemb(2)=column(mdatos,10);
 CPUE(2)=column(mdatos,12);
 Bcru(2)=column(mdatos,14);
 nm(2)=column(mdatos,16);
 nmc(2)=column(mdatos,17);

 cv_index(1,1)=column(mdatos,3); // definir como 3-array (zona, año, indice)
 cv_index(1,2)=column(mdatos,5);
 cv_index(1,3)=column(mdatos,7);

 cv_index(2,1)=column(mdatos,11);
 cv_index(2,2)=column(mdatos,13);
 cv_index(2,3)=column(mdatos,15);

 Linf=column(Par_bio,1); // definir estos como vectores
 k=column(Par_bio,2);
 M=column(Par_bio,6);
 h=column(Par_bio,7);

 Unos_tallas=1;// lo uso en operaciones matriciales con tallas
 Unos_year=1;// lo uso en operaciones matriciales con el año


RUNTIME_SECTION
  convergence_criteria 1.e-1,1.e-01,1.e-03,1e-3,1e-5
  maximum_function_evaluations 100,100,200,3000,3500

PROCEDURE_SECTION
// se listan las funciones que contienen los calculos
 Eval_Trans_talla_talla();
 Eval_selectividad();
 Eval_mortalidades();
 Eval_abundancia();
 Eval_biomasas();
 Eval_capturas_predichas();
 Eval_indices();
 Eval_logverosim();
 Eval_funcion_objetivo();

//-----------------------------------------------------------------------
FUNCTION Eval_Trans_talla_talla


 beta=mfexp(log_beta);

 int i, j, z;

 for (z=1;z<=nzonas;z++){

// matriz de transicion modelo normal

  delta=(Linf(z)-Tallas)*(1-mfexp(-k(z)));// incremento en tallas
  Lesp=Tallas+delta; // talla esperada luego del crecimiento
  sigmaL=delta(z)*beta(z);

  for (i=1;i<=ntallas;i++){
    for (j=1;j<=ntallas;j++){
      if(i==j){
         T(i,j)=1.0;}}
   }


  for (i=1;i<=ntallas;i++){

    for (j=1;j<=ntallas;j++){
     if(sigmaL(i)>0){
     T(i,j)=mfexp(-0.5*square((Lesp(i)-Tallas(j))/sigmaL(i)));}}
   }


  for (j=1;j<=ntallas;j++){
  T(j)/=sum(T(j));
```

```
  }

  Trans(z)=T;

 }


//-------------------------------------------------------------------------

FUNCTION Eval_selectividad
 int i,j,z;


//.................ZONA NORTE.....................................
// FLOTA...................

 for (j=1;j<=nbloques1n;j++){

 S1(j)=exp(-0.5*square(Tallas-exp(log_L50n(j)))/square(exp(log_sigma1n(j))));


    for (i=1;i<=ntallas;i++){

      if(Tallas(i)>=exp(log_L50n(j))){
      S1(j,i)= exp(-0.5*square(Tallas(i)-exp(log_L50n(j)))/square(exp(log_sigma2n(j))));
      }

 }}

   for (i=1;i<=ntime;i++){
      for (j=1;j<=nbloques1n;j++){
              if (yrs(i)>=ybloques1n(j)){
                Sel(1,i)=S1(j);}
       }
   }

 // CRUCERO...................

 for (j=1;j<=nbloques2n;j++){

 S2(j)=exp(-0.5*square(Tallas-exp(log_L50cn(j)))/square(exp(log_sigma1cn(j))));

    for (i=1;i<=ntallas;i++){

      if(Tallas(i)>=exp(log_L50cn(j))){
      S2(j,i)= exp(-0.5*square(Tallas(i)-exp(log_L50cn(j)))/square(exp(log_sigma2cn(j))));
      }

 }}

   for (i=1;i<=ntime;i++){
      for (j=1;j<=nbloques2n;j++){
              if (yrs(i)>=ybloques2n(j)){
                Selc(1,i)=S2(j);}
       }
   }


//.................ZONA SUR.....................................
// FLOTA...................

 for (j=1;j<=nbloques1s;j++){

 S3(j)=exp(-0.5*square(Tallas-exp(log_L50s(j)))/square(exp(log_sigma1s(j))));


    for (i=1;i<=ntallas;i++){

      if(Tallas(i)>=exp(log_L50s(j))){
      S3(j,i)= exp(-0.5*square(Tallas(i)-exp(log_L50s(j)))/square(exp(log_sigma2s(j))));
      }

 }}

   for (i=1;i<=ntime;i++){
      for (j=1;j<=nbloques1s;j++){
              if (yrs(i)>=ybloques1s(j)){
```

```
                Sel(2,i)=S3(j);}
        }
    }

 // CRUCERO...................

 for (j=1;j<=nbloques2s;j++){

 S4(j)=exp(-0.5*square(Tallas-exp(log_L50cs(j)))/square(exp(log_sigma1cs(j))));

    for (i=1;i<=ntallas;i++){

      if(Tallas(i)>=exp(log_L50cs(j))){
      S4(j,i)= exp(-0.5*square(Tallas(i)-exp(log_L50cs(j)))/square(exp(log_sigma2cs(j))));
      }

 }}



   for (i=1;i<=ntime;i++){
      for (j=1;j<=nbloques2s;j++){
              if (yrs(i)>=ybloques2s(j)){
                Selc(2,i)=S4(j);}
       }
   }


FUNCTION Eval_mortalidades

 for (int z=1;z<=nzonas;z++){

 F(z)=elem_prod(Sel(z),outer_prod(mfexp(log_F(z)),Unos_tallas));
 Z(z)=F(z)+M(z);

 S(z)=mfexp(-1.0*Z(z));

 }


FUNCTION Eval_abundancia
 int i, j, z;

 propR=exp(log_prec);// prop de reclutas que migran desde el sur

 //-----------------------------------------------------

 for (z=1;z<=nzonas;z++){

  Lr(z)=mfexp(log_Lr(z));
  sr(z)=mfexp(log_sr(z));

// genero la composicion de tallas del reclutamiento
  pre(z)=exp(-0.5*square((Tallas-Lr(z))/sr(z)));
  pre(z)/=sum(pre(z));
  }
 //-----------------------------------------------------


// Estimación de Bo y parámetros S/R
  z=2;
  Reqs=exp(log_Rmeds);//log_Rmed(z));
  No=pre(z)*Reqs*(1-propR);
  for (j=1;j<=5*nedades;j++){
  No=No*exp(-1.*M(z))*Trans(z)+pre(z)*((1-propR)*Reqs);
  SSBo(z)=sum(elem_prod(No*mfexp(-dt(z,1)*M(z)),elem_prod(Wmed(z),msex(z))));
  }

  z=1;
  Reqn=exp(log_Rmedn);//log_Rmed(z));
  No=pre(z)*(Reqn+propR*Reqs);
  for (j=1;j<=5*nedades;j++){
  No=No*exp(-1.*M(z))*Trans(z)+pre(z)*(Reqn+propR*Reqs);
  SSBo(z)=sum(elem_prod(No*mfexp(-dt(z,1)*M(z)),elem_prod(Wmed(z),msex(z))));
  }
```

```
 /*
 for (z=1;z<=nzonas;z++){
  alfa_sr(z)=4*h(z)*exp(log_Rmed(z))/(5*h(z)-1);//
  beta_sr(z)=(1-h(z))*SSBo(z)/(5*h(z)-1);// Reclutamiento
  }
 */
  z=1;
  alfa_sr(z)=4*h(z)*exp(log_Rmedn)/(5*h(z)-1);//
  beta_sr(z)=(1-h(z))*SSBo(z)/(5*h(z)-1);// Reclutamiento

  z=2;
  alfa_sr(z)=4*h(z)*exp(log_Rmeds)/(5*h(z)-1);//
  beta_sr(z)=(1-h(z))*SSBo(z)/(5*h(z)-1);// Reclutamiento



// -----------------primer año-----------------------------------------------

 /*
 Reclutas(2)=mfexp(log_Rmed(2)+log_desv_Rs)*(1-propR); //
 Reclutas(1)=mfexp(log_Rmed(1)+log_desv_Rn)+propR*mfexp(log_Rmed(2)+log_desv_Rs); //
 */

 Reclutas(2)=mfexp(log_Rmeds+log_desv_Rs)*(1-propR); //SUR

 Reclutas(1)=mfexp(log_Rmedn+log_desv_Rn)+propR*mfexp(log_Rmeds+log_desv_Rs); //NORTE




// genero una estructura de equilibrio inicial en torno a Z del primer año;

  z=2;// sur
  Neq=pre(z)*Reclutas(z,1);
  Migra=propR*Reclutas(z,1);

  for (j=1;j<=nedades;j++)
//  {Neq=(elem_prod(Neq,exp(-1.*Z(z,1))))*Trans(z)+pre(z)*(exp(log_Rmed(z)+log_desv_No(z,j))-
Migra(1));}
  {Neq=(elem_prod(Neq,exp(-1.*Z(z,1))))*Trans(z)+pre(z)*(exp(log_Rmeds)-Migra(1));}


  N(z,1)=Neq;
  NMD(z,1)=elem_prod(elem_prod(N(z,1),mfexp(-dt(z,1)*Z(z,1))),msex(z));
  BD(z,1)=sum(elem_prod(Wmed(z),NMD(z,1)));

  z=1;// norte
  Neq=pre(z)*Reclutas(z,1);
  for (j=1;j<=nedades;j++)
//  {Neq=(elem_prod(Neq,exp(-
1.*Z(z,1))))*Trans(z)+pre(z)*(exp(log_Rmed(z)+log_desv_No(z,j))+Migra(1));}
  {Neq=(elem_prod(Neq,exp(-1.*Z(z,1))))*Trans(z)+pre(z)*(exp(log_Rmedn)+Migra(1));}

  N(z,1)=Neq;
  NMD(z,1)=elem_prod(elem_prod(N(z,1),mfexp(-dt(z,1)*Z(z,1))),msex(z));
  BD(z,1)=sum(elem_prod(Wmed(z),NMD(z,1)));


// --------------------dinamica anual por zonas

  Rpred=Reclutas;
  Migra=propR*Rpred(2);

  for (i=2;i<=ntime;i++){

// ZONA SUR ---------------------------------------
  z=2;


  if(i>minedad){
  Rpred(z,i)=(alfa_sr(z)*BD(z,i-minedad)/(beta_sr(z)+BD(z,i-minedad)));
  Migra(i)=propR*Rpred(z,i)*mfexp(log_desv_Rs(i));}// lo que migra al norte

  Reclutas(z,i)=(Rpred(z,i))*mfexp(log_desv_Rs(i))- Migra(i);


  N(z,i)=(elem_prod(N(z,i-1),S(z,i-1)))*Trans(z)+pre(z)*Reclutas(z,i);
```

```
  NMD(z,i)=elem_prod(elem_prod(N(z,i),mfexp(-dt(z,1)*Z(z,i))),msex(z));
  BD(z,i)=sum(elem_prod(Wmed(z),NMD(z,i)));


// ZONA NORTE ---------------------------------------

  z=1;

  if(i>minedad){
  Rpred(z,i)=(alfa_sr(z)*BD(z,i-minedad)/(beta_sr(z)+BD(z,i-minedad)));}

//  Reclutas(z,i)=(Rpred(z,i)+ Migra(i))*mfexp(log_desv_Rn(i)) ;
  Reclutas(z,i)=Rpred(z,i)*mfexp(log_desv_Rn(i))+ Migra(i);
  // la migración viene con la fuerza de la zona sur y es independiente de la anomalía local

  N(z,i)=(elem_prod(N(z,i-1),S(z,i-1)))*Trans(z)+pre(z)*Reclutas(z,i);
  NMD(z,i)=elem_prod(elem_prod(N(z,i),mfexp(-dt(z,1)*Z(z,i))),msex(z));
  BD(z,i)=sum(elem_prod(Wmed(z),NMD(z,i)));

  } //

FUNCTION Eval_biomasas

 for (int z=1;z<=nzonas;z++){

 //--------------NORTE-------------------------------
 NMD(z)=elem_prod(N(z),mfexp(-dt(z,1)*Z(z)));
 NMD(z)=elem_prod(NMD(z),outer_prod(Unos_year,msex(z)));
 NVflo(z)=elem_prod(elem_prod(N(z),mfexp(-dt(z,2)*(Z(z)))),Sel(z));
 NVcru(z)=elem_prod(elem_prod(N(z),mfexp(-dt(z,3)*(Z(z)))),Selc(z));


// vectores de biomasas derivadas
 BMflo(z)=Wmed(z)*trans(NVflo(z));
 BMcru(z)=Wmed(z)*trans(NVcru(z));
 BT(z)=Wmed(z)*trans(N(z));

 RPRlp(z)=BD(z)/SSBo(z);

 }


FUNCTION Eval_capturas_predichas

 for (int z=1;z<=nzonas;z++){

// matrices de capturas predichas por edad y año
 pred_Ctot(z)=elem_prod(elem_div(F(z),Z(z)),elem_prod(1.-S(z),N(z)));

// vectores de desembarques predichos por año
 pred_Desemb(z)=Wmed(z)*trans(pred_Ctot(z));

// matrices de proporcion de capturas por talla y año
 pobs(z)=elem_div(Ctot(z),outer_prod(rowsum(Ctot(z)+1e-10),Unos_tallas));
 ppred(z)=elem_div(pred_Ctot(z),outer_prod(rowsum(pred_Ctot(z)+1e-10),Unos_tallas));

 pobsc(z)=elem_div(Ncru(z),outer_prod(rowsum(Ncru(z)+1e-10),Unos_tallas));
 ppredc(z)=elem_div(NVcru(z),outer_prod(rowsum(NVcru(z)+1e-10),Unos_tallas));

 Lmed_pred(z)=Tallas*trans(ppred(z));
 Lmed_obs(z)=Tallas*trans(pobs(z));

 Lmed_predc(z)=Tallas*trans(ppredc(z));
 Lmed_obsc(z)=Tallas*trans(pobsc(z));

 }


FUNCTION Eval_indices


 //------------------ NORTE-----------------------------

   for (int i=1;i<=ntime;i++){
      for (int j=1;j<=nqbloquesn;j++){
              if (yrs(i)>=yqbloquesn(j)){
                 pred_CPUE(1,i)=exp(log_qflon(j))*pow(BMflo(1,i),exp(log_b));}
```

```
        }
    }


    for (int i=1;i<=ntime;i++){
       for (int j=1;j<=nqbloquescn;j++){
              if (yrs(i)>=yqbloquescn(j)){
                 pred_Bcru(1,i)=exp(log_qcrun(j))*BMcru(1,i);}
        }
    }


 // ------------------SUR-----------------------

    for (int i=1;i<=ntime;i++){
       for (int j=1;j<=nqbloquess;j++){
              if (yrs(i)>=yqbloquess(j)){
                 pred_CPUE(2,i)=exp(log_qflos(j))*pow(BMflo(2,i),exp(log_b));}
        }
    }


    for (int i=1;i<=ntime;i++){
       for (int j=1;j<=nqbloquescs;j++){
              if (yrs(i)>=yqbloquescs(j)){
                 pred_Bcru(2,i)=exp(log_qcrus(j))*BMcru(2,i);}
        }
    }


FUNCTION Eval_logverosim
// esta funcion evalua el nucleo de las -log-verosimilitudes marginales para
// series con datos 0.
 int i;

 suma1=0; suma2=0; // suma 1 y suma 2 son vectores (1,nzonas)

 for (int z=1;z<=nzonas;z++){


 for (i=1;i<=ntime;i++)
 {
  if (CPUE(z,i)>0){
    suma1(z)+=square(log(CPUE(z,i)/pred_CPUE(z,i))*1/(cv_index(z,2,i)));}

  if (Bcru(z,i)>0){
    suma2(z)+=square(log(Bcru(z,i)/pred_Bcru(z,i))*1/(cv_index(z,3,i)));}
 }

 }

FUNCTION Eval_funcion_objetivo


 for (int z=1;z<=nzonas;z++){

 suma3=0; suma4=0; penalty=0;
 // likeval es ahora una matriz

 likeval(z,1)=0.5*suma1(z);//CPUE
 likeval(z,2)=0.5*suma2(z);//Bcru
 likeval(z,3)=0.5*norm2(elem_div(log(elem_div(Desemb(z),pred_Desemb(z))),cv_index(z,1)));//
desemb

 for (int i=1;i<=ntime;i++){

 suma3(z,i)=-nm(z,i)*sum(elem_prod(pobs(z,i),log(ppred(z,i)+1e-10)));
 suma4(z,i)=-nmc(z,i)*sum(elem_prod(pobsc(z,i),log(ppredc(z,i)+1e-10)));

 }

 likeval(z,4)=sum(suma3(z));//
 likeval(z,5)=sum(suma4(z));//
 //likeval(z,4)=suma3(z);//
 //likeval(z,5)=suma4(z);//

// lognormal Ninicial y Reclutas
```

```
// if(active(log_desv_Rn)){
 likeval(z,6)=1./(2*square(sigmaR))*(norm2(log_desv_Rn)+norm2(log_desv_Rs)); //}

 if(active(log_Lr)){
 likeval(z,7)=1./(2*square(cv_Par_bio(z,3)))*square(log_Lr(z)-log_Lr_prior(z));}

 }

 // Correlaciones en los desvíos
 likeval(1,8)=1./(2*square(sigma2R))*norm2(log_desv_Rn -log_desv_Rs);// desvios entre zonas

 penq=1./(2*square(cvq))*norm2(log_qcrun-log_qcrus);

 f=festim*(sum(likeval)+penq);




// if(last_phase){
// f=festim*sum(likeval)+200*square(log_desv_Rt(1,ntime));}



REPORT_SECTION

 report << "Años" << endl;
 report << yrs << endl;
 report << "Bcrucero_obs & pred" << endl;
 report << Bcru << endl;
 report << pred_Bcru << endl;
 report << "CPUE_obs & pred" << endl;
 report << CPUE << endl;
 report << pred_CPUE << endl;
 report << "Desemb_obs & pred" << endl;
 report << Desemb << endl;
 report << pred_Desemb << endl;
 report << "Lmed_obs & pred FLOTA" << endl;
 report << Lmed_obs << endl;
 report << Lmed_pred << endl;
 report << "Lmed_obs & pred CRUCERO" << endl;
 report << Lmed_obsc << endl;
 report << Lmed_predc << endl;
 report << "Biomasa_desovante" << endl;
 report << BD << endl;
 report << "Biomasa_total" << endl;
 report << BT << endl;
 report << "Biomasa_explotable" << endl;
 report << BMflo << endl;
 report << "Reclutamiento" << endl;
 report << Reclutas<< endl;
 report << Rpred<< endl;
 report << "Migrantes" << endl;
 report << Migra<< endl;
 report << "desv_reclutamiento" << endl;
 report << log_desv_Rn<< endl;
 report << log_desv_Rs<< endl;
 report << "F " << endl;
 report << exp(log_F) << endl;


 report<<"Tallas"<<endl;
 report<<Tallas<<endl;

 report<<"Abundancia a la talla"<<endl;
 report<<N<<endl;

 report<<"Selectividad a la talla Flota"<<endl;
 report<<Sel<<endl;

 report<<"Selectividad a la talla Crucero"<<endl;
 report<<Selc<<endl;

 report << "Prop_obs FLOTA" << endl;
 report << pobs<< endl;
 report << "Prop_pred FLOTA" << endl;
```

