

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 were 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* (Wehrmann *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; Encarnação *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 (n)	Effort (km)	Biological samples		Depth (m)		Latitude (°S)		Period	
	Zone 1	Zone 2			(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

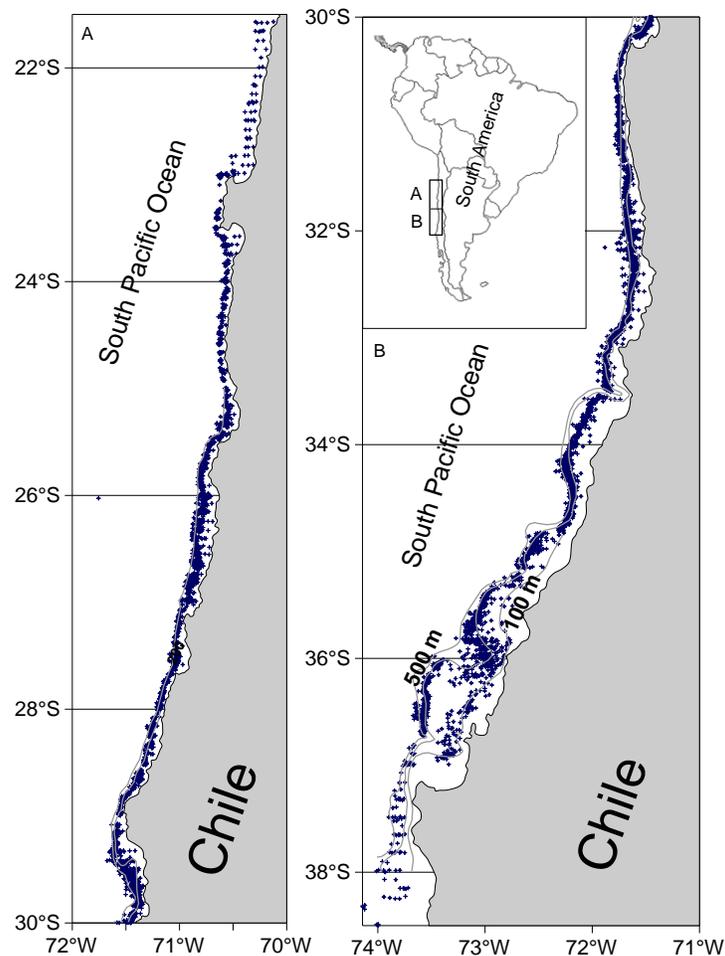


Figure 1. Study area and geographic location of fishing hauls (dots) of *Heterocarpus reedi* in trawl surveys carried out at the central southern zone of Chile between 1996 and 2011.

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, $D = 2R \operatorname{asin} \sqrt{a^2 + b^2 \cos(\operatorname{lat}_1) \cos(\operatorname{lat}_2)}$, where $a = \sin [0.5(\operatorname{lat}_2 - \operatorname{lat}_1)]$ and $b = \sin [0.5(\operatorname{long}_2 - \operatorname{long}_1)]$, 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.

