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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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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.

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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
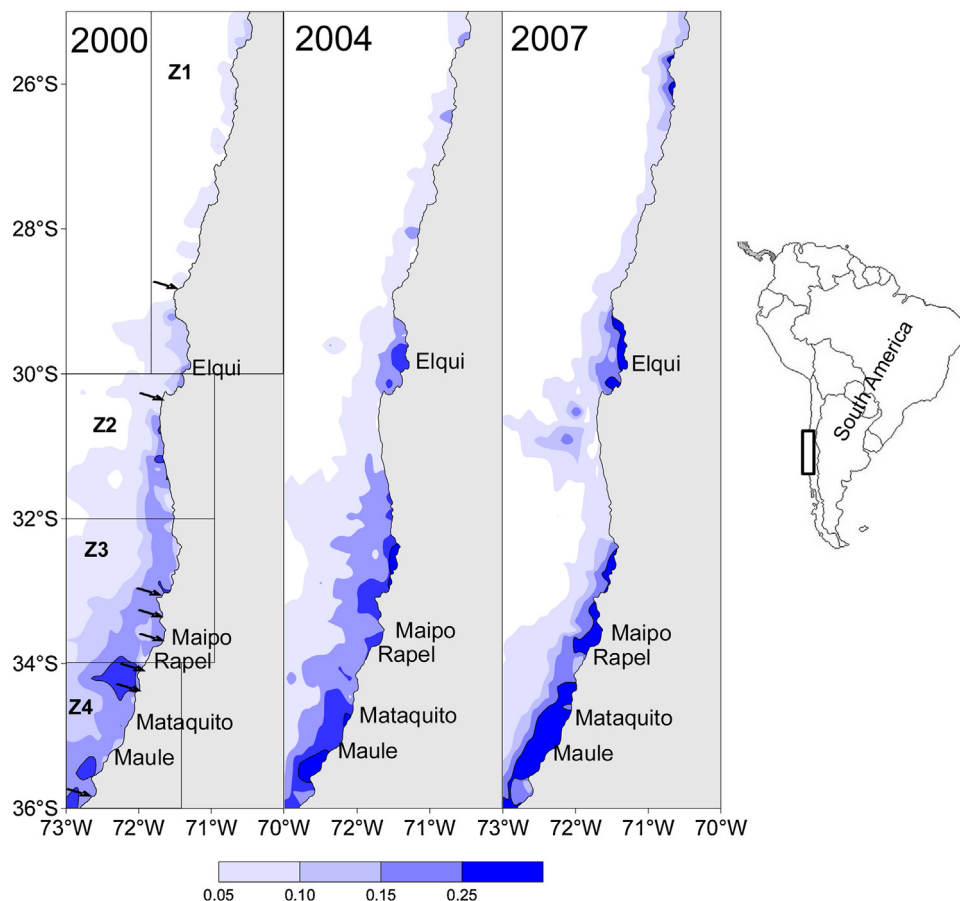

Fig. 1. Study zone and distribution of cumulative organic matter and dissolved detritus between September and December in three years, with the main river names included. The black arrows indicate the main upwelling zones. The rectangles make reference to subzones of analysis.