```
 report << ppred<< endl;

 report << "Prop_obs CRUCERO" << endl;
 report << pobsc<< endl;
 report << "Prop_pred CRUCERO" << endl;
 report << ppredc<< endl;

 report << "BD virgen largo plazo" << endl;
 report << SSBo << endl;

 report << "Reducción del stock (BD/BDo) de LP " << endl;
 report << RPRlp << endl;
 report << " " << endl;

 report << "Tallas medias por grupo y desviación" << endl;
 report << Lesp << endl;
 report << sigmaL << endl;


 report << "-----------------------------------------------" << endl;
 report << "Tallas y función de reclutamiento a la talla" << endl;
 report << Tallas<< endl;
 report << pre<< endl;

 report << "-----------------------------------------------" << endl;

 report << "P(talla-talla)" << endl;
 report << Trans(1) << endl;
 report << "-----------------------------------------------" << endl;
 report << "alfa  beta   propR  " << endl;
 report << alfa_sr<<" "<<beta_sr<<" "<<propR<< endl;
 report << "-----------------------------------------------" << endl;

 report << "-----------------------------------------------" << endl;
 report << "bCPUE  Lr  Sr  beta  " << endl;
 report << exp(log_b)<<" "<<exp(log_Lr)<<" "<<exp(log_sr)<<" "<<exp(log_beta)<< endl;
 report << "-----------------------------------------------" << endl;
 report << "Componentes de verosimilitud" << endl;
 report << likeval << endl;
 report << "sigmacorr  propR  h" << endl;
 report << sigma2R <<" "<<exp(log_prec)<<" "<<h<< endl;