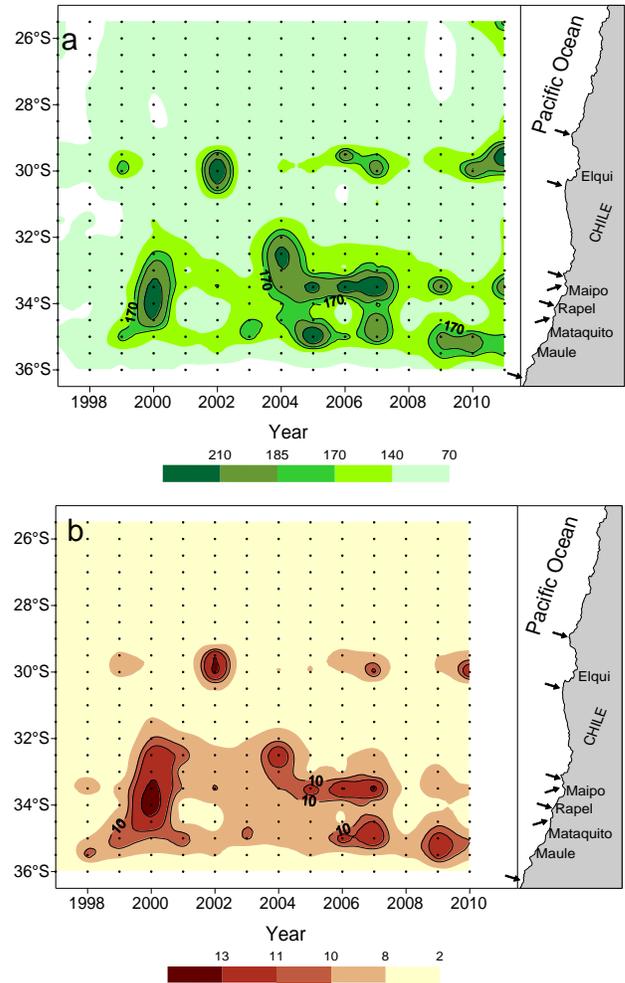


Figure 2. a) Isopleths of absorption coefficient of chlorophyll-*a* concentration (mg m^{-3}), and b) organic matter and dissolved detritus (m^{-1}). Dots represent the information nodes. Over the map the main river names are displayed. The small black arrows correspond to main upwelling zones.

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

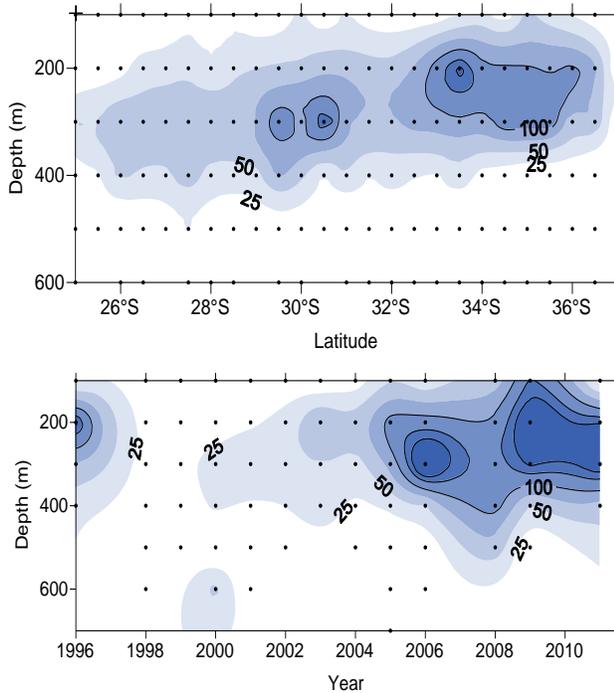


Figure 3. Isopleths of abundance (kg km-linear^{-1}) of *Heterocarpus reedi* estimated in surveys using swept area method by depth, latitude, and year. Dots represent the information nodes.