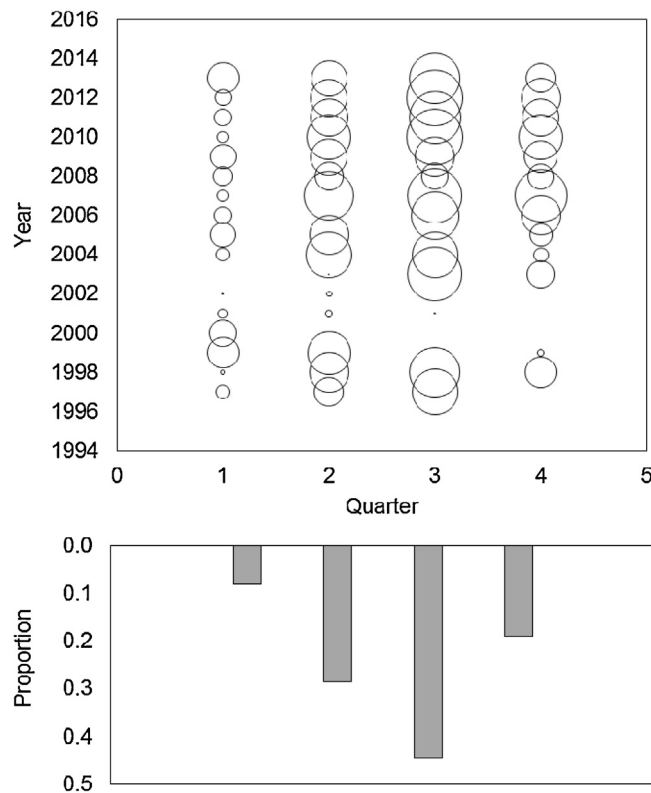
Fig. 2. Proportion (average) of mature females of *Heterocarpus reedi* by year and quarter. The bubble size represents the relative importance within the year, estimated by dividing the number of mature females by the number of total females each quarter and year. The bars represent the expected value 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
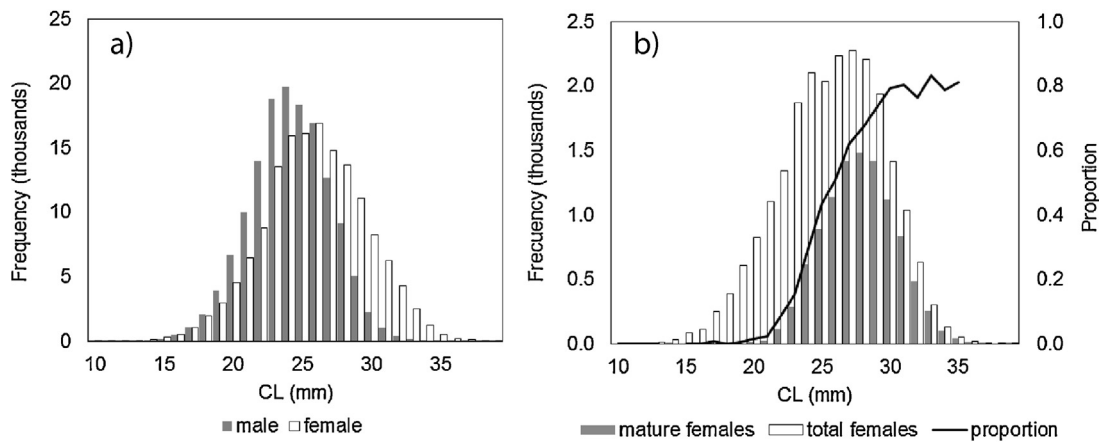
Fig. 3. Histogram of carapace length (CL) of biological samples of *H. reedi*. (a) Males ($n = 142927$) and females ($n = 152000$), (b) mature females ($n = 10249$) and total females ($n = 23005$) measures in the third quarter of each year. The solid line represents the proportion of mature females.