FINAL_SECTION

 time(&finish);
 elapsed_time=difftime(finish,start);
 hour=long(elapsed_time)/3600;
 minute=long(elapsed_time)%3600/60;
 second=(long(elapsed_time)%3600)%60;
 cout<<endl<<endl<<"*****************************************"<<endl;
 cout<<"--Start time:  "<<ctime(&start)<<endl;
 cout<<"--Finish time: "<<ctime(&finish)<<endl;
 cout<<"--Runtime: ";
 cout<<hour<<" hours, "<<minute<<" minutes, "<<second<<" seconds"<<endl;
 cout<<"*****************************************"<<endl;
```

Appendix V (Publication of Chapter II.1)

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Research Article

Population structure of nylon shrimp *Heterocarpus reedi* (Crustacea: Caridea) and its relationship with environmental variables off Chile

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ABSTRACT. The population structure of fishery resources and the impact of environmental factors over its productivity are important processes to be considered in fisheries management. Environmental factors could determine both, the success of larval drift as the population spatial structure and its changes of biomass. In this paper we show the environmental effect over distribution, abundance and spatial structure of nylon shrimp population (*Heterocarpus reedi*) off central Chile (25°-37°S) from trawling surveys carried out between 1996 and 2011. Environmental variables considered where sea surface concentration of chlorophyll-*a* and dissolved organic matter. Results show a geographical separation in population around 32°S. Shrimp density is higher in the southern zone, where concentration of chlorophyll-*a* and dissolved organic matter are high due to presence of river tributaries and coastal upwelling zones. In this area, the bulk of the adult population is concentrated, which could act as "source" population and thereby its influence on larval drift could explain both, the preponderance of juveniles in the northern area as the smallest size of its population ("pseudo-sink" population). In the southern area, a process of spatial and bathymetric expansion had driven the increase in population size over time, where the colonization and individual somatic growth had been the main mechanisms. We found that periods of good environmental conditions explain high densities of shrimp with a delay of two years, which might be related mainly with larval survival and enhanced recruitment and somatic growth. The aim of this study was to understand the spatial-temporal variability of the nylon shrimp density in the study area.

Keywords: *Heterocarpus reedi*, nylon shrimp, abundance, distribution, environment, metapopulation, river tributaries.

Estructura poblacional del camarón nailon *Heterocarpus reedi* (Crustacea: Caridea) y su relación con variables ambientales frente a Chile

RESUMEN. La estructura poblacional de recursos de interés pesquero y el impacto de los factores ambientales sobre su productividad son procesos claves a considerar en la gestión pesquera. Los factores ambientales pueden determinar tanto el éxito de la deriva larval como la estructura espacial de la población y sus cambios de biomasa. Se muestra el efecto del medio ambiente sobre la distribución, abundancia y estructura espacial de la población de camarón nailon (*Heterocarpus reedi*) en Chile central (25°-37°S), considerando como variables la concentración de clorofila-*a* y la materia orgánica disuelta, respecto a los cruceros de arrastre realizados entre 1996 y 2011. Los resultados muestran una separación geográfica de la población alrededor de 32°S. En la zona sur, la densidad del camarón es mayor, donde los altos niveles de concentración de clorofila-*a* y de materia orgánica disuelta se deben, entre otros, a la presencia de afluentes de ríos y a surgencia costera. En esta área, se concentra la mayor parte de la población adulta, que podría actuar como población "fuente" y por lo tanto, su influencia en la deriva larval podría explicar tanto la preponderancia de juveniles en la zona norte, como el tamaño más pequeño de su población (población "pseudo-sumidero"). En la zona sur, un proceso de expansión espacial y batimétrica habría impulsado el aumento de tamaño de la población a través del tiempo, donde los principales mecanismos habrían sido la colonización y crecimiento somático individual. Se determinó que los períodos de buenas condiciones ambientales explican las altas densidades de camarones con un retraso de dos años, aspecto que estaría relacionado principalmente con la supervivencia larval, reclutamiento y crecimiento

somático. El objetivo de este estudio es comprender la variabilidad espacio-temporal de la densidad de camarón nailon en el área de estudio.

Palabras clave: *Heterocarpus reedi*, camarón nailon, abundancia, distribución, medio ambiente, metapoblación, aporte fluvial.

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INTRODUCTION

Nylon shrimp (*Heterocarpus reedi*) is a decapod crustacean Caridea, distributed off the coasts of Chile, between 25° and 38°S, on clay, sedimentary rock, sandy and muddy bottoms. This species inhabit mainly the external border of the continental shelf and the upper slope, at a depth range that varies between 100 and 500 m. It can be found in the intersection area of Equatorial Subsurface Water (ESSW) and Antarctic Intermediate Water (AAIW), which are cold (10-12°C) and saline (34.5-34.9) (Bahamonde & Henríquez, 1970; Arana, 2012; Silva, 2012). This species is described as a predatory detritivore with an omnivore diet (Andrade & Báez, 1980), while in its larval stage; the diet is mainly based on phyto and zooplankton. As described by authors such as Bahamonde & Henríquez (1970), Arana *et al*. (1975), and Roa & Ernst (1996), the carapace length (CL) of *H. reedi* varies in the range 15-40 mm, being the females larger than males and slightly predominant in the catches. Mature females carry eggs in the pleopods by a couple of month, within a reproductive season that takes place between May and December and whose peak is registered between June and September (Arana *et al*., 1975, 1976; Acuña *et al*., 1997). Mean size at maturity is reported between 24.3-25.1 mm CL (Arana & Tiffou, 1970; Arana *et al*., 1976; Canales *et al*., 1999). The presence of Caridea larvae in the plankton -with *H. reedi* being the most abundant species of the group-, has been reported in different areas (*e.g.,* Palma, 1980; Mujica *et al*., 2011), particularly in the middle of the southern spring, with the highest percentages on October.

The fishery of *H. reedi* is one of the oldest and most important among the group of demersal crustaceans in Chile, along with the red squat lobster (*Pleuroncodes monodon*) and the yellow squat lobster (*Cervimunida johni*). This resource started to be exploited in the 1950's, with catches showing important fluctuations: the highest values around 10,000 annual tonnes in the middle of the 1990's, while the lowest has been recorded over the last decade around 4,000 ton yr^{-1}, due to regulations on fishing quotas caused by the reduction in the population of *H. reedi* (Wehrtmann *et al*., 2012).

One of the most important sources of scientific information is the trawling survey programme carried out since the mid-1990s. The data derived from these surveys allow to study changes in magnitude and spatial-temporal distribution of the population across years. Estimates of biomass of these surveys show important variations, whose highest increase is registered southward of 32°S since 2006 (Acuña *et al*., 2012). This increase could have been facilitated, among others, by the reduction in exploitation levels, the closure of some fishing areas since 2000, and depletion of the common hake (*Merluccius gayi*), species that has been noted as an important predator of *H. reedi* (Arana & Williams, 1970; Bahamonde & Henríquez, 1970; Arancibia & Neira, 2008). In the same time period, northward of this parallel, estimates show a smaller population about half the biomass estimates in the south zone (Table 1).

The relationship between environmental variables and abundance have been reported in some crustaceans (*e.g.,* Loneragan & Bunn, 1999; Mujica, 2008; De Juan & Cartes, 2011; Encarnacão *et al*., 2013), but the relationship between spatial and temporal distribution in *H. reedi*, as well as the environmental aspects and those related to its population structure, are still under incipient research; particularly, and as an example, those related to the impact that environmental effects of river discharges and coastal upwelling could have on early life stages, given the evidence found on the studies of fisheries of penaeid crustaceans in waters of the Indian-Pacific (Grimes & Kingsford, 1996; Evans *et al*., 1997; Myers, 1998; Loneragan & Bunn, 1999) and in the Eastern Pacific (Mora-Lara *et al*., 1984; Gracia, 1989; Mendo & Tam, 1993). In this context, this paper summarizes the information collected by scientific surveys during thirteen years and surface environmental data coming from dissolved organic matter, detritus and chlorophyll-*a* obtained by satellite telemetry, aiming to study relationships between variations in distribution and abundance of *H. reedi*, regarding environmental conditions off Chile, and its connection with the population structure of this important crustacean.

MATERIALS AND METHODS

Survey information

The information used corresponds to records from trawling scientific surveys on the continental shelf off central Chile (25°30´, 37°30´S) between 1996 and 2011. The data were provided by the Fisheries Research

Table 1. Biomass of *Heterocarpus reedi* by zone and general details of assessment surveys carried out off Chilean coast between 1996 and 2011. In years, 1997, 2007 and 2010 surveys were not carried out. Zone 1: 24°00 -32°10'S, Zone 2: 32°10'-37°00'S, fp: female proportion.

Year	Biomass (ton)		Hauls	Effort	Biological samples		Depth (m)		Latitude (°S)		Period	
	Zone 1	Zone 2	(n)	(km)	(n)	(fp)	(min)	(max)	(min)	(max)	start	end
1996	24557	10873	297	400	74587	0.45	170	440	25.9	38.5	May	Aug
1998	2593	6809	274	456	36415	0.70	46	649	21.6	38.2	Aug	Dec
1999	876	20872	248	439	18449	0.67	122	505	21.7	38.5	Jul	Sept
2000	725	21086	780	1427	152816	0.65	74	604	23.0	37.0	Jun	Oct
2001	3224	19575	348	740	23989	0.58	84	617	21.7	38.3	Jun	Jul
2002	8348	18256	1156	2308	97860	0.66	51	584	23.0	37.0	Aug	Oct
2003	7465	18079	442	805	266416	0.63	148	497	23.0	36.7	Aug	Sept
2004	8281	21545	502	855	151041	0.60	120	562	23.0	36.9	Jul	Sept
2005	14382	27561	562	1235	208964	0.57	110	640	25.2	37.0	Jul	Aug
2006	19486	37111	407	376	19045	0.50	118	648	24.2	36.7	Oct	Dec
2008	15809	28772	515	531	54991	0.51	125	518	25.3	36.7	Jun	Dec
2009	27718	38058	490	513	49567	0.56	108	575	25.1	36.7	Aug	Nov
2011	23515	35048	379	538	39662	0.56	131	652	25.2	36.7	Oct	Dec

Fund (FIP, for Fondo de Investigación Pesquera), corresponding to 6.400 geo-referenced trawling hauls (Fig. 1, Table 1). As reported by Canales & Arana (2010), these surveys have been conducted to assess the exploitable biomass of the *H. reedi* using the swept area method, conducted by commercial vessels and following sampling designs, such as systematic sampling where the hauls follow a set of parallel transect (each 10° of latitude) and perpendiculars to the coast (Canales & Arana, 2009), complemented since 2006 by an adaptive sampling strategy, where the number of transects is increased in those areas where a predefined minimum capture is obtained (Acuña *et al*., 2012). Sampling method has been throughout the time, in which vessels have had few technological innovation (Quiroz *et al*., 2005), which suggests that the fishing efficiency have not had major variations in time and thus without major impact on catch rates as measures of relative abundance. For each trawling survey, hauls duration is standardized to 30 min and speed of 2.0-2.5 knots. The start and end position of each fishing haul were recorded, at the time of stop and turn on the cable winch of the fishing net.

These fishing surveys have been carried out during the second half of each year, and although one of the shortcomings in these have been the variations in the month of start and end of each survey (Table 1), the period -winter and spring at southern hemisphere- coincides with the season that intensifies the process of egg carrying by females of *H. reedi* (Arana *et al*., 1975; Acuña *et al*., 1997) and increases the flow of the main rivers that discharge in the area where this species inhabits. Given the above and that the reproductive period in this species is mainly extended in the second semester, for practical purposes, measurements of relative abundance and biological attributes of *H. reedi* derived from survey data assumed to be representative of reproductive activity peak.

Biological sampling recorded carapace length (CL), sex, and presence of eggs at pleopods of females and individuals weight. The information collected shows that, on the average, around 92,000 individuals have been analysed by survey, 60% of which were females (Table 1). It is important to highlight that the 2002 survey was particularly aimed at assessing three commercial decapod crustaceans at the same time (*Pleuroncodes monodon*, *Cervimunida johni* and *Heterocarpus reedi*), which required changes of the sampling design/strategy along with a significant increase in the number of fishing hauls, which could have explained some results shown later.

Environmental data

The geo-referenced environmental surface information was taken from free-access database, obtained from satellite telemetry available since 1997 in NASA-Giovanni Portals website, particularly the data referred to absorption coefficients of organic matter and dissolved detritus (OMD), as well as the concentration of chlorophyll-*a* (Chl-*a*) between 1997 and 2011, under the assumption they represent indirectly the food availability for larvae and adults of *H. reedi*. This information was selected for the geographic quadrant 26°-36°S, 70°-73°W and represents the accumulated value between September and December of each year after the surveys were carried out (Table 1), coinciding

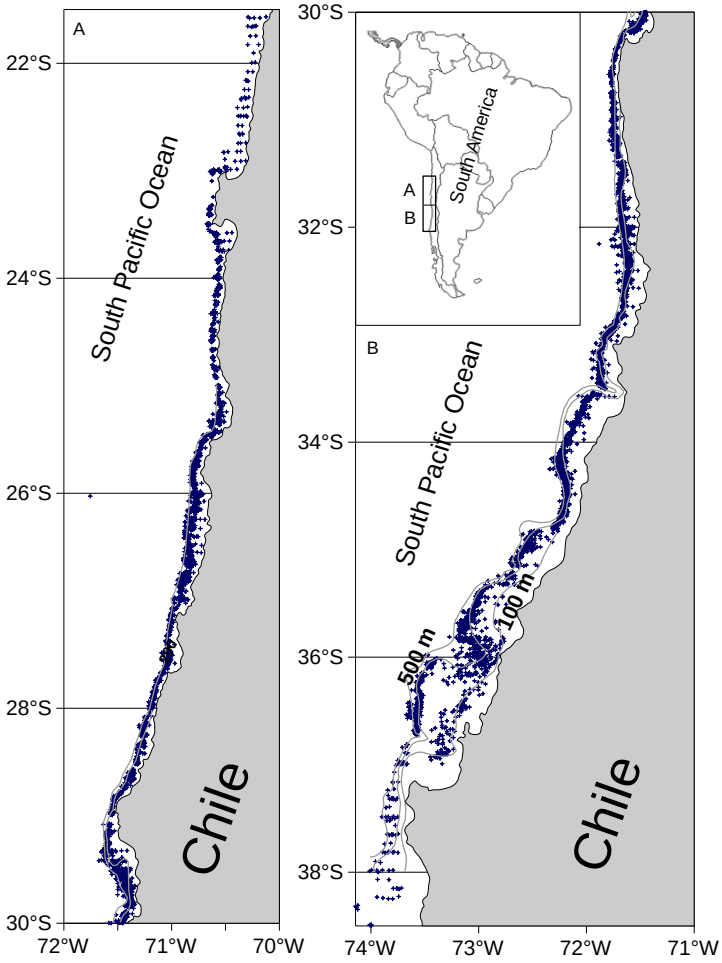

Figure 1. Study area and geographic location of fishing hauls (dots) of *Heterocarpus reedi* in trawl surveys carried out at the central southern zone of Chile between 1996 and 2011.

with the peak of the reproductive cycle of this species and where both coastal upwelling as the effluents of rivers increase, both variation sources of OMD and Chl-*a*.

Abundance index

As a measure of relative abundance, the ratio between the catch (kg) and the linear distance travelled on every fishing haul was considered. The advantages of this measure are: it is independent of net-opening performance, it is standardized to the distance travelled by the vessel, and it is not influenced by the criteria of time or effective hauling (Canales & Arana, 2010). The distance travelled in linear kilometres is measured once the geographic coordinates of start and end of the haul are known through the Haversine equation, $D = 2\,R\,asin\sqrt{a^2 + b^2\,cos(lat_1)cos(lat_2)}$, where $a = sin[0.5(lat_2\text{-}lat_1)]$ and $b = sin[0.5(long_2\text{-}long_1)]$, where lat and long represent latitude and longitude, respectively, both converted to radians; sub-indices 1 and 2 refer to the respective variable measure at the beginning and end of the fishing haul; while R = 6,371 corresponds to the radius of the Earth measured in km.

Exploratory analysis

In order to explore abundance patterns and link them with depth and environmental conditions, both the fishing hauls information (abundance and CL) as environmental data were stratified by year, geographic latitude (each 30 nautical miles) and depth range (each 100 m). For each of these nodes (year-latitude-depth), a simple average was computed with the purpose to represent in a discrete scale, changes in abundance, individual size (CL) and environmental variables (OMD and Chl-*a*). From this, a kriging representation was used to explore spatial-temporal patterns in the data and summarize the extensive information available. On the other hand, and in order to explore the relationship between environment and shrimp abun-

dance, a correlation analysis was conducted between anomalies of environmental variables and anomalies of relative abundance of *H. reedi*, with a temporal lag between 0 and 3 years.