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-

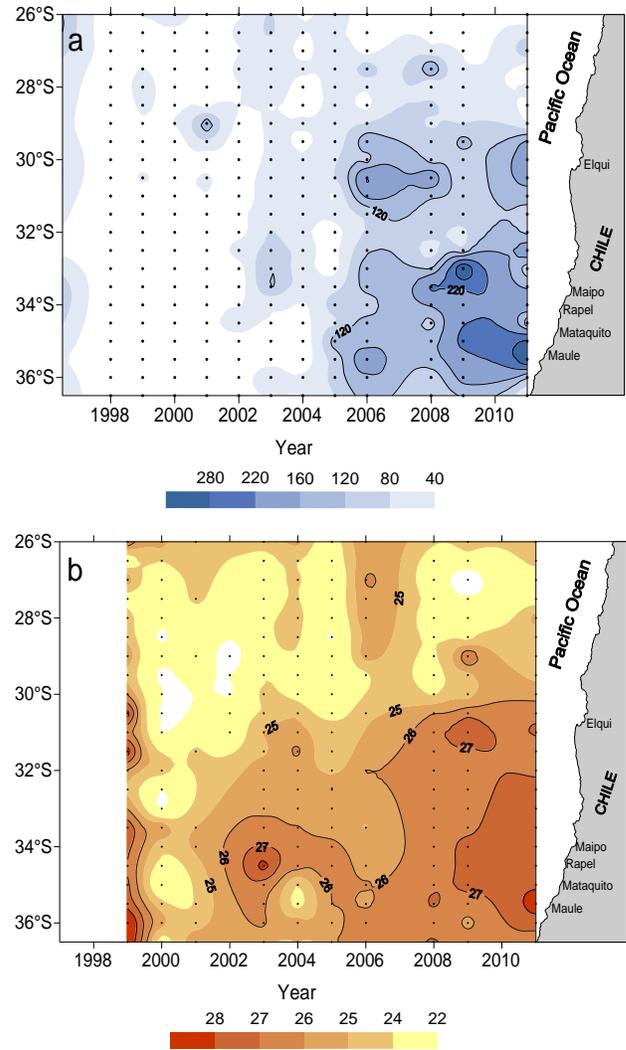


Figure 4. a) Isopleths of abundance (kg km-linear^{-1}), and b) mean carapace length (mm) (both genders) of *Heterocarpus reedi* estimated in surveys using swept area method by latitude and year. Dots represent the information nodes.

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

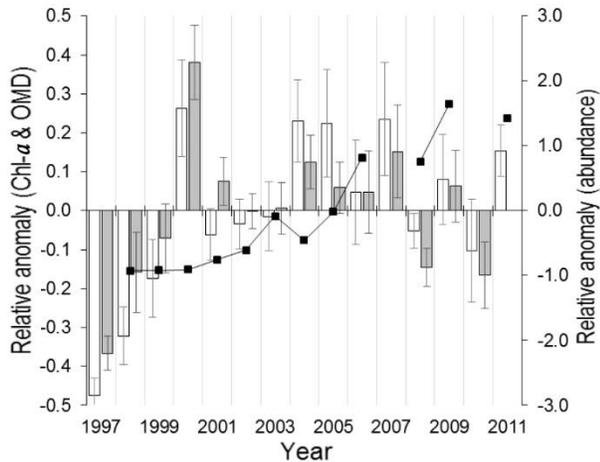


Figure 5. Anomalies of environmental variables and abundance of *Heterocarpus reedi* by year in zone 32°-36°S. The white and gray bars represent Chl-*a* and organic matter and dissolved detritus (OMD), respectively. The black line corresponds to shrimp abundance. Error bars represent two times the standard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

lag (yr)	Autocorrelation coefficients			Correlation coefficients			
	OMD	Chl- <i>a</i>	Abundance	All data		Excluding year 2000	
				OMD	Chl- <i>a</i>	OMD	Chl- <i>a</i>
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

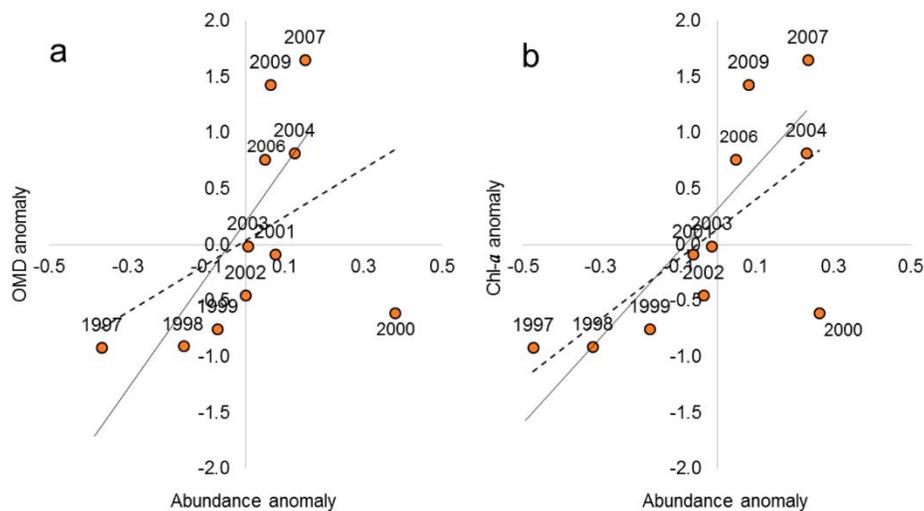


Figure 6. Linear relationship between anomalies of shrimp abundance *Heterocarpus reedi* vs a) organic matter and dissolved detritus (OMD), and b) chlorophyll-*a* (Chl-*a*). Environmental variables are delayed two years relative to the abundance anomalies. The year labels are related to environmental 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 they 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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