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 ($p < 0.001$, $F = 16.1\text{e}3$) and zone ($p < 0.001$, $F = 7.3\text{e}3$); 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 ($F > 12\text{E}3$, $p < 0.001$, 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 $32\,^\circ$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 $32\,^\circ$S, $CL_{50\%}$ ranged from 24.1 mm (Z2) to 20.9 mm CL (Z1), whereas south of $32\,^\circ$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
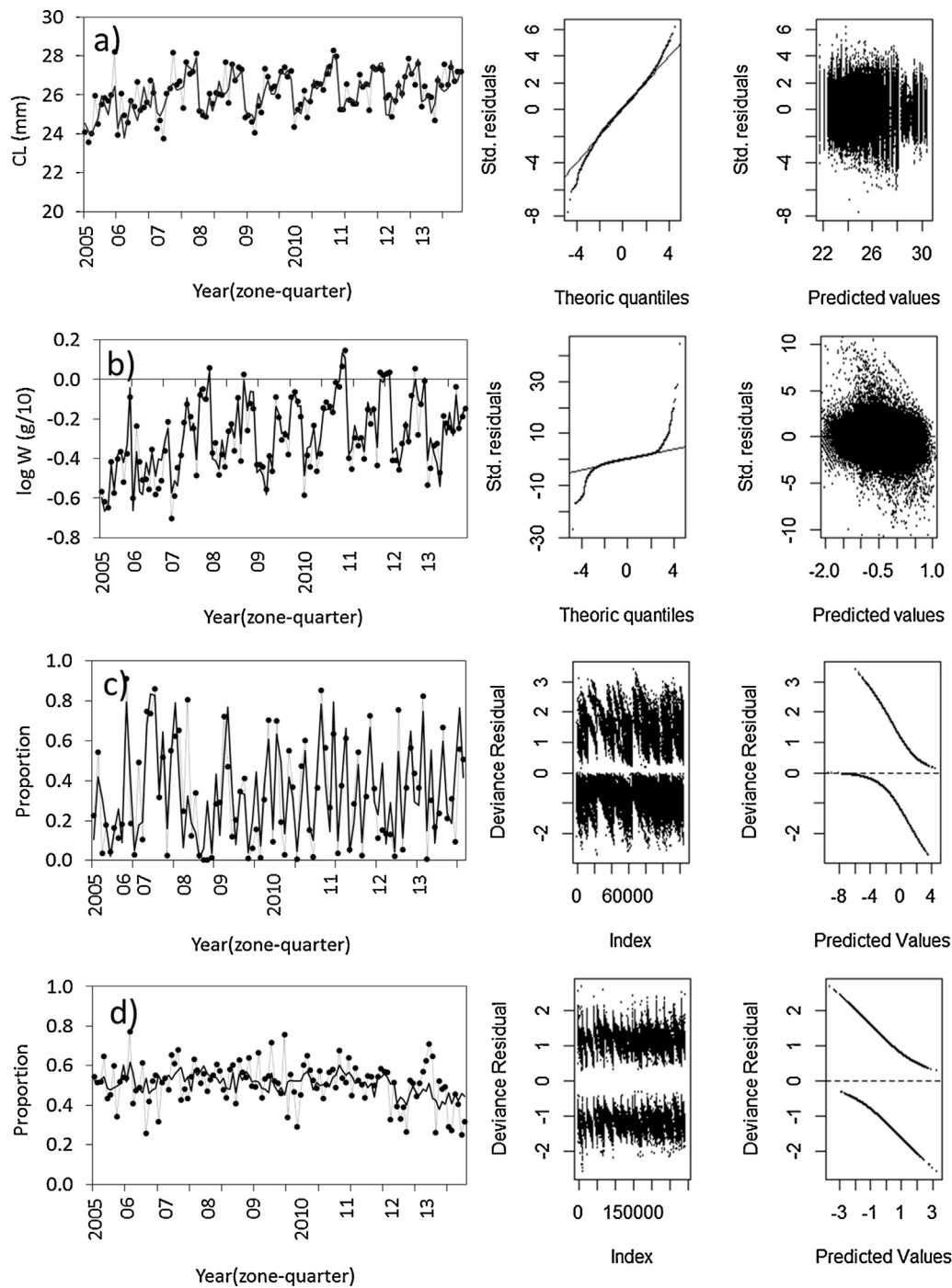
Fig. 4. Model fit diagnostics. Each row corresponds to a different variable: a) carapace length (CL), b) log-weight (W), c) maturity ratio, d) females proportion. Left panels represent the average values by year, zone and quarter (the line is the model fit and the dots are data), where time scale was 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).