The use of anomalies was preferred because more accurately describes climate variability over larger areas, and they give a frame of reference that allows more meaningful comparisons between locations and more accurate calculations of environmental trends. These anomalies for each year were calculated as A = (V-E(V)) / E(V) where V represents the average of the interest variable for each year while E(V) corresponds to the expected value represented here by a simple average. The Pearson correlation coefficient was used as statistic, while its significance level was verified with Pyper & Peterman (1998) methodology, who proposed a critical correlation (r*) based on an effective sample size (N*), used as hypothesis test considering the autocorrelation degree of the explanatory variables (OMD and Chl-*a*). The analysis was also complemented by *F*-Fisher and *P*-value tests.

RESULTS

Environmental conditions and *Heterocarpus reedi* distribution

The surface distribution of organic matter and dissolved detritus (OMD) and Chl-*a* between 1997-2011 showed concentration zones near the affluent of the main rivers and at coastal upwelling areas mentioned by Silva & Valdenegro (2003), and Moraga *et al*. (2001), and as a result of this, a higher number of OMD and Chl-*a* concentration areas were registered southward of 32°S (Fig. 2). The accumulated value of OMD and Chl-*a* per latitude and year (Sept-Dec) shows three foci near the coast and located around the 30°S (Elqui River), 33°30'S (Maipo and Rapel rivers) and 35°S (Mataquito and Maule rivers) respectively (Fig. 2). The spatial-temporal variability of these indices show that southward 32°S the highest concentrations of OMD and Chl-*a* were recorded in 2000 and 2004-2007, while north and off the Elqui River (30°S) high concentrations were recorded in 2002, 2006-2007 and 2010-2011 (Fig. 2).

In terms of *H. reedi* depth distribution, the bathymetric information shows that the highest nylon shrimp abundance (>50 kg km-linear^{-1}) is located in depths of 200-400 m and between the 25°30' and 37°00'S, showing a pattern in which, at a lower latitude, the foci of highest abundance are obtained at deeper depths (Fig. 3). The temporal variations in the bathymetric range indicate that since 2004, the abundance has gradually expanded towards higher depths, reaching a peak in 2008.

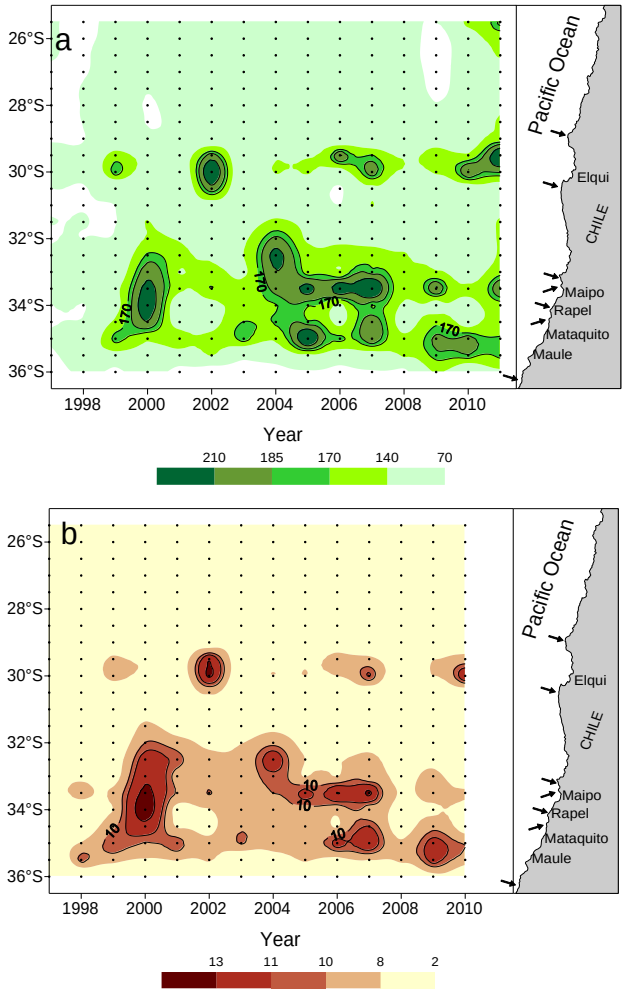

Figure 2. a) Isopleths of absorption coefficient of chlorophyll-*a* concentration (mg m^{-3}), and b) organic matter and dissolved detritus (m^{-1}). Dots represent the information nodes. Over the map the main river names are displayed. The small black arrows correspond to main upwelling zones.

In addition, across most of years analysed, an important discontinuity is observed in the abundance of *H. reedi*, whose reference points are around parallel 32°S. The increase in abundance reported since 2006, affected all the distribution area, but the increase southward 32°S was the most important reaching maximum values over 220 kg km-linear^{-1} in 2009 around the 33°S, and after in 2011 near the 35°30´S (Fig. 4a). In the southern zone, the displacement of the isopleth of 120 kg km-linear^{-1} registered a gradual northward movement according to the increase of abundance from 2006 around 35°S, to near 32°S in 2011 (Fig. 4a).

Spatial-temporal changes in size composition

In general, larger individuals have been found south 32°S reaching over 27 mm CL as average, while in the

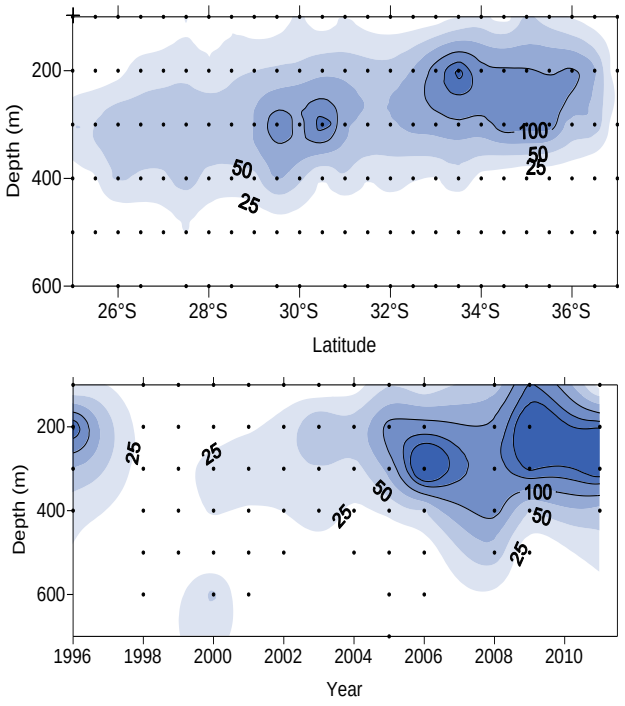

Figure 3. Isopleths of abundance (kg km-lineal^{-1}) of *Heterocarpus reedi* estimated in surveys using swept area method by depth, latitude, and year. Dots represent the information nodes.

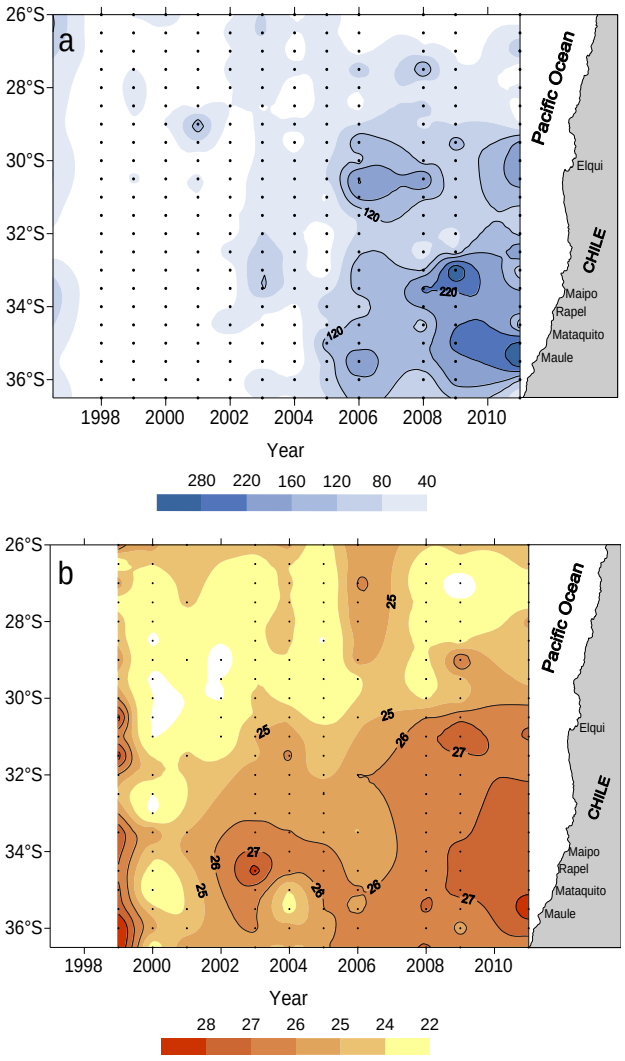

Figure 4. a) Isopleths of abundance (kg km-lineal^{-1}), and b) mean carapace length (mm) (both genders) of Heterocarpus reedi estimated in surveys using swept area method by latitude and year. Dots represent the information nodes.

north zone, size of *H. reedi* has varied almost always below the 25 mm CL (Fig. 4b). The information shows an important spatial-temporal dynamic in this variable southward 32°S, where isopleths of 25 and 26 mm CL show a displacement in the south-to-north axis since 2001, similar to the behaviour of the isopleth of relative abundance of 120 kg km-linear^{-1} mentioned above. This situation coincides with the increase of population abundance and is explained by the individual somatic growth alongside the contribution of juveniles located towards the borders of the population expansion. An example of this, is the gradual increase that shows the average CL through years at the 34°-36°S latitudinal range, which goes up from 24 mm in 2000 to 28 mm CL in 2011 (Fig. 4b). Is important to note that in this species the growth rate is moderate (Roa & Ernst, 1996), so that the mean CL by year is enough robust to minimize the impact of lack of temporal coincidence at the survey period, as was described earlier.

Relative abundance *vs* sea surface environmental variables

Since 2006 and particularly southward 32°S, both the relative abundance of *H. reedi* as the environmental variables (OMD and Chl-*a*) have registered positive anomalies, but with different inter annual variability and some temporal lag between them (Fig. 5). In spatial-temporal terms, the environmental and population abundance distribution suggest a spatial correlation, which not only means latitudinal coherence in the concentration nuclei of this species, but also episodes where favourable environmental conditions are followed by high abundances of *H. reedi*.

Different year-lags were analyzed (0-3 years). The partial correlation analysis shows that the highest level of linear relationship (0.43-0.67) between the environmental variables and the population abundance southward 32°S are obtained when a 2-year lag is considered (Table 2). This situation improves significantly when the survey of 2002 (year 2000 for environmental variable) is addressed as an out layer and excluded from the analysis, in which case the annual

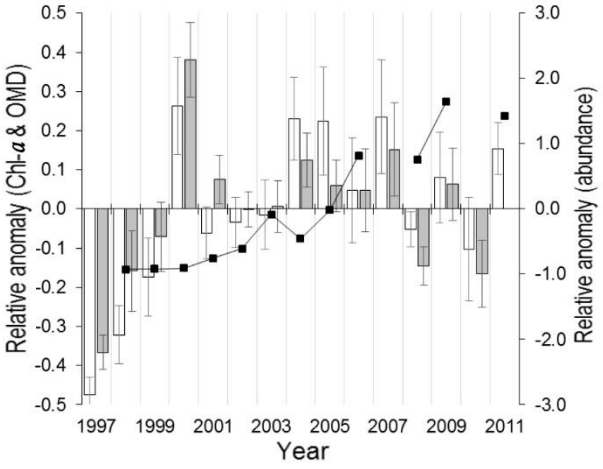

Figure 5. Anomalies of environmental variables and abundance of *Heterocarpus reedi* by year in zone 32°-36°S. The white and gray bars represent Chl-*a* and organic matter and dissolved detritus (OMD), respectively. The black line corresponds to shrimp abundance. Error bars represent two times the standard error.

variability of relative abundance of *H. reedi* presents a considerable and significant positive correlation with respect to the anomalies of OMD and Chl-*a*, reaching coefficients of r = 0.78 (*P*-value = 0.0086, *F* = 11.93) and r = 0.86 (*P*-value = 0.0012, *F* = 24.06) respectively (Fig. 6). The significance level is also confirmed because the correlation coefficients are larger than the critical correlation (r^*) of Pyper & Peterman (1998), estimated in 0.75 (N^* = 3.67, $t_{(0.975,11)}$ = 2.02) for OMD and 0.79 (N* = 2.90) for Chl-*a*. Here, two probable reasons could explain the lack of a relationship between the environmental conditions in 2000 and the abundance of *H. reedi* in 2002: modifications in the survey sampling design as mentioned earlier, or the population inelasticity to respond the large positive environmental anomaly recorded in 2000.

DISCUSSION

The highest increase of population biomass of *H. reedi* over the last years is registered since 2006, mainly southward 32°S (Table 1), increase that was joined by the south-to-north geographic expansion through a colonization of less dense areas and expanding the range of its bathymetric distribution (Figs. 3, 4). This agreed with report in Roa & Bahamonde (1993), who observed the same orientation in the population expansion of red squat lobster (*Pleuroncodes monodon*) at the central-southern zone of Chile. The colonisation of areas as expansion mechanism of populations has been extensively discussed on the scientific literature (*e.g.*, Rockwood, 2006), and particularly on crustaceans decapods by authors such as Fogarty & Botsford (2006), Fëlix-Hackradt *et al.* (2010) and Lavesque *et al.* (2010).

The main nuclei of aggregations of the *H. reedi* were located nearby the mouths of rivers and upwelling zones, which is a characteristics in other coastal decapods by Haas *et al.* (2001); Medina-Reyna (2001); Ramírez-Rodríguez *et al.* (2003) and Carvalho *et al.* (2011). In this context, at the southern area of the distribution of *H. reedi* where the main river effluents and upwelling zones are located (southward 32°S), a significant correlation between abundance and concentrations of OMD and surface Chl-*a* was found (Table 2, Fig. 6). This correlation was maximum (r = 0.78-0.86) when a two-year lag was considered among the variables, which coincides with the age at which the shrimp reach around 11.5 mm CL size (*e.g.*, Ziller, 1993; Roa & Ernst, 1996; Canales *et al.*, 1999) and starts to be available at recruitment zone and/or fishing gear. Similar findings have been reported by Company *et al.* (2008) and Díaz-Ochoa & Quiñones (2008), who found important correlations with temporal lags, between environmental variables and abundance of depth crustaceans.

The possible explanation to the relationship found is that, when there are good surface environmental conditions of OMD and Chl-*a*, derived probably from the discharge of rivers and the coastal upwelling mentioned above (Fig. 2), the conditions would be favourable for feeding and spawning of adults and for the survival of larvae and post-larvae. Later, these would settle following the course of the larval drift and would recruit to the fishing gear or zone as juveniles of two years old. As a consequence of the south-to-north direction of the Humboldt Current System (Glantz, 1998; Lorca *et al.*, 2004; Fuenzalida *et al.*, 2008; Silva, 2012), whose mean maximum surface speed can be higher than 15 cm s^{-1} (Fuenzalida *et al.*, 2008), larvae could be transported more than one thousand km in three months, which would explain the direction and orientation of the spatial expansion of the *H. reedi* population indicated above.

One of the most important differences in the population characteristics is the predominance of adults (>25 mm de CL) southwards 32°S (Fig. 4b), where most biomass increases are explained by somatic growth and a higher abundance, thus constituting the bulk of the parental population. Here, the absence of main predators as common hake (Arancibia & Neira, 2008) could have facilitated a faster growth in the shrimp population. Following the idea of Pulliam (1988), Hanski & Gilpin (1997), and Hanski (1998), this area could be compatible with the concept of "source habitat", while the zone northward 32°S could

Table 2. Autocorrelation's coefficients for explanatory variables and Pearson's correlation coefficients of environmental variables organic matter and dissolved detritus (OMD) and chlorophyll-*a* (Chl-*a*) *vs Heterocarpus reedi* abundance in zone 32°-36°S for two analysis cases. In bold the highest scores are indicated.

	Autocorrelation coefficients			Correlation coefficients			
lag (yr)	OMD	Chl-*a*	Abundance	All data		Excluding year 2000	
				OMD	Chl-*a*	OMD	Chl-*a*
0	1.00	1.00	1.00	-0.15	0.29	0.15	0.49
1	-0.05	0.18	0.89	-0.05	0.36	0.15	0.51
2	-0.58	-0.49	0.89	**0.43**	**0.67**	**0.78**	**0.86**
3	-0.29	0.00	0.93	0.24	0.57	0.43	0.70

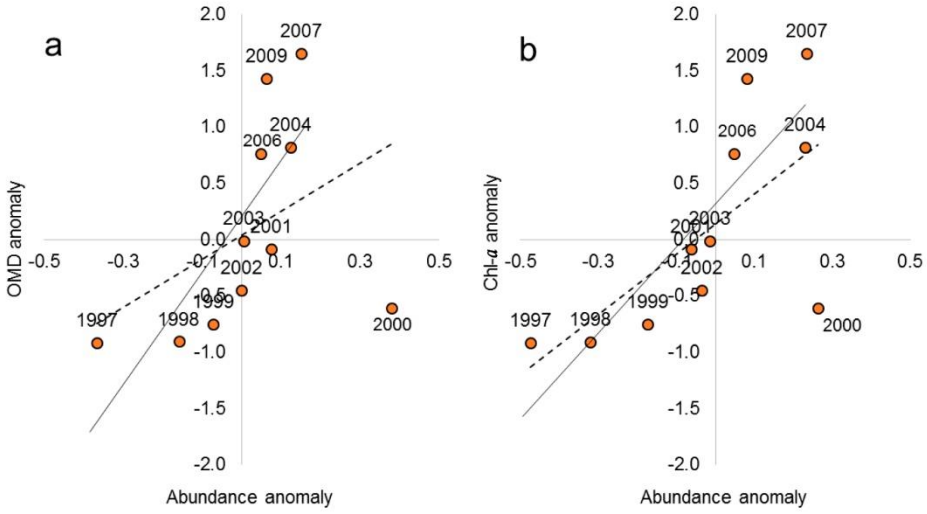

Figure 6. Linear relationship between anomalies of shrimp abundance *Heterocarpus reedi vs* a) organic matter and dissolved detritus (OMD), and b) chlorophyll-*a* (Chl-*a*). Environmental variables are delayed two years relative to the abundance anomalies. The year labels are related to environmental variables. Continuous line represents the situation when year 2000 is excluded from analysis.

receive part of the contribution of larval drift coming from the southern zone, conforming a "pseudo-draining habitat", which may explain the lower population size and the higher presence of juveniles in that area. In this context, Rockwood (2006) indicated that a heterogeneous quality of the habitat can generate larger and more productive populations as a source of migrants towards poorer zones, and that the spatial expansion and colonization in decapods is ruled by the process of larval dispersion (Epifanio *et al*., 1984; Ernst *et al*., 2005; Fogarty & Botsford, 2006, 2007). Therefore, both the dynamics of length compositions as the spatial patterns in the population abundance suggest that the *H. reedi* could constitute a metapopulation, with at least two sub-populations located northward and southward of 32°S. The most important of them would locate between the mouths of Maipo and Maule rivers (33°43'-35°18'S), and the smallest one with a nucleus located between the mouths of Elqui River and Punta Lengua de Vaca (30°23'-31°12'S). This proposal of population structure could be complemented by the basin model of McCall (1990), in which there is a central nuclei with the highest density of individuals, and the population growth is generated by the "overflow" of biomass toward areas less dense. In this model, advection it is one of the mechanisms described and therefore larval drift could give support to the metapopulation hypothesis. Another evidences were given by Acuña *et al*. (1997), who investigated morphometric aspects in *H. reedi* and found out significant differences between the sample coming from the region Caldera-Coquimbo (27°03'-29°58'S) and from the region Quintero-Tomé (32°46'-36°35'S). These authors complemented their results with a genetic analysis, determining that population heterogeneity would be explained by a migratory process along the spatial distribution, but at rates that are insufficient to revert the effect of dispersive-genetic factors.

CONCLUSIONS

The extensive amount of information analysed in this paper, which was obtained from thirteen years of trawling surveys on *H. reedi* off Chile, correlated with data of environmental variables (Chl-*a* and OMD) obtained through satellite telemetry, shed light on aspects of population dynamics of this species. Noticeable patterns in environmental conditions along shrimp distribution were identified, mainly in those areas close to rivers mouth and upwelling zones southward 32°S, which would be related with fluctuations in abundance and distribution of *H. reedi*.

This evidence was supported by good correlation levels between abundance and distribution of environmental variables, and whose explanation could be given by the relationship between good environmental conditions, larval survival success and its later settlement before to reach the recruitment size at two years old. The shrimp population is likely to be constituted by a metapopulation structure with at least two subunits located each north and southward 32°S, and whose connectivity would be explained by larvae drift through Humboldt Current System in south-north direction, situation very relevant for fishery management when them are considered as independent stock units. In this sense, given the level of relationship found between the environmental variables and the abundance of the *H. reedi*, including the population structure, it is concluded that is need to further investigate and strengthen this evidence, since this could become as a forecasting tool in the management of this fishery when poor environmental anomalies be detected. To reinforce that, also it is suggested to develop a more detailed research on the early development stages of this crustacean related to its larval drift along the coast of Chile and its dependence with environmental factors.

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Appendix VI (Publication of Chapter II.2)

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Spatio-temporal modelling of the maturity, sex ratio, and physical condition of nylon shrimp *Heterocarpus reedi* (Decapoda, Caridea), off Central Chile

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ABSTRACT

Two key elements in the adequate, sustained exploitation of any fishery should be considered; the biological attributes of the species and how these vary over time and space. Research is needed to obtain a more thorough understanding of these effects, how they vary, and how they relate to environmental factors. For 17 years, biological information has been collected for *Heterocarpus reedi* (nylon shrimp) caught off central Chile (25–37 °S). Here, we analyze these data using generalized linear models and determine the factors responsible for changes in carapace length, body weight, maturity, and sex ratio. The environmental and alimentary conditions are better south of 32 °S, and this is probably associated with the better physical condition and reproductive attributes of *H. reedi* there. For example, individuals are larger, females are longer at first maturity ($CL_{50\%}$), and mature females are less prevalent. We outline a theoretical foundation that can guide future research on *H. reedi*. We also suggest that future conservation measures consider biological attributes within a spatial context.

1. Introduction

Important changes in the abundance and distribution of many marine benthic species are determined by substrate, environmental characteristics, and exploitation (e.g., Loneragan and Bunn, 1999; Diaz-Ochoa et al., 2004; Encarnacao et al., 2013; Sancinetti et al., 2014; Canales et al., 2016). These factors also affect seasonal differences in, and the persistence of, biological parameters (e.g., Company et al., 2001, 2004; Araújo et al., 2014) and may even give rise to discrete population units or metapopulations (e.g., Fogarty and Botsford, 2006; Josileen, 2011; Sethi et al., 2013; Sal-Moyano et al., 2014).

Heterocarpus reedi (nylon shrimp) is one of the most important decapod crustaceans exploited in Central Chile (25–37 °S), with catches of ~4000 tons year^{-1}. This species is distributed continuously on the continental shelf and upper slope, between 200 and 400 m depth (Fig. 1), occupying a heterogeneous habitat made up of clay soil, sedimentary rock, sand, and mud. The water column in this area contains both equatorial subsurface waters, which are low in dissolved oxygen, and Antarctic intermediate waters, which are cool (10–12 °C), but have relatively high salinity (34.5–34.9 g kg^{-1}) (Silva, 2012). In the south of the study area, river discharge (Canales et al., 2016) and coastal upwelling (mainly in spring) (Silva and Valdenegro, 2003) lead to important amounts of organic matter.

Our understanding of the biology of *H. reedi* is varied. Much information is restricted to finite time periods, for example the early works on reproductive process, growth, and condition factor of *H. reedi* (Arana and Tiffou, 1970; Bahamonde and Henríquez, 1970; Arana et al., 1976). Those authors suggested, among other things, probable spatial heterogeneity in length at first maturity as a response to environmental conditions. Nonetheless, research that extends the space-time dimension or that focuses on other biological attributes (e.g., physical condition, sex ratio, length at maturity) and their variations in time and space remains limited.

We analyzed 17 years of biological information gathered while monitoring the extraction activities of *H. reedi* to understand the patterns and trends of the factors and variables that determine the spatio-temporal changes in its biological attributes, maturity state, physical condition, body length, and sex ratio. Our results contribute to understanding the spatial heterogeneity of these attributes as affected by the environmental conditions observed off the coast of Chile between 1997 and 2013.

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2. Materials and methods

2.1. Data source

Biological samples were taken by the Fisheries Development Institute (Instituto de Fomento Pesquero, IFOP). Samples were taken in south-central Chile (25°–36°S) between 1997 and 2013, as part of a program that not only monitors fishing activity at the main landing ports and processing plants, but also performs on-board sampling. The individuals used for biological samples were selected to represent, in a nonrandom manner, the greatest size range possible. Specimens were taken from the final haul of each fishing trip, allowing us to measure variables that would have been difficult to measure on land (e.g., body weight, morphometric measurements). Statistically, this sample was consistent with prior studies that showed, for example, weight and state of maturity to be heavily dependent on individual carapace length. Because of this, more observations should be made at either end of the size frequency spectrum. For each individual, we recorded: the date and geographic location of capture, sex, carapace length (CL) in millimeters, and total wet weight in grams. For females, the reproductive status (mature or immature) was also recorded, as determined by the presence or absence of eggs in the abdomen.

2.2. Statistical analysis

We used Generalized Linear Models (GLM; McCullagh and Nelder, 1984) to analyze four biological response variables (CL, individual weight, maturity, sex ratio), in the same sense as several other authors have used GLM to analyze maturity at size (or age) and the sex ratio (e.g., ICES, 2008; Lambert et al., 2009; Wheeler et al., 2009; Stewart et al., 2010). The models were specified and fit using the language and environment for statistical computation and graphics R (R Development Core Team, 2009). An analysis of deviance was used to evaluate the importance and significance of each predictor variable included in the model. This was complemented by an Akaike Information Criterion (AIC) analysis (Akaike, 1974), which was used to evaluate the relative increase of AIC after excluding specific terms from the full model through the *drop1* function included in R language.

This analysis considered four factors as discrete predictor variables: year (Y), quarter (Q), zone (Z), and sex (M: male, F: female, MF: mature female); and carapace length (CL) as a continuous predictor variable. The models describing the proportion of mature females, total females, and body weight included CL. While analysis focused on model main effects, the first-order interaction defined by quarter × zone also was evaluated to know if seasonality of some dependent variable is determined by spatial influences (zones). Other interactions were not considered to avoid decompensation of the design matrix. Both CL and the logarithm of weight were assumed to be normally distributed (Gaussian error model) with link functions "log" and "identity", respectively, whereas the proportions (of mature and of total females) were assumed to have a binomial distribution with a "logit" link function (Table 1).

Only females (126,252 individuals) were used for the analysis of the proportion of mature individuals. Maturity was designated as a binary variable (p) according to the presence (1) or absence (0) of eggs in the pleopods. After fitting the model and regardless of the year, the length at first maturity was calculated in each zone and for quarter (Q^*) with the highest proportion of mature females, using

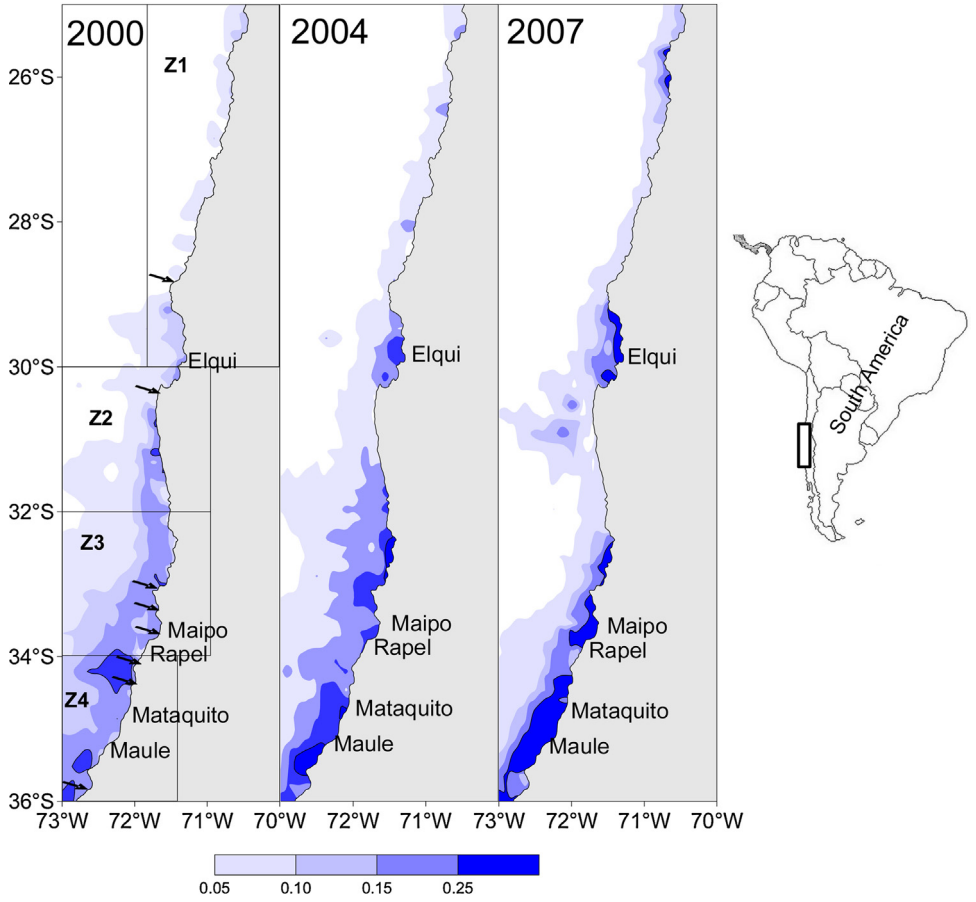

Fig. 1. Study zone and distribution of cumulative organic matter and dissolved detritus between September and December in three years, with the main river names included. The black arrows indicate the main upwelling zones. The rectangles make reference to subzones of analysis.

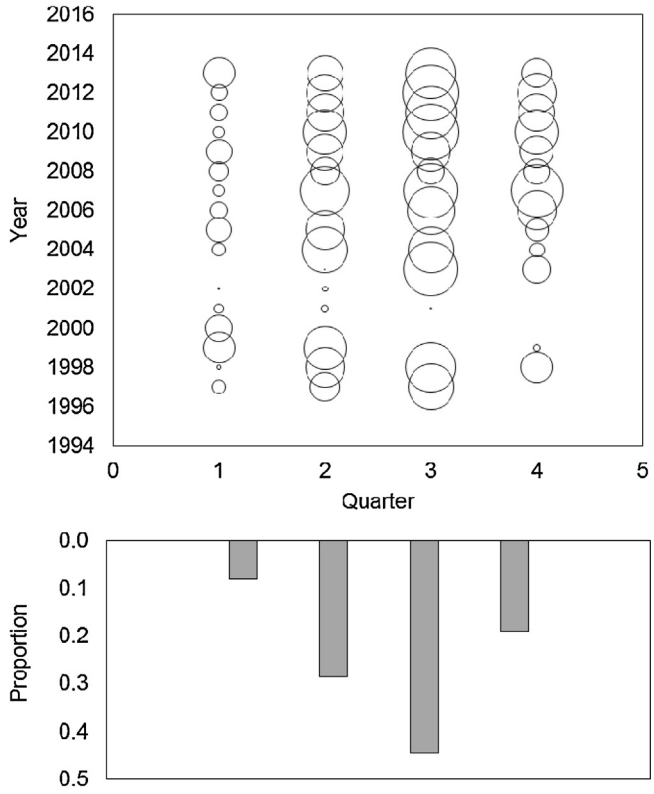

Fig. 2. Proportion (average) of mature females of *Heterocarpus reedi* by year and quarter. The bubble size represents the relative importance within the year, estimated by dividing the number of mature females by the number of total females each quarter and year. The bars represent the expected value across the years.

Table 1
Generalized Lineal Models used to describe variability of carapace length (CL), weight, maturity and sex ratio of *Heterocarpus reedi*.

Response variables	Error	Link	Predictor variables
CL	Gaussian	Log	Year + quarter + zone + sex
log(weight)	Gaussian	Identity	Year + quarter + zone + sex + log(CL)
Maturity	Binomial	Logit	Year + quarter + zone + CL
Sex ratio	Binomial	Logit	Year + quarter + zone + CL

the estimator $CL_{50\%} = \beta^{-1}\left(-\alpha + \bar{Y} + Q^* + Z\right)$, where α is the model intercept and β is the coefficient CL. $\bar{Y}$ is the average of year factor coefficients, including value zero for reference treatment (first level of each factor). Similarly, for the analysis of the proportion of females in the samples, the same statistical attributes of the maturity model were considered, but this time applied to all the individuals measured. The binary response variable corresponded to presence ($p = 1$) or absence ($p = 0$) of females in the samples.

3. Results

3.1. Preliminary data treatment

The information was classified by year, quarter, and zone (Z1: 25°–30 °S; Z2: 30°–32 °S; Z3: 32°–34 °S; Z4: 34°–36 °S) (Fig. 1), considering both the latitudinal distribution of the fishery and whether or not sufficient observations were made in each stratum. A total of 295,000 individuals were collected and measured during the study period. Of these, 52% were females and 21% of those were mature. The highest incidence of maturity (45%) was recorded in the third quarter (July–September) of each year (Fig. 2). Due to the low spatial representation of the samples taken between 2000 and 2002 (Fig. 2), these data were discarded from the maturity analysis, reducing the sample size to ~126,000 individuals.

In general, the H. reedi carapace length (CL) measured between 10 and 40 mm CL, averaging nearly 25 mm CL and 7.25 g. Females were more prevalent in catches over 26 mm CL and were, on average, larger than males (up to 38 mm CL vs. about 33 mm CL) (Fig. 3a). The prevalence of ovigerous females was greater during the third quarter, with mature individuals starting at 22 mm CL and reaching a maximum incidence of 80% at lengths >30 mm CL (Fig. 3b). It is likely that not all mature females were included in the count because the larger individuals may have released their eggs before sampling.

3.2. Model fit diagnostics

The models fitted the data adequately both in variability and trend (left panels Fig. 4). For CL and W, normal quantile-quantile plots (qq-plot) and studentized residuals were considered, while only deviance residuals were considered for the logistic models. The qq-plots for CL and W suggested that the assumed error model appears adequate (center panels Fig. 4a,b), while the studentized residuals did not show significant trends against the predicted values (right panels Fig. 4a,b). For logistic models the same situation was observed (center panels Fig. 4c, 4d), where there no trends in residuals within each groups (binary response), and the dispersion diagram between predicted values against residuals shows an expected profile, with two curves with monotonic decrement around zero (right panels Fig. 4c,d).

3.3. Carapace length and body weight

According to the GLM models, all the factors considered were significant (Table 2). In particular, the main factors determining the variability of *H. reedi* carapace length (CL) and body weight were

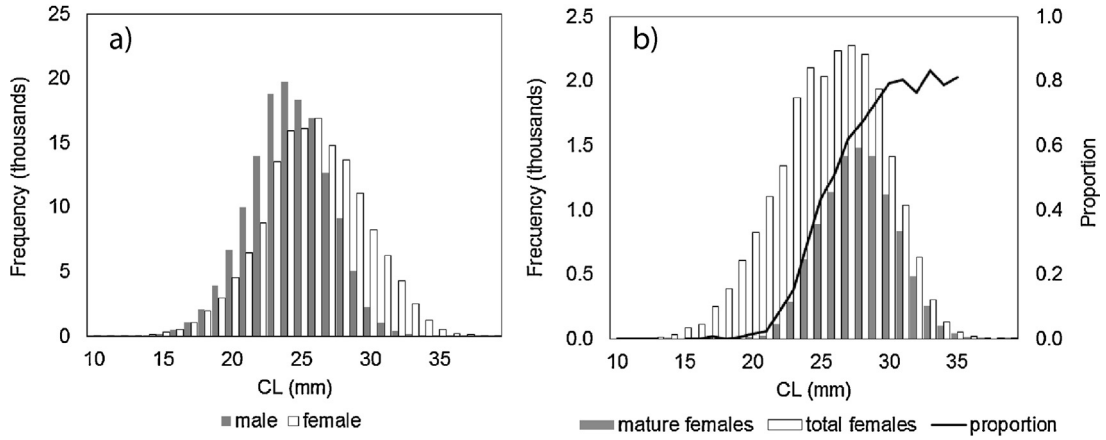

Fig. 3. Histogram of carapace length (CL) of biological samples of *H. reedi*. (a) Males (n = 142927) and females (n = 152000), (b) mature females (n = 10249) and total females (n = 23005) measures in the third quarter of each year. The solid line represents the proportion of mature females.

Table 2
Main statistics of generalized linear models applied to carapace length (CL), log(weight), maturity, and sex ratio of *Heterocarpus reedi*. ΔAIC shows the porcentual increment of AIC when from the full model a predictor variable is excluded.

Predictor variable	Level	Response variable: Carapace length			log(weight)			Maturity			Sex ratio		
		ΔAIC	Coeff.	*t*	ΔAIC	Coeff.	*t*	ΔAIC	Coeff.	*t*	ΔAIC	Coeff.	*t*
Intercept			3.142	2482.4		−7.527	−976.2		−9.277	−109.9		−3.862	−97.2
Quarter (Q)		0%			1%			21%			0%		
	Q2		−0.029	−52.3		−0.033	−44.9		2.170	94.4		−0.013	−1.3
	Q3		−0.031	−45.8		−0.042	−45.9		3.462	127.1		0.050	4.1
	Q4		−0.013	−22.9		−0.008	−10.6		1.506	63.2		0.001	0.1
Zone (Z)		2%			8%			6%			0%		
	Z2		0.032	41.3		0.017	16.5		−0.830	−27.6		−0.261	−18.4
	Z3		0.068	110.7		0.069	82.1		−2.028	−73.2		−0.469	−40.9
	Z4		0.093	147.1		0.125	141.4		−1.361	−55.8		−0.417	−34.0
Year		1%			5%			4%			1%		
Sex		2%			11%								
	F		0.042	95.1		0.032	53.7		–	–		–	–
	MF		0.122	182.1		0.181	179.8		–	–		–	–
CL			–	–		–	–	10%	0.263	95.1	5%	0.180	130.9
log(CL)			–	–	187%	2.907	1210.3		–	–		–	–
$Z \times Q$		0%			1%			5%			0%		

AIC: Akaike information criterion. F: females. MF = mature females.

sex (p < 0.001, F = 16.1e3) and zone (p < 0.001, F = 7.3e3); and CL was the co-variable in the GLM for body weight (Table 2).

The GLM coefficients showed that the average length and weight of *H. reedi* individuals increased significantly from north to south. The individuals from Z4, the southernmost zone, were, on average, 12% longer and heavier than those from Z1, the northernmost zone (Table 2, Fig. 5b). Overall, females were 4% longer and heavier than males. Likewise,and irrespective of the CL, the coefficients of the model indicated that berried (mature) females weighed 16% more than resting females (Fig. 5d), whereas the coefficient of the length-weight ratio (b = 2.90, s.e. = 0.002) indicated negative allometric growth for *H. reedi* (b < 3) (Table 2).

Seasonally, both CL and body weight decreased significantly towards the second and third quarters of each year (Fig. 5a), coinciding with the period of greatest reproductive activity (Fig. 2). Annually, CL growth was found to follow a linear trend (slope > 0, p-value = 0.00035), particularly from 2007 to 2013, while in the weight's model, the annual effect shows that this can vary independently to body size (Fig. 5c), as for example, when annual variations of condition factor occur. In these GLMs, the first-order interaction (quarter*zone) had few contribution in the model's deviance explanation (ΔAIC < 1%).

3.4. Maturity and sex ratio

According to the GLM that described both the variability of maturity and the proportion of females, CL and quarters were the most relevant and significant variables in the model (F > 12E3, p < 0.001, ΔAIC > 5%). The magnitude of the coefficients revealed that the third quarter was the most influential in the proportion of mature females (Table 2, Fig. 6a). The proportion of mature females decreased significantly from north to south, particularly south of 32 °S (Z3, Z4) (Fig. 6b). The results also indicated, though with less influence on the model, that the annual effect on the proportion of gravid *H. reedi* females was variable and increasing over time (Fig. 6c). Also, a small but significant AIC variation (ΔAIC = 5%) was observed when the quarter × zone interaction was excluded from full model, it that might suggest that shrimp maturity depends on spatial and temporal covariates.

Taking the third quarter to be the period when reproductive activity peaked for *H. reedi*, estimates of size at 50% maturity ($CL_{50\%}$) were significantly different between zones. North of 32°S, $CL_{50\%}$ ranged from 24.1 mm (Z2) to 20.9 mm CL (Z1), whereas south of 32 °S, $CL_{50\%}$ was significantly higher, ranging from 28.6 mm (Z3) to 26.1 mm CL (Z4) (Fig. 6d). These data explain the greater proportion of gravid females observed in the

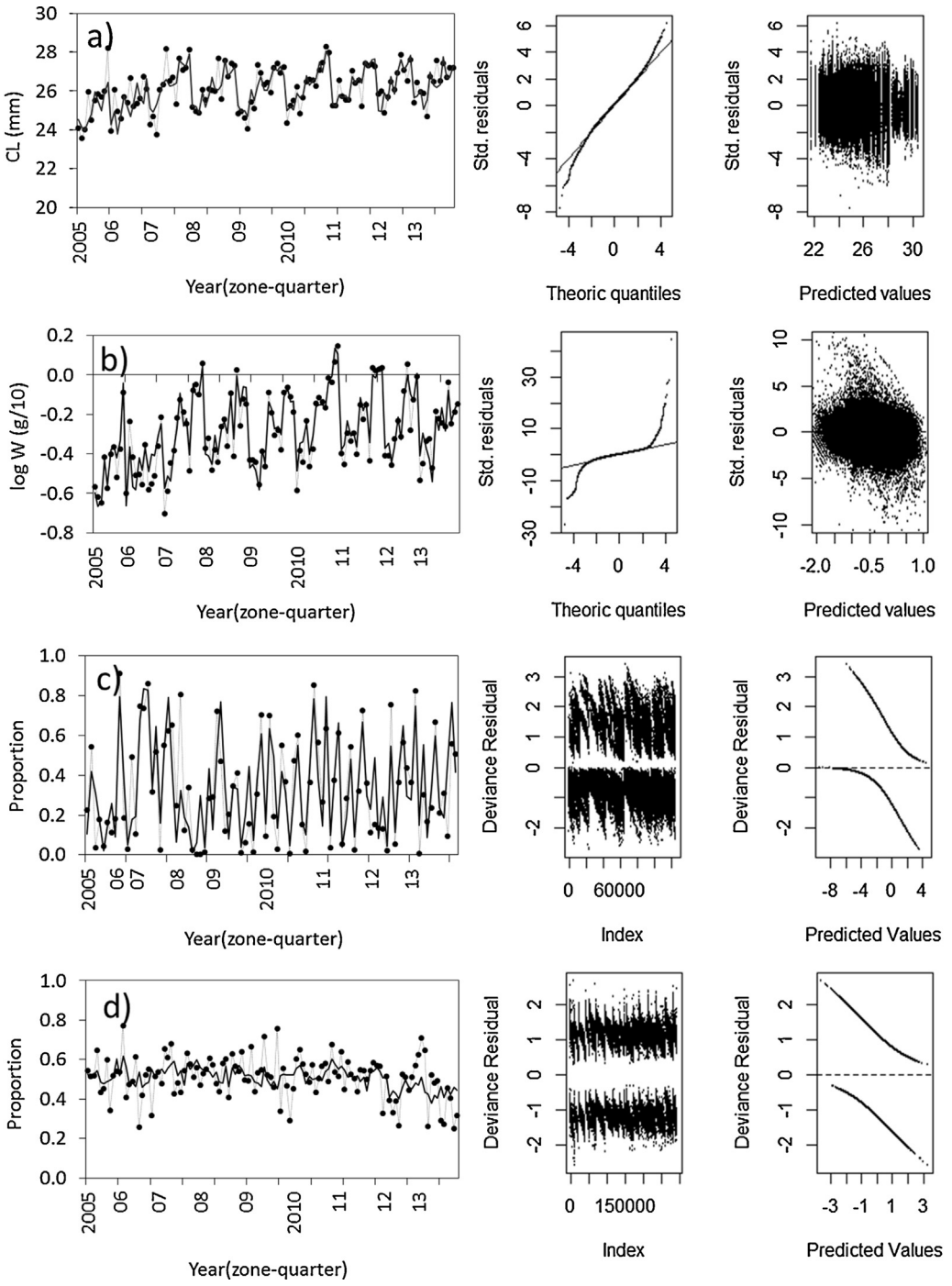

Fig. 4. Model fit diagnostics. Each row corresponds to a different variable: a) carapace length (CL), b) log-weight (W), c) maturity ratio, d) females proportion. Left panels represent the average values by year, zone and quarter (the line is the model fit and the dots are data), where time scale was reduced for improve visualization of model fit. The center panels show respectively the normal quantile-quantile plots for CL and logW, whereas the plots in the 3th and 4th rows are residuals over time. The right panels show the residuals versus the predicted values.

north, since the lower the $CL_{50\%}$ value, the greater the fraction of mature individuals for the size ranges considered. Combining all years and zones, the model that described the proportion of maturity at size for *H. reedi* during the third quarter was $P(CL) = \exp(-6.53 + 0.26CL)/(1 + \exp(-6.53 + 0.26CL))$, in which the parameter −6.53 was the sum of the value of the GLM intercept plus the average of the coefficients of the factors of the model: year, zone, and third quarter. $CL_{50\%}$ was estimated to be 24.9 mm CL (Fig. 7a). Annually, the results suggested a negative trend for $CL_{50\%}$ ($r^2 = 0.65$, $p = 0.005$), as this fell by 32% between 2008 and 2013 (Fig. 7b, 7c).

With respect to the sex ratio (female), CL was the most important variable ($\Delta AIC = 5\%$). Two other factors, Zone ($F = 483$) and Year ($F = 95$), had a lesser, albeit still significant influence on the model, indicating a lower proportion of *H. reedi* females south of 32°S (Fig. 7b). When combining all the factors, the logistic relationship between CL *vs.* sex ratio showed that females were dominant in the population (> 50%) beginning at 25 mm CL; this figure was similar to the $CL_{50\%}$ reported earlier (Fig. 7a).

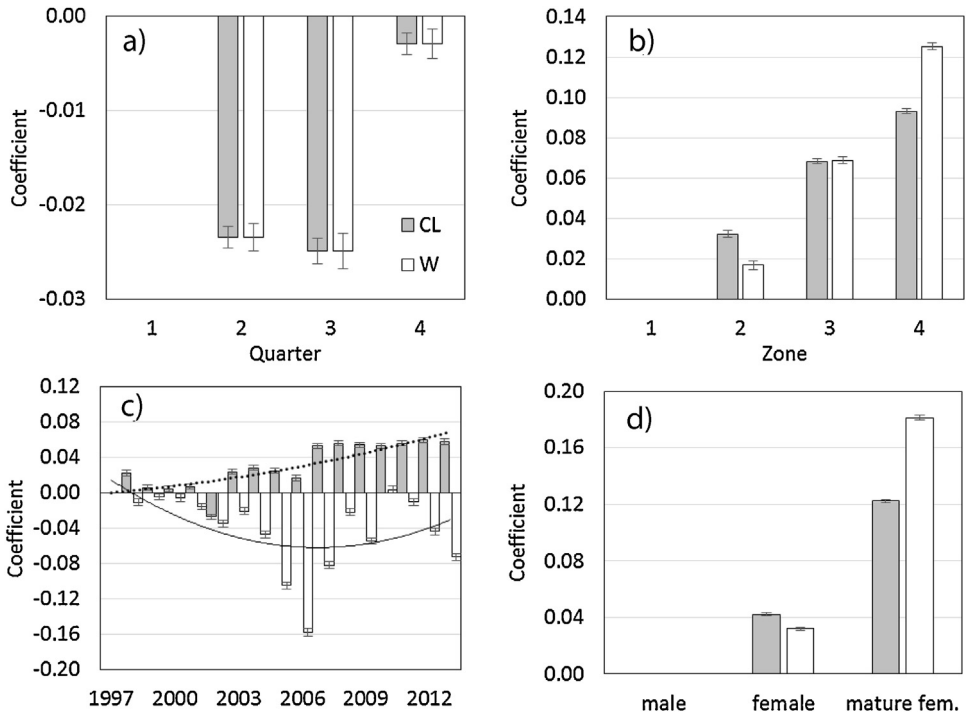

Fig. 5. GLM's coefficients related to carapace length (gray bars) and individual weight (white bars) for *H. reedi*. The effects are: (a) quarter, (b) zone, (c) year, and (d) sex. The trend lines represent the annual factor by year (c).

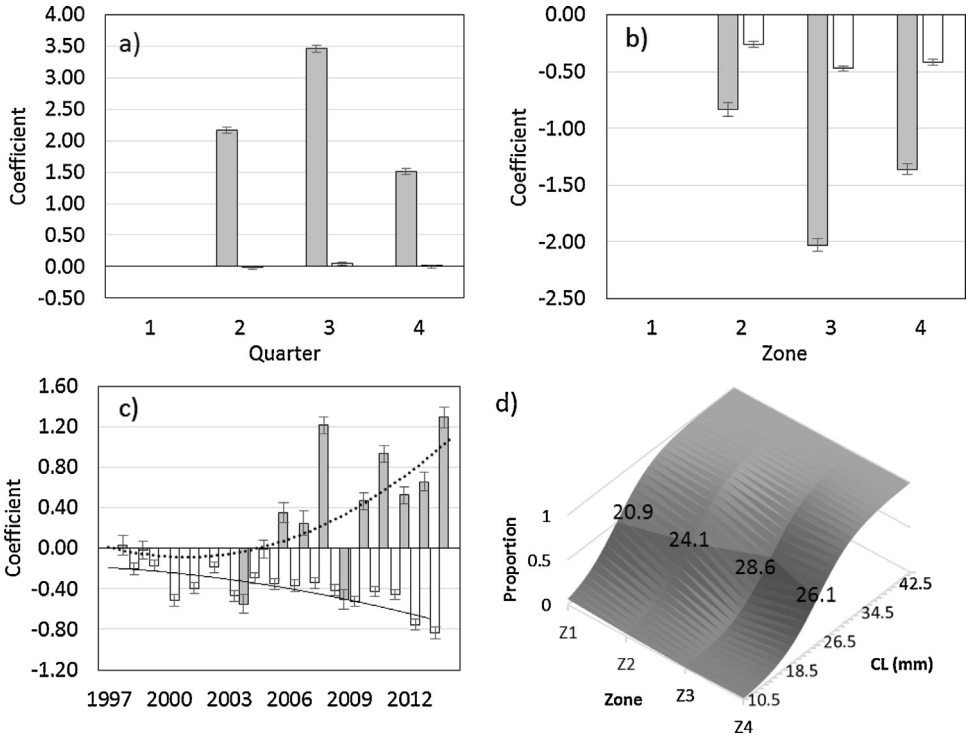

Fig. 6. GLM's coefficients related to maturity (gray bars) and the proportion of females (white bars) for *H. reedi*. The effects are: (a) quarter, (b) zone, and (c) year. The trend line represents the annual factor by year (c). Panel (d) shows the maturity ogive by zone where are included the $CL_{50\%}$ estimations.