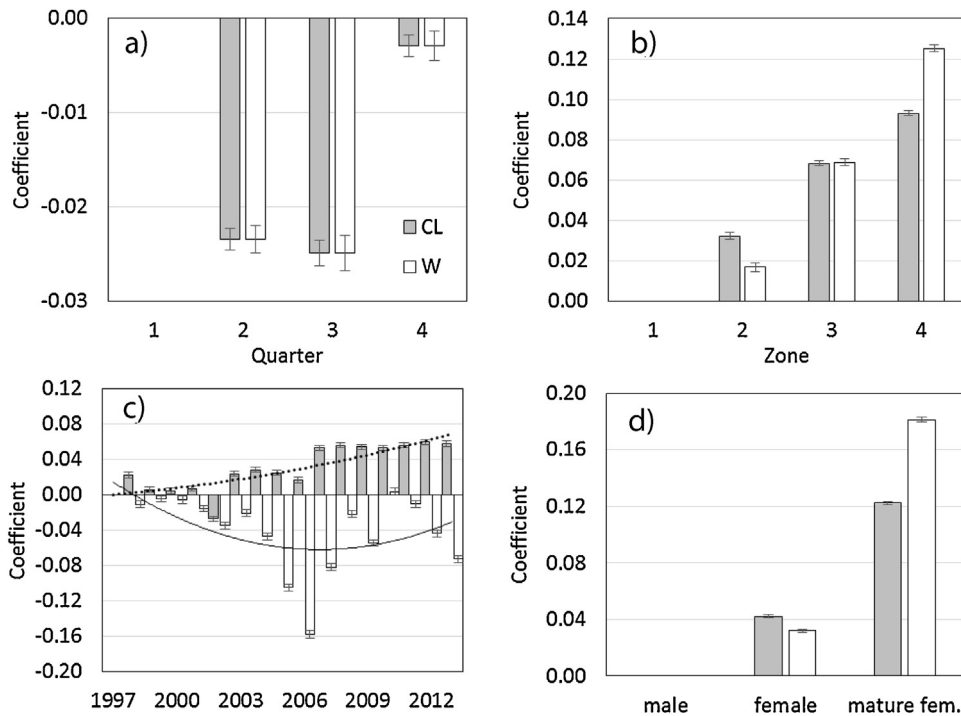
Fig. 5. GLM's coefficients related to carapace length (gray bars) and individual weight (white bars) for *H. reedi*. The effects are: (a) quarter, (b) zone, (c) year, and (d) sex. The trend lines represent the annual factor by year (c).
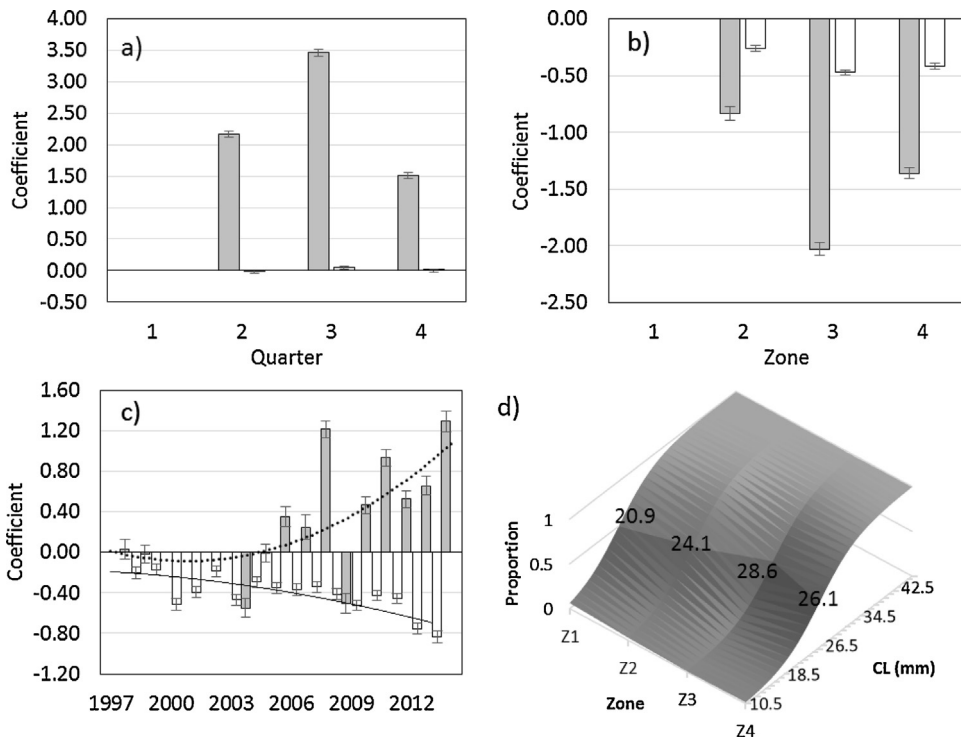

Fig. 6. GLM's coefficients related to maturity (gray bars) and the proportion of females (white bars) for *H. reedi*. The effects are: (a) quarter, (b) zone, and (c) year. The trend line represents the annual factor by year (c). Panel (d) shows