4. Discussion

The main biological attributes of *H. reedi*, particularly those related to physical condition and maturity, showed significant spatial and temporal heterogeneity, as evidenced through biological information obtained with samples taken from commercial catches over the course of 17 years. The spatial pattern for the physical conditions of *H. reedi* could be related to environmental heterogeneity observed along its distribution, which among others could determine food availability. Similar findings have been reported in other marine decapods, where bottom conditions seem explain seasonal and spatial differences in some biological parameters (e.g.,

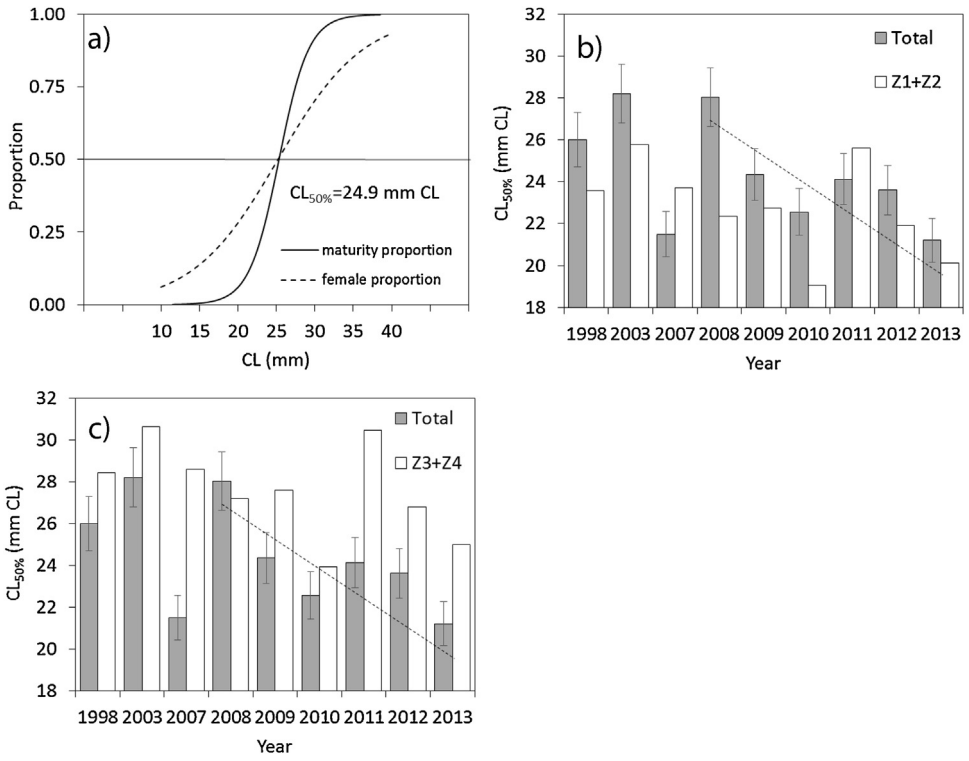

Fig. 7. (a) Proportion of mature females by size of *H. reedi* in the third quarter, for all years and combined zones, plus the proportion of females by size. In panels b) and c), comparative annual changes in maturity size (CL50%) by zones: total vs Z1+Z2 combined (b), total vs Z3+Z4 combined (c). The dotted line represents the annual trend, and error bars show the 95% confidence interval.

Company et al., 2001, 2004; Encarnacao et al., 2013; Sancinetti et al., 2014). In our analysis area, north of 32 °S there is a semi-desertic weather, low precipitations and a narrow continental shelf, while south, several tributary rivers and coastal upwelling zones contribute with important amounts of organic matter and detritus, and probably determining an important food source (Canales et al., 2016) (Fig. 1). Both individual CL and weight differed significantly on spatial and seasonal scales, with individuals of both sexes being longer and in better physical condition south of 32 °S, although these conditions were largely reversed in the third quarter, coinciding with the peak of the reproductive process. Weight loss during the reproductive process can be attributed to increased energy consumption while carrying eggs (females) or producing sperm (males) (Bauer, 2004), to the detriment of energetic investments in individual growth. In common with Gaete and Arana (1986), Anger (1998), Paschoal et al. (2013), and Grabowski et al. (2014), the males in this study were smaller than the females and, starting at 25 mm CL, the females made up a larger proportion of the *H. reedi* population. Also, further investigations seem be necessary to evaluate the apparent relationship between maturity, zone and quarter.

The proportion of females in the samples showed no significant seasonality and, therefore, no apparent connection to the reproductive process. Instead, a weak geographic pattern was observed: the relative predominance of females decreased gradually from north to south, and was heavily dependent on CL. An early study by Gaete and Arana (1986) that looked at the sex ratio of *H. reedi* reported that females were dominant with no significant differences between months. Those authors also found that females were predominant in the size ranges over 25 mm CL, corroborating the findings of the present work.

Many aspects relative to the maturity of *H. reedi* have already been well documented (e.g. Arana and Tiffou, 1970; Bahamonde and Henríquez, 1970; Arana et al., 1976; Canales et al., 1998). Our results for the period of greatest reproductive activity and size at maturity $CL_{50\%}$ (24.9 mm CL) were similar to those found in previous works: 25.5 mm CL (Arana and Tiffou, 1970), 24.3 mm CL (Canales et al., 1998), and 25.1 mm CL (Arana et al., 1976). Our results also confirmed the spatial pattern suggested by Bahamonde and Henríquez (1970), where length at maturity $CL_{50\%}$ increased significantly from north to south. Tuck et al. (1997), Kuhulmann and Walker, 1999, and Queirós et al. (2013) described variations of this parameter in other regions of the world. Those authors offered different explanations for this phenomenon: from the impact of overexploitation of the larger individuals of a population, which would reduce the average length at age, to the importance of habitat in determining life parameters as a result of discrete population units. In the case of *H. reedi*, the latter may be the more likely scenario since commercial fishing does not seem to have generated significant changes in the population structure, given the low level of exploitation recorded in the last decade (Montenegro et al., 2014) and the increased biomass reported by Acuña et al. (2012).

Queirós et al. (2013) noted that spatial variations of $CL_{50\%}$ were not yet well understood, but were related to recruitment and hydrodynamic conditions (Hill et al., 1997), sediment characteristics (Campbell et al., 2009), and food availability (Tuck et al., 1997). According to Canales et al. (2016), *H. reedi* has a heterogeneous population structure, with the greatest densities and largest individuals located south of 32 °S, where the food supply and probably the sediment quality were greater, in turn, determining the larger sizes of $CL_{50\%}$ mentioned above. The better quality of the habitat may lead to delayed maturity, allowing individuals to allocate more of their energy consumption to growth and, thereby, explaining why few large individuals were found north of 32 °S and why females in that area were smaller at maturity. As indicated by Kuhulmann and Walker, 1999, latitudinal differences in $CL_{50\%}$ result in implicit changes in the growth patterns and could have important implications for management of *H. reedi* fisheries since the level of fishing

mortality that would allow sustainability of this resource depends on both the maturity ogive and life history parameters.

Our results also showed annual trends in key biological attributes. For example, the proportion of mature females has been greater since 2008, in response to a decline in $CL_{50\%}$ observed in the same period. Such changes in biological parameters have often been related with environmental stress factors and exploitation. Indeed, both Phillip (2013) and Zheng (2008) noted that temperature, food, and population density may have led to changes in $CL_{50\%}$. This situation was also studied by Castilho et al. (2007), who established, for example, that the characteristics of the rearing period for *Artemesia longinaris* were correlated with the availability of food for the potential larvae of this decapod. Those authors indicated that $CL_{50\%}$ was the result of a process of reproductive adaptation to the aforementioned environmental factors. For *H. reedi*, Canales et al. (2016) provided environmental indicators associated with the area south of 32 °S, showing a suggested decrease in the anomalies of chlorophyll-a and organic matter dissolved since 2008, which could explain in some way the decline in $CL_{50\%}$ mentioned above.

5. Conclusion

This research identified spatio-temporal patterns in the main biological attributes of *H. reedi*, the causes of which seemed to be determined mainly by environmental factor related to the habitat. Better conditions in the southern portion of the distribution area could explain the higher $CL_{50\%}$ and the presence of individuals in better physical condition, thereby suggesting that future studies of *H. reedi* growth parameters and natural mortality be conducted on a similar spatial scale. Finally, our results support the hypothesis of the *H. reedi* population structure proposed by Canales et al. (2016): in brief, the *H. reedi* population structure is spatially heterogeneous, particularly north and south of 32°S. This reveals the importance of considering these characteristics when developing future conservation and fisheries management measures.

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Appendix VII (Publication Chapter II.3)

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Using a length-based stock assessment model to evaluate population structure hypotheses of nylon shrimp *Heterocarpus reedi* (Decapoda, Caridea) exploited off central Chile

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ABSTRACT

Spatial processes are rarely considered explicitly in the evaluation and management of marine invertebrate populations. This is particularly true when larval drift acts as one of the main mechanisms of population expansion. The ecological concept *metapopulation* is widely used and accepted for understanding low-mobility marine populations. This study uses a length-based dynamic analysis model for nylon shrimp (*Heterocarpus reedi*) exploited off central Chile (25°–37°S) to contrast various hypotheses of population structure and spatial connectivity. The two subpopulations studied are located to the north and south of 32°S. The model is fitted to the historical fishery data (from the mid-1940s to the present), the results of monitoring of fishing activities (1970s-present), and research surveys (1990s-present). Statistically, several hypotheses can explain the data. The most likely hypothesis is that of a metapopulation in which the south zone acts as a source population (reproductive refuge) and determines, partially or totally, the recruits in the north zone, thereby explaining the population increase over the last decade. Empirical evidence will strengthen the hypothesis of spatial connectivity and special attention should be paid to the biological-fishery conditions recorded south of 32°S given the implications for managing the fishery for this resource.

1. Introduction

The spatial attributes of populations are not often explicitly considered in the classical approach to stock assessment used for marine invertebrates. Instead, the discussion focuses on the size of the spatial scales of analysis, presuming that the principal biological processes (e.g., spawning and larval settlement) occur within these limits (e.g., Legendre, 1993; Tuck and Possingham, 1994; Caddy and Defeo, 2003). However, larval drift has been identified as the main mechanism of expansion for many decapod crustacean populations (Fogarty and Botsford, 2006). Thus, the influence of nearby areas defined as reproductive refuges or sources (Walters, 1998; Caddy, 1999) should be considered when explaining variations in this type of marine resource. Not knowing the levels of spatial connectivity specific in a metapopulation could, for example, provide an incorrect perception about the poor recruitments in a specific zone, when really this are a function of a nearby source population that has been overexploited (Orensanz and Jamieson, 1998; Caddy and Defeo, 2003).

Data for nylon shrimp (*Heterocarpus reedi*) date back to the mid-1940s and constitute one of the longest data sets available for a decapod crustacean exploited off Chile's central coast (25°S–37°S) (Fig. 1). The commercial fleet that fishes nylon shrimp is made up of small-scale industrial trawlers and concentrates operations between 200 and 400 m depth over the continental shelf and the upper edge of the slope (Bahamonde and Henríquez, 1970; Arana et al., 1976; Arana, 2012). *H. reedi* has a continuous latitudinal distribution with largely bathymetric and meridional migratory cycles (Arana et al., 1975). The nylon shrimp aggregations seem to depend on river mouths and have a juvenile-led population expansion from south to north. Moreover, they are likely influenced by the Humboldt Current System, which moves in a general south-to-north direction at the surface and acts as an advective mechanism for eggs and larvae. Thus, Canales et al. (2016b) proposed a metapopulation population structure with two sub-populations: one north

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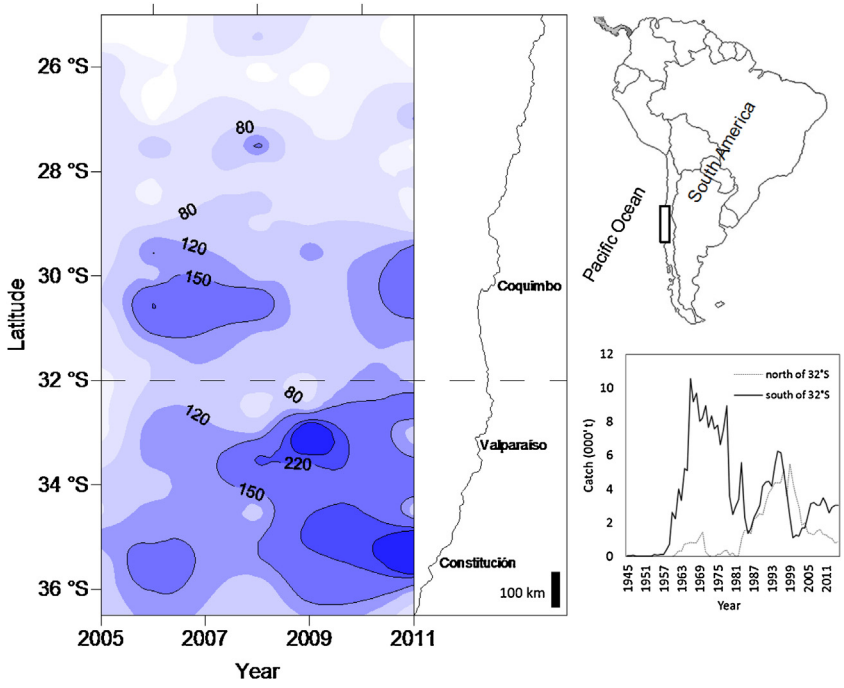

Fig. 1. Spatial distribution and catches of nylon shrimp (*Heterocarpus reedi*) off Chile. In the map, contour lines represent the density isopleths (kg km^{-1}) estimated from scientific survey data (source: Canales et al. (2016a,b)). The horizontal dashed line (32°S) represents the hypothetical spatial separation of the population.

and one south of 32°S. In this set-up, the south zone acts as the main habitat or *source* population.

The *H. reedi* fishery is administered as if it were two independent stock units separated at 32°10′S. Stock assessments consider each of these stock units to be closed and rely on a model that integrates age-structured dynamics with size observations (Montenegro et al., 2015) similar to the A-SCALA model proposed by Maunder and Watters (2003). An analysis of the data – mainly the signals found in abundance indices from the commercial fishery and scientific trawling surveys – reveals that population variations between these zones are similar, suggesting some level of correlation and/or spatial connectivity (Montenegro et al., 2015).

In this paper, we analyze the data and historical information for the nylon shrimp using a length-based population dynamics model (e.g., Sullivan et al., 1990; Punt and Kennedy, 1997; Zheng and Siddeek, 2011; Turnock and Rugolo, 2011). We evaluate probable relations between spatially neighboring sub-populations and determine whether the information used in the stock assessment can be explained by more than one hypothesis of the population structure. Our results permit evaluation of the implications that this situation could have on management of this resource and contributes to our understanding of the *H. reedi* biological-fishery data from a novel analytical perspective.

2. Materials and methods

2.1. Study area and data analyzed

We use data from three independent sources: landing statistics recorded by the Chilean National Fisheries Service (SERNAPESCA), fishing activities as monitored by the Fisheries Development Institute (Instituto de Fomento Pesquero, IFOP) since the early 1970s, and scientific trawling surveys funded by the Fisheries Research Fund (Fondo de Investigación Pesquera, FIP) since the 1990s. These data cover the area where *H. reedi* is distributed and fished (northern central Chile), but are divided into two zones separated by the latitude 32°S (Fig. 1). For modeling purposes, we consider the series of landings back to 1945, length frequencies (combined sexes) for the commercial landings and scientific surveys combined, the standardized series of annual catch per unit of effort (CPUE) (tons per hour of trawling) (Montenegro et al., 2015), and annual indices of relative abundance (catch in kg per linear km trawled) calculated from the fishing logs during scientific surveys (Canales et al., 2016b) (Table 1).

For each survey, the abundance index is calculated by zone and year using the ratio estimator (Cochran, 1978), where the density of shrimp (kg km^{-1}) in a given zone (z) and year (y) corresponds to the ratio of the sum of the landings of all hauls made in a given zone and year, to the sum of the individual linear distances trawled for all hauls made in the same zone and year. The seasonal and technological considerations of this indicator are ignored because, in general, the surveys are conducted during the second half of the year, are based on stratified designs, and use vessels with similar operational characteristics (Canales and Arana, 2010; Canales et al., 2016b).

2.2. Biological parameters

The biological parameters of *H. reedi* such as growth, the proportion maturity at size, and weight at size are assumed to be the same between years but to differ by zone (Canales et al., 2016b) (Table 1). The growth parameters by zone were estimated outside the model based on an analysis of modal compositions (Fournier et al., 1990; Gayanilo et al., 1994; Canales and Arana, 2009) from size frequencies from the commercial fishery and scientific surveys. The natural mortality rate was fixed at $M = 0.36\,\text{yr}^{-1}$ (Montenegro et al., 2015), and assumed to be invariant between years, sizes, and zones.

2.3. Population model

The model of the population dynamics was implemented using AD Model Builder (C++) (Fournier et al., 2012) and is based the models proposed by Sullivan et al., (1990), Punt and Kennedy (1997),

Table 1
Years of available information and biological parameters of nylon shrimp (*Heterocarpus reedi*) by zone (north (n) and south (s) 32°S) used for stock assessment.

Catches	Northward 32°S (n) 1961–2015	Southward 32°S (s) 1945–2015
Length compositions	Fleet: 1970–71; 1984–86; 1993–2014 Surveys: 1999–2006; 2008–2009; 2011–2012	Fleet: 1970–1981; 1984–1987; 1989–1990; 1992–2015 Surveys: 1999–2006; 2008–2009; 2011–2012
Abundance indexes	Fleet: 1969–1971; 1974–1975; 1978–1979; 1981–2014 Surveys: 1998–2006; 2008–2009; 2011	Fleet: 1968–1978; 1980–2000; 2002–2015 Surveys: 1998–2006; 2008–2009; 2011
Maturity proportion at-length (50%–95%)	22.0 mm–33.0 mm CL	27.0 mm–36.0 mm CL
Coefficients of weight-at-length relationship	a = 5.19E-4, b = 2.91	a = 5.67E-4, b = 2.91
Growth parameter[a]		
l_∞ *(mm)*	41.1	42.3
k (yrs^{-1})	0.14	0.15
Lo (mm)[b]	20.1	18.2
Sr[c]	2.0	1.8

[a] Estimated outside the model.
[b] Mean carapace size of the first modal-group.
[c] Standard error of the first modal-group.

Zheng and Siddeek (2011), Haddon (2011), and Turnock and Rugolo (2011), amongst others. Recruitment in this model is distributed over a range of sizes and occurs at the start of the year after the survivors of fishing and natural mortality have grown. The advantage of this model is that all processes are based on size, regardless of age (Punt et al., 2013). The model includes spatial considerations (e.g., Haist et al., 2009; McGarvey et al., 2010; Lestang et al., 2012), and their main formulation is expressed by zone ($z = n,s$) as:

$$N_{y,z} = T_z\left(S_{y-1,z}N_{y-1,z}\right) + R_{y,z} \quad (1)$$

$$R_{y,z} = r_{y,z}\varphi_z \quad (2)$$

$$r_{y,z} = \begin{cases} \hat{r}_{y,z} + \pi\,\hat{r}_{y,z=2} & z = n \\ \hat{r}_{y,z}(1-\pi) & z = s \end{cases} \quad (3)$$

$$0 \le \pi \le 1 \quad (4)$$

$$\hat{r}_{y,z} = \frac{\alpha_z SSB_{y-\tau,z}}{\beta_z + SSB_{y-\tau,z}} e^{\varepsilon_{y,z}} \quad (5)$$

where $N_{y,z}$ is a column vector containing the number of individuals per size interval at the start of year y; n and s are related respectively the north and south zones; T_z is the transition matrix that determines the annual growth between the size classes, based on a normal probability distribution (e.g., Luke et al., 2014; Haddon, 2011; Punt and Kennedy, 1997; Punt et al., 2010); $S_{y\text{-}1,z}$ is a diagonal matrix with the proportion of survivors (of fishing and natural mortality) by length interval and zone in year y-1; and $R_{y,z}$ is a vector that represents the annual distribution of recruits by size and zone (z). The size-specific selectivity and catchability coefficients of both the commercial fleet and scientific surveys are assumed to vary by zone but not over time. Selectivity is modeled logistically in both cases (see Appendix B, B.2).

The annual distribution of recruits by size and zone ($R_{y,z}$) defined in Eq. (2) comprises an annual number of recruits in each zone ($r_{y,z}$) and a column vector (φ_z) that describes the relative proportion of the $r_{y,z}$ in each class interval following a normal distribution with mean L_0 and standard deviation S_r ($\sim N(L_0, S_r)$) for each zone. Eq. (3) defines the spatial connectivity between zones and is a function of the theoretical recruits ($\hat{r}_{y,z}$) for each zone and the parameter π, whose domain is defined in Eq. (4). Depending on the hypothesis, this parameter determines the fraction of the recruits generated in the south zone (z = s) that move (through larval advection) to the north zone (z = n), or the proportion of allocated recruits to the north zone under a single-stock scenario (Fig. 2). The expected umber of recruits per year and zone $\hat{r}_{y,z}$ is modeled by the Beverton and Holt stock-recruitment relationship (Eq. (5)), where SSB is the spawning stock biomass, τ is the time lag (assumed to be 2 years) (Canales et al., 2016b) between recruitment and spawning, and $\varepsilon_{y,z}$ is an annual deviation on the logarithmic scale ($\sim N(0,\sigma_R)$). The parameters α and β are calculated in terms of steepness ($h = 0.75$), virgin recruitment estimated by the model ($R_{0,z}$), and the spawning stock biomass ($SSB_{0,z}$) calculated in each zone (Francis, 1992).

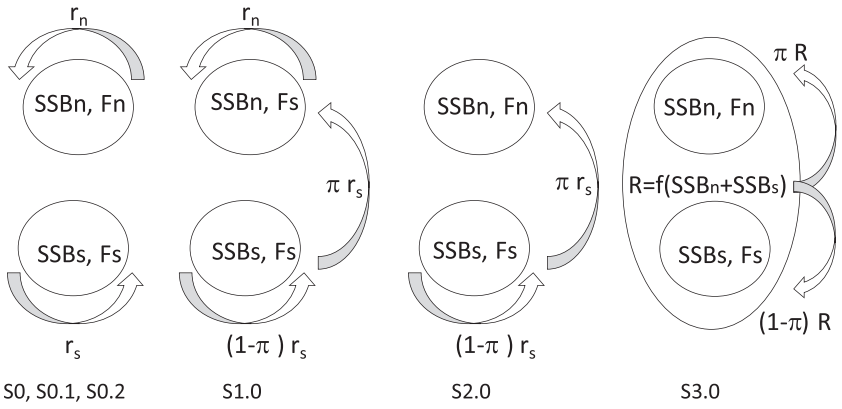

Fig. 2. Illustration of four hypotheses of nylon shrimp population structure. SSB represents the population spawning biomass, *n* and *s* are sub-indexes for 'north' and 'south', respectively, *r* is recruitment, F is the zone-specific fishing mortality and π is the proportion of south recruitment that migrated to the north (S0, S1.0, S2.0) or an allocation coefficient (S3.0). Recruitment occurs in scenarios S0, S0.1, S0.2 and S1.0 in each zone while in scenario S2.0 all recruitment to the north zone comes from south zone. S3.0 is the representation of a single stock where recruitment to each zone is a proportion of a total recruitment as a function of a combined biomass.

Table 2
Configuration of key model parameters for different hypotheses of shrimp population structure. σ_x represents deviates the standard error (log scale) of recruitments between zones (z), π is the proportion of migrant recruits from southern zone, R_0 is the virginal recruitment, and $\varepsilon_{y,z}$ is the annual deviate of recruitment (in log-scale). Letters F and E indicate if the parameter was fixed or estimated, respectively.

Population structure	Scenario	σ_x	π	$R_{0,z=n}$	$R_{0,z=s}$	R_0	$\varepsilon_{y,z=n}$	$\varepsilon_{y,z=s}$	ε_y	Number of parameter
Cross-correlated recruitments	S0.0	1.0	0 (F)	E	E	–	E	E	–	303
	S0.1	0.5	0 (F)	E	E	–	E	E	–	303
	S0.2	0.2	0 (F)	E	E	–	E	E	–	303
Metapopulation	S1.0	1.0	E	E	E	–	0 (F)	E	–	233
	S2.0	1.0	E	0 (F)	E	–	0 (F)	E	–	232
Single stock	S3.0	–	E	–	–	E	–	–	E	231

The model assumes that the stock was in an unfished state in 1945 and SSB_0 is calculated by projecting the survival (only from natural causes) of the distribution of annual recruits for as many years as necessary to reach a stable biomass value (Fig. 3).

2.4. Error model

Different log-likelihood functions are considered to capture the data, penalties, and *a priori* distributions of the parameters of interest (Appendix C). The size proportions of the commercial landings and scientific surveys are represented using a multinomial distribution with an effective sample size of n = 30, which was calculated using the estimator of Gavaris and Ianelli, (2002). The log likelihood of both abundance indices and landings assumes normality of the log-transformed variable. The standard deviation of the abundance indices is assumed not to vary between years and zones, and the values ($\sigma = 0.3$ for CPUE; $\sigma = 0.15$ for surveys) are verified *a posteriori* by calculating the standard deviation of the log-deviations. For catches, this standard deviation is assumed to be $\sigma = 0.05$ (see Appendix C, C.2).

The objective function further includes three penalty terms related to: (1) the recruitment deviations on a logarithmic scale ($\varepsilon_{y,z}$); (2) the deviations in the catchability coefficients of the scientific surveys between zones; and (3) the deviations in the random errors of annual recruitment on a logarithmic scale between zones (Appendix C, C.3). The deviation in catchability of the surveys between zones is assumed to be normally distributed on the log-transformed scale subject to a low coefficient of variation (cv = 0.05), which is justified because it allows the biomass estimates for each zone to be represented by the scale of local densities. The deviations in the random errors of the recruitment defined in (3) allow us to evaluate different levels of correlation for recruitment between zones, with values of cv equal to 1.0, 0.5, and 0.2, given low, medium, and high cross-correlation scenarios (Appendix C, C.3.2)

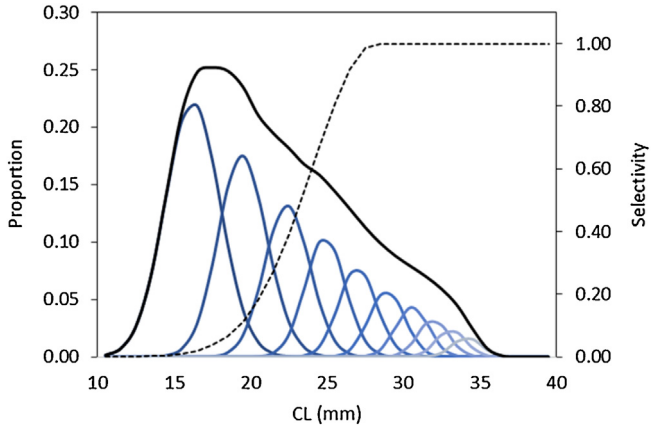

Fig. 3. Example of modal groups present in virgin length composition of nylon shrimp together to fleet selectivity (scenario S0, north). Bold line represents total population, thin lines represent each modal group and the dashed line corresponds to selectivity. Recruitment at length is represented by the first modal group.

The values of the parameters are estimated by minimizing the objective function consisting of the sum of the marginal components of the negative log-likelihood, the penalties mentioned above, and an *a prior* distribution of the $\log\_L_0$ parameter assumed to be normal with a mean $\log\_L_r$ (baseline information) and a standard error of 0.1 (Table 2). In this sense and considering the nonlinearity of the model, a set of start parameters was selected given the predicted variables by the model compared to the observations, as a function of some key parameters, as the selectivity coefficients, distribution of recruitment at length, migration/allocation coefficient, and the average of fishing mortality by zone.

2.5. Evaluation of different population structures

Six different model configurations were used to represent alternative hypotheses for the dynamics of *H. reedi* recruitment and population structure. Three models involve independent populations (S0) with three magnitudes of cross-correlation (low, medium and high) in recruit recruitment (S0.1, S0.2, S0.3); the fourth is a metapopulation with a population/habitat pseudo-sink (Fig. 2); the fifth is a typical source-and-sink metapopulation (Fogarty and Botsford, 2006); and the sixth is a single-stock. Specifically, there is a cross-correlation of recruitments among zones in scenarios S0, represented by assuming that deviations in recruitment between zones follow a normal distribution (mean zero) with different variance assumption (see Appendix C, C.3.2). Scenarios S1.0 and S2.0 represent a metapopulation with different magnitudes of connectivity. In S1.0, the north zone is a pseudo-sink where, although the scale of local recruitment is determined by the zone's spawning biomass through Eq. (5), its variability depends only on the recruits generated in the south zone (source population). In scenario S2.0, the northern population is a sink (no local generation of recruits, $R_{0,z=1} = 0$) and recruitment depends on a proportion of annual recruits generated by the south zone. In the last two cases, the number of model parameters are reduced by approximately 23% since deviations of annual recruitment in the north are not estimated (Table 2).

Particular considerations were taken account when the hypothesis of a single-stock (S3.0) in nylon shrimp was implemented, given its widespread distribution (25°–37°S) and its low level of latitudinal migrations. The main assumption was to consider that there a single theorical annual recruitment (with process error) as function (S/R) of a combined spawning biomass (both zones), while recruitments by zone are determined by applying a spatial allocation factor (π) assumed to be time invariant (north: $\pi\hat{r}_y$; south: $(1-\pi)\hat{r}_y$). After the recruitments to each zone, the exploitation levels depend on local fishing mortality.

Table 3
Estimates of key parameters (log scale) model, marginal likelihood components and indexes of information criterion (AIC & BIC) for each scenario. The parameter standard error are given in parenthesis. The lowest scores are indicated in bold.

				Hypothesis (scenario)					
Parameter	*Source*	*name*	*stock*	*S0*	*S0.1*	*S0.2*	*S1.0*	*S2.0*	*S3.0*
Selectivity	fleet	log (μ)	north	3.28 (0.01)	3.28 (0.02)	3.27 (0.02)	3.31 (0.02)	3.27 (0.02)	3.29 (0.03)
		log (θ_1)		1.14 (0.06)	1.14 (0.06)	1.12 (0.06)	1.52 (0.19)	1.15 (0.08)	1.67 (0.21)
		log (μ)	south	3.41 (0.02)	3.41 (0.02)	3.41 (0.02)	3.41 (0.02)	3.42 (0.02)	3.42 (0.02)
		log (θ_1)		1.47 (0.04)	1.47 (0.04)	1.48 (0.04)	1.47 (0.04)	1.47 (0.04)	1.50 (0.05)
	survey	log (μ)	north	3.34 (0.03)	3.34 (0.03)	3.34 (0.03)	4.09 (0.52)	3.37 (0.04)	5.26 (1.18)
		log (θ_1)		1.43 (0.09)	1.43 (0.09)	1.43 (0.09)	3.19 (0.79)	1.55 (0.13)	4.53 (1.36)
		log (μ)	south	3.41 (0.02)	3.41 (0.02)	3.41 (0.02)	3.42 (0.03)	3.39 (0.02)	3.46 (0.03)
		log (θ_1)		1.37 (0.07)	1.38 (0.07)	1.39 (0.07)	1.41 (0.07)	1.34 (0.06)	1.48 (0.08)
Virginal recruitment		log (R_0)	north	7.75 (0.11)	7.78 (0.11)	7.85 (0.11)	6.94 (0.18)	–	–
			south	8.23 (0.08)	8.28 (0.08)	8.32 (0.09)	8.61 (0.07)	8.77 (0.08)	–
			single	–	–	–	–	–	8.60 (0.06)
Migrant rate/allocation		log (π)		–	–	–	−1.24 (0.16)	−0.97 (0.11)	−0.71 (0.05)
Catchability	fleet	log (q_f)	north	−11.16 (0.11)	−11.24 (0.13)	−11.44 (0.09)	−11.88 (0.12)	−11.74 (0.08)	−12.12 (0.11)
			south	−10.34 (0.13)	−10.39 (0.12)	−10.44 (0.12)	−10.32 (0.13)	−10.45 (0.12)	−10.34 (0.13)
	survey	log (q_s)	north	−5.57 (0.13)	−5.64 (0.12)	−5.75 (0.11)	−5.54 (0.19)	−5.94 (0.11)	−5.18 (0.16)
			south	−5.55 (0.13)	−5.61 (0.12)	−5.7 (0.11)	−5.53 (0.18)	−5.86 (0.11)	−5.18 (0.16)
Recruitments		log (l_r)	north	2.79 (0.05)	2.8 (0.05)	2.83 (0.05)	3.04 (0.03)	2.91 (0.04)	3.07 (0.02)
			south	2.79 (0.04)	2.78 (0.05)	2.77 (0.06)	2.81 (0.04)	2.78 (0.05)	2.82 (0.04)
Transition matrix		log (ω)	north	−2.31 (0.21)	−2.33 (0.22)	−2.36 (0.21)	−2.63 (0.17)	−2.48 (0.22)	−2.59 (0.18)
			south	−1.33 (0.19)	−1.45 (0.23)	−1.64 (0.29)	−1.35 (0.19)	−1.59 (0.26)	−1.44 (0.22)
Maximum gradient component				7.16e-04	1.82e-05	5.67e-05	2.58e-04	8.05e-05	3.91e-05
Log-likelihood components									
	cpue			30.77	32.16	35.62	42.32	45.78	41.94
	survey			52.14	53.91	61.16	40.08	59.70	41.93
	catch			0.73	0.90	1.52	0.63	2.27	2.70
	prop_catch			5,432.65	5,438.14	5,449.73	5,472.23	5,461.33	5,487.90
	prop_survey			1,930.41	1,930.82	1,933.58	1,950.42	1,937.24	1,958.35
	Total likelihood			7,446.7	7,455.9	7,481.6	7,505.7	7,506.3	7,532.8
Number of parameters				303	303	303	233	232	231
Index of information criterion									
	AIC			15,499.4	15,517.9	15,569.2	15,477.4	**15,476.6**	15,527.6
	BIC[a]			17,912.4	17,930.8	17,982.2	17,332.9	**17,324.2**	17,367.2

[a] Based on 2406 observations.

Models are compared statistically using Akaike's Information Criterion (AIC) (Akaike, 1974) and Schwartz's Bayesian Information Criterion (BIC) (Schwarz, 1978). Both metrics satisfy the fundamental criteria for model selection: goodness of fit, parsimony, and objectivity (Langitoto et al., 2000).

$$AIC = 2L_{max} + 2p \quad (6)$$

$$BIC = 2L_{max} + p\log(n) \quad (7)$$

where L_{max} is the minimum of the negative of the total log-likelihood function of the data (not considering penalties or *a priori* distributions), p is the number of parameters, and n is the number of observations.

3. Results

3.1. Overall model fit

In all considered cases the model converges on a feasible solution with maximum gradient values that are lower than $2.58^{*}10^{-4}$ for all scenarios (Table 3). The fit of the model to the data is adequate, and the model appears to reproduce the abundance index of the commercial fleet (CPUE) and research surveys well, as well as the average carapace length (CL) for these two data sources per year and zone (Fig. 4). The 95% confidence intervals suggest that the assumed observation errors of the abundance indices are adequate given that these contain most of the predictions. The consistency between the pieces of information (abundance indices, landings, size compositions), particularly for the growing trend of the indicators beginning in 2000, is also worthy of note. Similarly and as an example, the fit of the length compositions under the hypothesis of independent populations (S0) is notable, first, for the slight tendency of the model to over-estimate the frequency of individuals greater than 30.5 mm CL and, second, because the *H. reedi* recruits are distributed around 16 mm CL (Fig. 5). Also and without large impact in results, the residual pattern observed in model fit to abundance indexes for the south (Fig. 4b and d) would represent hyper-stability effects in CPUE, which could be modelling under appropriate justifications.

3.2. Population parameters

H. reedi is characterized by reduced biomass in both zones until the mid-1990s and a subsequent population increase and expansion from 2000 onwards (Fig. 6a, b). As expected, the hypotheses of population structure appear to have a greater impact for the north zone, with S1.0 and S2.0 (metapopulation) presenting the greatest sensitivity on the biomass scale, differing by more than 30% from the hypothesis of independent populations (S0) (Fig. 6a). Average biomass estimates in the south zone are around 50,000 tons, which is 24% higher than in the north zone. The results also show that the main changes in biomass are explained by large pulses of recruits recorded throughout the decade of the 2000s in both zones, even when (and depending on the hypothesis), recruits in the north are influenced by recruits in the south (S1.0 and S2.0) (Fig. 6c, d).

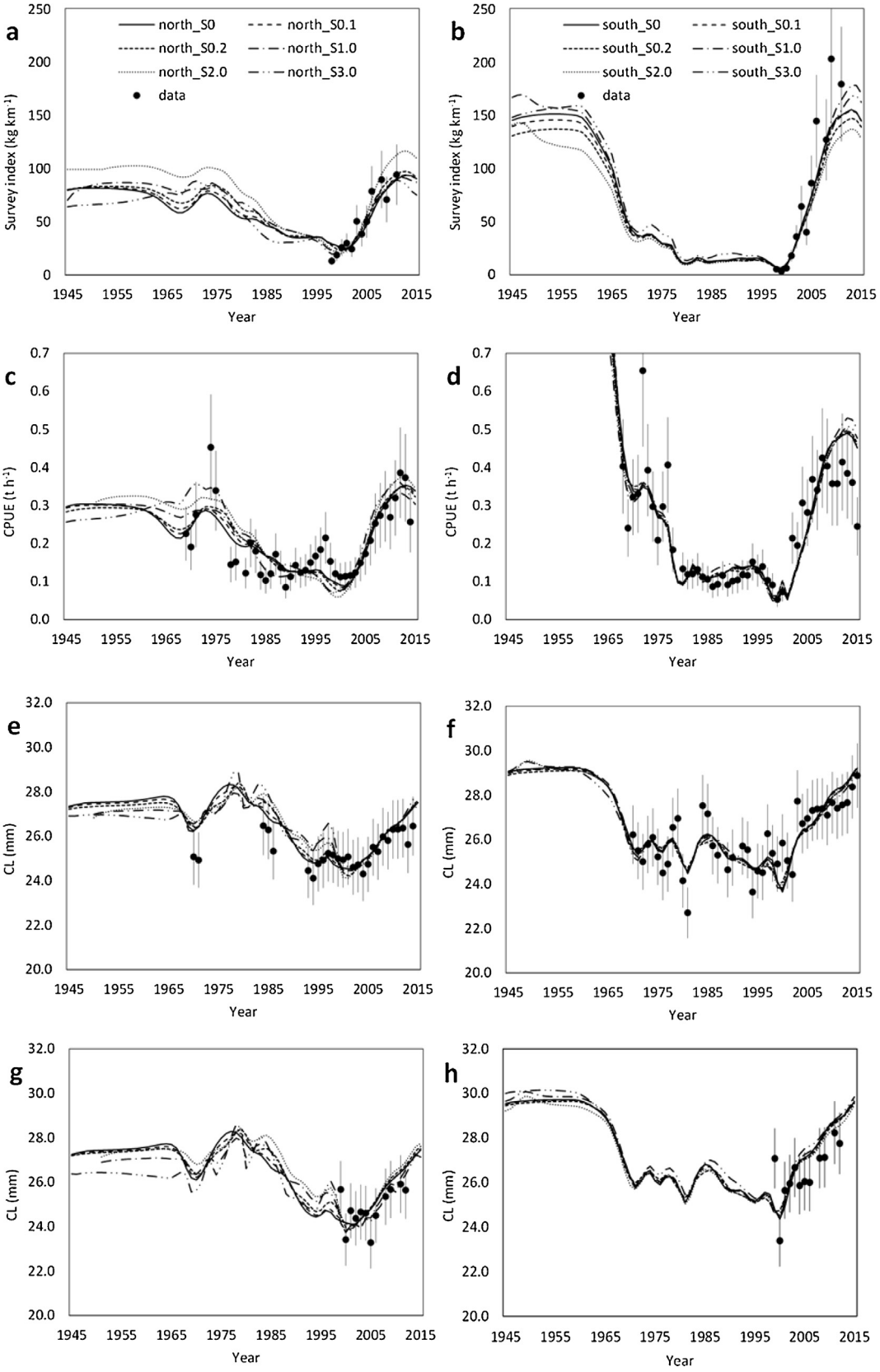

Fig. 4. Fit of the model to nylon shrimp information. Dots represent the information and lines the expected values (model) related to the different hypothesis. The lengths compositions in this figure are represented by the mean carapace length (*e* and *f* for catches, *g* and *h* for surveys). Right and left panels correspond to north and south zones, respectively. Vertical lines represent 95% confidence interval.

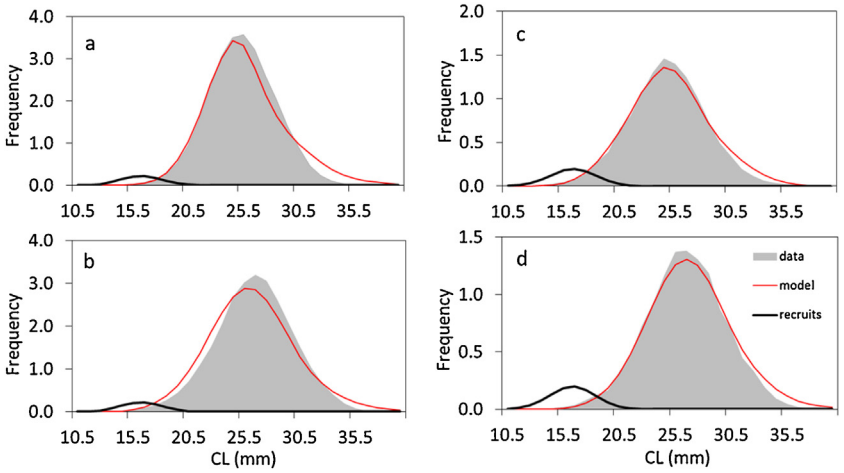

Fig. 5. Summary of model fit (S0) to the length compositions of nylon shrimp for all years combined (marginal compositions). The shading represents the data and thin lines represent the predicted values by the model. The bold black lines represents the recruitment distribution by size. The left panels show results for the catches and the right panels the results for the trawl surveys. The upper panel corresponds to north zone while the lower one the south zone.