the maturity ogive by zone where are included the $CL_{50\%}$ 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.,
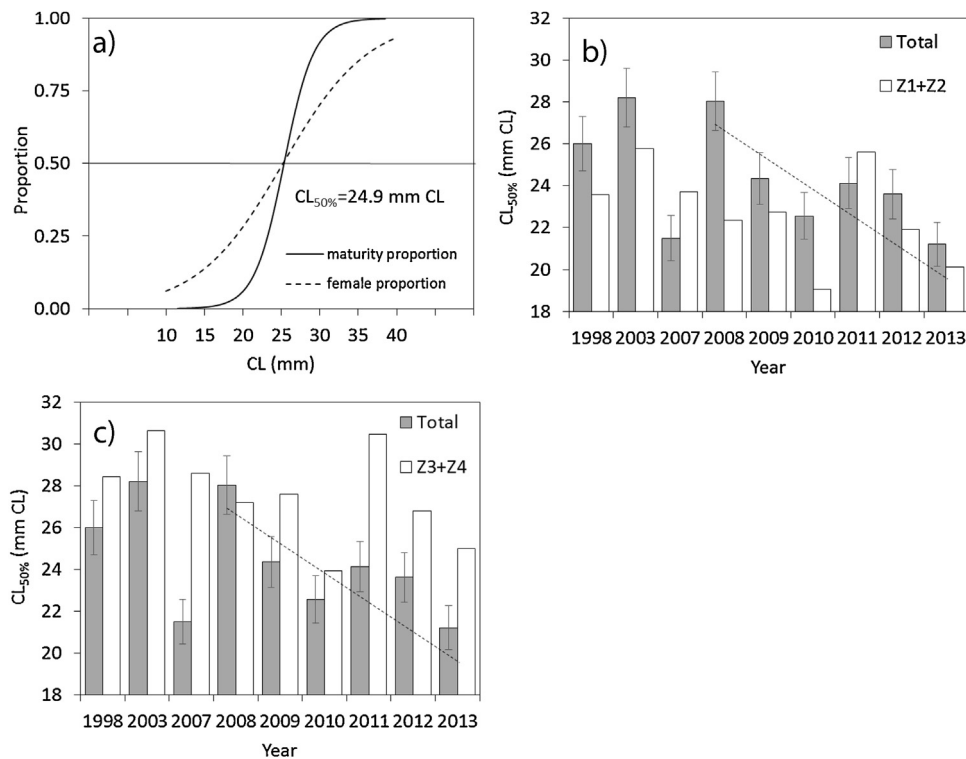
Fig. 7. (a) Proportion of mature females by size of *H. reedi* in the third quarter, for all years and combined zones, plus the proportion of females by size. In panels b) and c), comparative annual changes in maturity size (CL50%) by zones: total vs Z1+Z2 combined (b), total vs Z3+Z4 combined (c). The 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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