The estimates of selectivity, catchability, and virgin recruitment are robust to the scenarios analyzed. In the south zone, size at 50% of selectivity of the commercial fleet (30.1 mm average CL) is estimated to be 14% higher than in the north zone, whereas the research surveys report a difference of only 6% (Table 3). In this sense, while in the recent years the catches between zones have had similar levels, the fishing mortality at south zone is the larger in each scenario (Fig. 6e, f) and this is to due to selectivity in this zone being focused on larger shrimps (see the estimates of log(μ) in Table 3). The average virgin recruitment (R_0) in the south zone is estimated to be more than twice that of the north (Table 3), partly explaining the different biomass estimates for these two zones (Fig. 6a, b). Considering all the scenarios, the average CL that determines recruitment (L_r) is estimated to be slightly higher in the north zone (near 17.7 mm) than in the south (16.2 mm). In both cases, the estimates of this parameter (*a posteri*) are lower than the *a priori* assumptions (Table 2). The low standard error of L_r (<0.06) (Table 3) suggests that the data contain relevant information with respect to the size range covered in nylon shrimp recruitment. In the same sense, the results also show that, regardless of the zone and scenario, the size composition of the exploitable population of *H. reedi* could be sustained in up to 10 modal groups (or states of average annual molt) (Fig. 3).

As for the hypothesis of spatial connectivity, the value of the parameter that measures the proportion of migrant recruits (π) in the two metapopulation scenarios (in natural scale) is estimated to be 0.28 (S1.0) and 0.37 (S2.0) (Table 3). This means that, under the hypothesis of a metapopulation with a pseudo-sink (S1.0), the average proportion of recruits moving from the south to the north zone (which would explain the increased recruits in this area) is 28%, $CI_{95\%}$ = [21%–39%]. In the case of a metapopulation with a sink zone (i.e., no generation of recruits) in the north, the contribution from the south reaches 37%, $CI_{95\%}$ = [30%–47%]. Nonetheless, and in agreement with the amplitude of the intervals determined by the standard error of these parameters, these measures seems to be not statistically different. In the same sense but in the single-stock hypothesis (S3.0), the spatial allocation coefficient was estimated in 49% and whose $CI_{95\%}$ = [44%–54%] indicates that recruitments would have equal allocation among zones.

3.3. Statistical discrimination

The value of the functions of log-likelihood and its marginal components (log-l), referring only to the fit of the model to the data, indicates that the hypothesis of population independence (S0) fits the data best (Table 3). When including recruits correlated between zones (S0.1 and S0.2), the model fit (Δ *log-l* > 2) is significantly poorer for the same hypothesis, with estimated correlation coefficients of 27% (S0), 53% (S0.1), and 86% (S0.2). Furthermore, and although the metapopulation scenarios (S1.0 and S2.0) have larger *log-l* values, probably due to the smaller number of parameters estimated, the best fit of the abundance index of the surveys is obtained under the hypothesis of a pseudo-sink metapopulation (S1.0). This log-likelihood value (*log-l* = 40.1) is more than two points lower than the rest of the scenarios considered (Table 3). The results also show that goodness fit (negative log likelihood) of the model to length compositions in S2.0 is better than S1.0, this because the model in S2.0 have larger value of R_0 (in log scale, Table 3) and larger annual variation of recruitment, which leads to more flexibility in the model to fit the length comps. Also, the results show that single-stock hypothesis (S3.0) has a poor fit to abundance indexes due to the assumption that a time-invariant spatial distribution applied on a single recruitments series can explain the data in two zones at same time.

Notwithstanding the above and considering the criteria for model selection, the hypothesis of metapopulation defined in scenarios S1.0 and S2.0 is the most likely with regard to the hypothesis of population independence (S0), since the values of the AIC and BIC are both significantly lower. The result is expressed in terms of a balance between the number of parameters in each model (303 vs. 233), the number of observations (2406 recorded), and the goodness of fit of the model to the data (log likelihood). The AIC values are identical (AIC = 15,477) for both metapopulation cases, whether pseudo-sink (S1.0) or sink (S2.0), but 23 points lower than that of the null hypothesis (two units of independent stock, S0) and 51 point lower than the single-stock scenario (S3.0). In this same context, the difference in the BIC between scenarios is noticeably higher, as reflected in the 617.6 points (on average) below S0 and in favor of the metapopulation hypothesis (S1.0, S2.0). Thus, S2.0 (metapopulation-sink) seems the most likely alternative since it has the lowest score (BIC = 17,324) (Table 3).

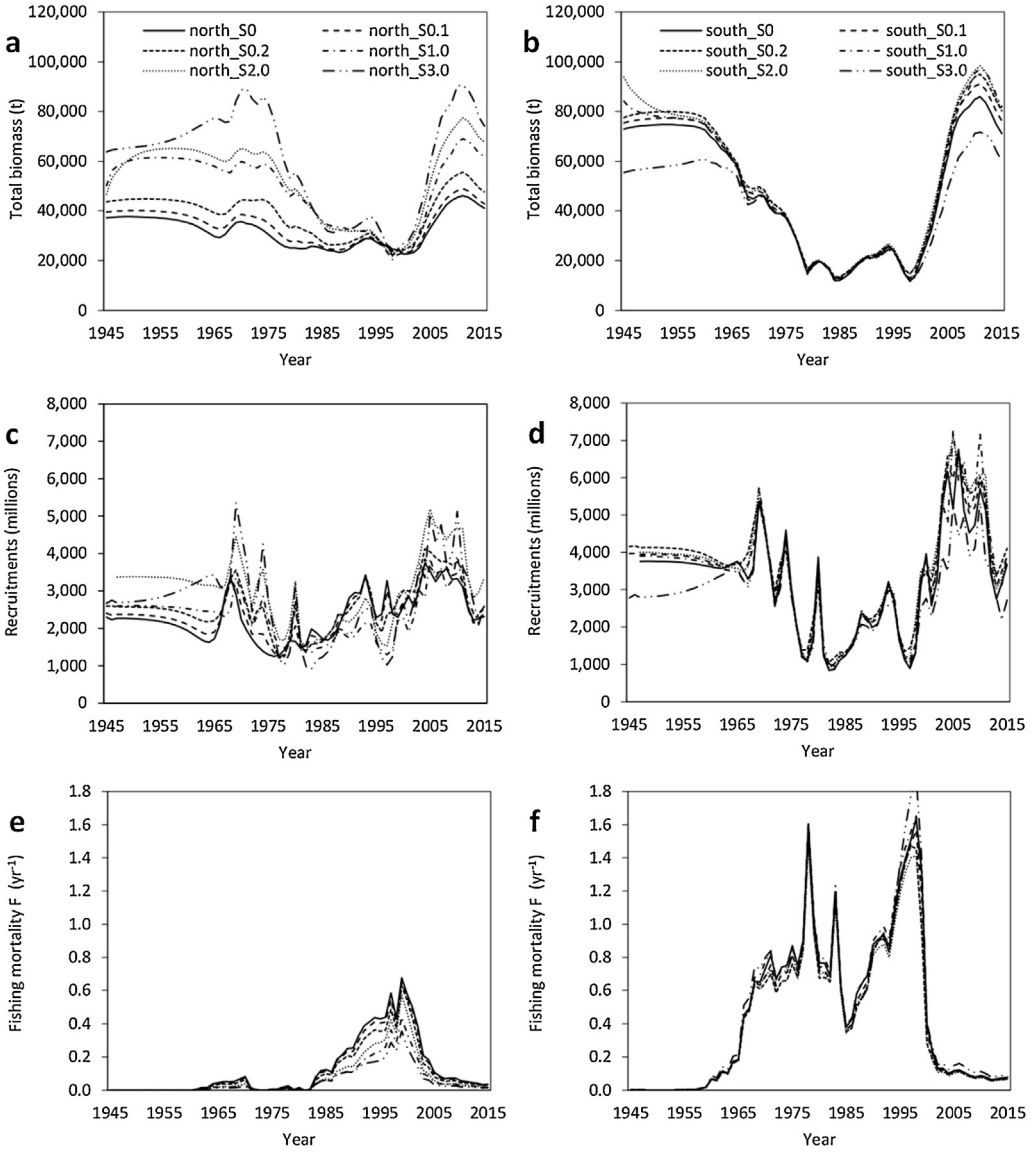

Fig. 6. Total biomass, recruitments and fishing mortality of nylon shrimp by zone and year for each scenario. The right and left panels correspond to north and south zones, respectively.

4. Discussion

The model-based analysis of the data from the commercial fishery and research surveys for *H. reedi* caught off central Chile reveals that, in general, the historical record can be explained by alternative hypotheses as to population structure and spatial connectivity between zones, with the metapopulation hypothesis being the most likely in statistical terms. The model used allows us to investigate the spatial distribution of recruits, obtain more details about the population structure, and learn about the biological processes based on length regardless of the age structure (Punt et al., 2013). In general, the model performs well for all of the scenarios, although the fit of the compositions of lengths improves when considering, for example, changes in functional types and/or temporal variations in selectivity (Lee et al., 2014; Wang et al., 2014) at the expense of a greater number of parameters. Nonetheless, in this work, we favor the use of a model with the greatest possible parsimony and the best goodness of fit to the data.

Our analysis shows that the subpopulations to the north and south of 32°S experience important variation caused by pulses of recruits, with the south acting as a source population. Although the abstraction of a model generates results that can only be considered in a relative or referential way, it gives an idea of the probable theoretical contribution of the larvae that could be drifting northward, estimating this to be, on average, between 28 and 37%, depending on the type of metapopulation. For the hypothesis of population independence (S0), the likely synchrony of recruitment between zones is rejected given the lower goodness of fit of the model under the scenarios of forced correlations of recruitment (S0, S0.1, and S0.2). In this sense, while we cannot rule out that large scale environmental variation could be equally responsible for temporal synchrony recruitment spatially. The metapopulation hypothesis is further supported by local oceanographic characteristics, where the orientation of advective flow would influence larval transport and hence connectivity between both zones. Likewise, environmental changes probably would determine annual variation in the migrant

proportions that in this work were assumed to be time-invariant, being necessary to develop further empirical researches to respond this scientific interrogant.

Although the hypothesis of an *H. reedi* metapopulation proposed by Canales et al. (2016b) requires more empirical evidence, it is based on observations that coincide with proposals made by Orensanz et al. (2006) and Defeo and Cansado (2015) as to the type of characteristics that can be expected in populations with spatial connectivity patterns. For nylon shrimp, the gradual expansion of the population towards the north from 1995 to 2005 as a result of greater recruitment is of particular interest and is reflected in the increased presence of juveniles in this zone, as a response the region's predominantly northward surface flow determined by the Humboldt Current (Fuenzalida et al., 2008), and the association of zones with greater abundances located south of 32°S (source population) with areas of improved environmental conditions in terms of chlorophyll-a and dissolved organic material (Canales et al., 2016b). Lipcius et al. (1997) reports the importance of source populations in the process of population expansion of *Panulirus argus* from the perspective of a metapopulation, and Caddy and Defeo (2003) use this concept to explain the increased biomass of *Homarus americanus* and its expansion to previously less abundant areas.

Considering the region south of 32°S to be a reproductive refuge or a source population of larvae and post-larvae that partially or totally supplies the area north of 32°S (sink or pseudo-sink population) generates important challenges for the future management of the fishery. Priority should be given to management mechanisms such as increased caution in exploitation and continuous monitoring of the reproductive refuge (e.g., Campbell, 1986; McGarvey et al., 1992; McGarvey and Willison, 1995; Kjelland et al., 2015). Proposals such as those of Gutiérrez and Defeo (2003), for example, regarding the rotation and closure of areas, should be considered. Yakubu and Fogarty (2006) demonstrate, theoretically and mathematically, that the conservative management of larval source populations can contribute to the resilience of exploited species. Other extensions of this idea can be found in Kough et al. (2013), who explored the relevance of considering larval drift when managing resources of economic importance such as the Caribbean spiny lobster (*Panulirus argus*). Likewise, the works of Goethel et al. (2011) and Guan et al. (2013) explore how considering the spatial structure in stock assessment and management impacts a population and fishery. Finally, these findings should be considered to extend the research on other demersal crustaceans of commercial relevance, such as the red squat lobster (*Pleuroncodes monodon*) and yellow squat lobster (*Cervimunida johni*) among others, those who inhabit similar bottom conditions than nylon shrimp.

5. Conclusion

This research generates statistical evidence supporting the proposal by Canales et al. (2016b) that the area south of 32°S could be considered a source population or reproductive refuge. The biological and fishery data available for nylon shrimp since 1945 are evaluated in terms of two population structure hypotheses. Of these, the metapopulation hypothesis is better supported statistically. Although further empirical evidence is necessary to sustain the proposal of Canales et al. (2016b), the ecological grounds given in the literature along with our results and observations suggest that the hypothesis of a reproductive refuge area for *H. reedi* south of 32°S should not be discarded. Therefore, fisheries management should focus on this area in order to ensure the generation of recruits across the resource's distribution, thereby endowing the fishery with resilience and sustainability

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Appendix A.

See Table A1.

Table A1
Parameter of the size-based model applied to nylon shrimp data exploited off Chile. The letter F indicates if the parameter was fixed.

Parameter	Nomenclature	Parameters number(1)	Initial values	Prior (in log scale)
Selectivity (fleet and survey by zone) (mm)	μ	4	25.0	U[−∞,+∞]
	θ_1	4	4.0	U[−∞,+∞]
	θ_2	4	1000 (F)	
Fishing mortality by year (y) and zone (z)	$F_{cr,y,z}$	142	0.2	U[−∞,+∞]
Virgin recruitment by zone	$R_{0,z}$	2	5000	U[−∞,+∞]
Recruitment annual deviates by zone (z)	$\varepsilon_{y,z}$	142	0.0	U[−∞,+∞]
Steepness	h	1	0.75 (F)	
Migrant proportion	π	1	0.0	U[−∞,0]
CPUE catchability by zone (z)	qf_z	2	0.01	U[−∞,+∞]
Survey catchability by zone (z)	qs_z	2	0.01	U[−∞,+∞]
Recruitment length distribution by zone(2)	L_0(3)	2	[20.1; 18.2]	$N(\log L_0, 0.1)$
	S_r(4)	2	[2.00; 1.80] (F)	
Transition matrix (growth) by zone(2)	l_{oo}	2	[41.1; 42.3] (F)	
	K	2	[0.14; 0.15] (F)	
	ω	2	0.5	U[−∞,+∞]
Natural mortality	M	1	0.35 (F)	

(1) based on S0; (2) [north; south]; (3) Mean carapace size of the first modal-group; (4) standard error of the first modal-group.

Appendix B. Observation model

B.1 Predicted catches in number at-size (l), by year (y) and zone(z)

$$\hat{c}^{f}_{l,y,z} = N_{l,y,z}F_{l,y,z}(1 - e^{-F_{l,y,z}-M})/(F_{l,y,z} + M) \quad (8)$$

N is the population abundance at the start of the year, F is fishing mortality rate and M is natural mortality rate. The fishing mortality at-size, by year (y) and zone (z) is modelled as

$$F_{l,y,z} = F_{cr,y,z}O^{f}_{l,z} \quad (9)$$

F_{cr} is the fully recruited fishing mortality and $O^{f}_{l,z}$ the selectivity of the fleet (f) by size and zone.

B.2 The selectivity at-size, by year (y), zone (z) and source type (fleet (f) or survey(s)) is formulated as double normal function

$$O^{f,s}_{l,z} = \begin{cases} \exp\left(-0.5\dfrac{\left(l-\mu^{f,s}_{z}\right)^{2}}{\theta^{f,s}_{1,z}}\right) & l \le \mu^{f,s}_{z} \\ \exp\left(-0.5\dfrac{\left(l-\mu^{f,s}_{z}\right)^{2}}{\theta^{f,s}_{2,z}}\right) & l > \mu^{f,s}_{z} \end{cases} \quad (10)$$

μ is the fully recruited size and θ is the dispersion parameter for each normal distribution. $\theta^{f,s}_{2,z} = 1000$ (fixed to produce a logistic model).

B.3 Available abundance for surveys in number at-size, by year (y) and zone (z)

$$\hat{c}^{s}_{l,y,z} = N_{l,y,z}O^{s}_{l,z}e^{-0.5(F_{l,t,z}+M)} \quad (11)$$

B.4 Predicted catches of the fleet in weight by year (y) and zone (z)

$$\hat{Y}_{y,z} = \sum_{l}\hat{c}^{f}_{l,y,z}w_{l,z} \quad (12)$$

$w_{l,z}$ is the expected weight at-size by zone.

B.5 Predicted proportions at-size, by year (y), zone (z) and source (fleet (f) or survey(s))

$$\hat{p}^{f,s}_{l,y,z} = \hat{c}^{f,s}_{l,y,z}/\sum_{l}\hat{c}^{f,s}_{l,y,z} \quad (13)$$

B.6 Abundance indices (CPUE or density of shrimp in surveys) by year (y), zone(z) and source (fleet (f) or survey(s))

$$\hat{I}^{f,s}_{y,z} = q^{f,s}_{z}\sum_{l}N_{l,y,z}e^{-0.5(F_{l,t,z}+M)}w_{l,z}O^{f,s}_{l,z} \quad (14)$$

$q^{f,s}_{z}$ is catchability coefficient by zone and source (fleet (f) or survey(s)).

B.7 Spawning biomass by zone

$$SSB_{y,z} = \sum_{l}N_{l,y,z}e^{-0.67(F_{l,y,z}+M)}w_{l,z}m_{l,z} \quad (15)$$

$m_{l,z}$ is maturity at size. 0.67 indicates the fraction of the year when the spawning occurs

B.8 Transition matrix

The individual growth is driven by a transition matrix T defined by zone as:

$$\mathrm{T_z} = \int_{l(i)}^{l(i+1)} \frac{1}{\sqrt{2\pi\delta_l}}\exp\left(-\frac{[l-(l+\Delta(l))]^2}{{\delta_l}^2}\right)dl \quad (16)$$

where $\Delta(l) = (l_{oo} - l)(1 - e^{-k})$ which reflecst the marginal increment in a year of individuals with size l. The variance of this increment is given by $\delta_l = \omega\Delta(l)$, ω being a scale factor to be estimated, while l_{oo} and k are parameters of Von Bertalanffy growth model.

Appendix C. Error model (negative log-likelihood functions)

C.1 Catch at-size proportions

$$\mathrm{L^{f,s}_p} = -\mathrm{n}\sum_{\mathrm{l}}\sum_{\mathrm{y}}\sum_{\mathrm{z}}\mathrm{p^{f,s}_{l,t,z}}\log(\mathrm{\hat{p}^{f,s}_{l,y,z}}) \quad (17)$$

n = 30.

C.2 Abundance indices and annual catches (y) by zone

$$\mathrm{L^{f,s}_I} = \frac{0.5}{(\sigma^{\mathrm{f,s,y}})^2}\sum_{\mathrm{y}}\sum_{\mathrm{z}}\left(\frac{\log\{\hat{\mathrm{I}}^{\mathrm{f,s}}_{\mathrm{y,z}}\}}{\log\{\mathrm{I}^{\mathrm{f,s}}_{\mathrm{y,z}}\}}\right)^2 \quad (18)$$

$\sigma^{f} = 0.3$, $\sigma^{s} = 0.15$, $\sigma^{y} = 0.05$.

C.3 Penalties & priors:

C.3.1 Annual deviates of stock-recruitment relationship

$$\mathrm{p_1} = \frac{0.5}{{\sigma_\mathrm{R}}^2}\sum_{\mathrm{y}}\sum_{\mathrm{z}}{\varepsilon_{\mathrm{y,z}}}^2 \quad (19)$$

$\sigma_\mathrm{R} = 0.6$

C.3.2 Annual recruitment deviates between zones (cross-correlation)

$$\mathrm{p_2} = \frac{0.5}{{\sigma_\mathrm{x}}^2}\sum_{\mathrm{y}}(\varepsilon_{\mathrm{y,z=n}} - \varepsilon_{\mathrm{y,z=s}})^2 \quad (20)$$

$\sigma_\mathrm{x} = [1.0; 0.5; 0.2]$

C.3.3 Surveys catchability deviates between zones

$$\mathrm{p_3} = \frac{0.5}{{\sigma_\mathrm{q}}^2}\left(\log\left(\mathrm{q^{s}_{z=n}}\right) - \log\left(\mathrm{q^{s}_{z=s}}\right)\right)^2 \quad (21)$$

$\sigma_\mathrm{q} = 0.05$

C.3.4 Size of recruitment deviates by zone

$$p^{z}_{4} = \frac{0.5}{{\sigma_{\mathrm{Lo}}}^2}(\log(\mathrm{Lr_z}) - \log(\mathrm{Lo_z}))^2 \quad (22)$$

$\sigma_{\mathrm{Lo}} = 0.10$

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