



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)**

Cristian M. Canales

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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.

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## 1. Introduction

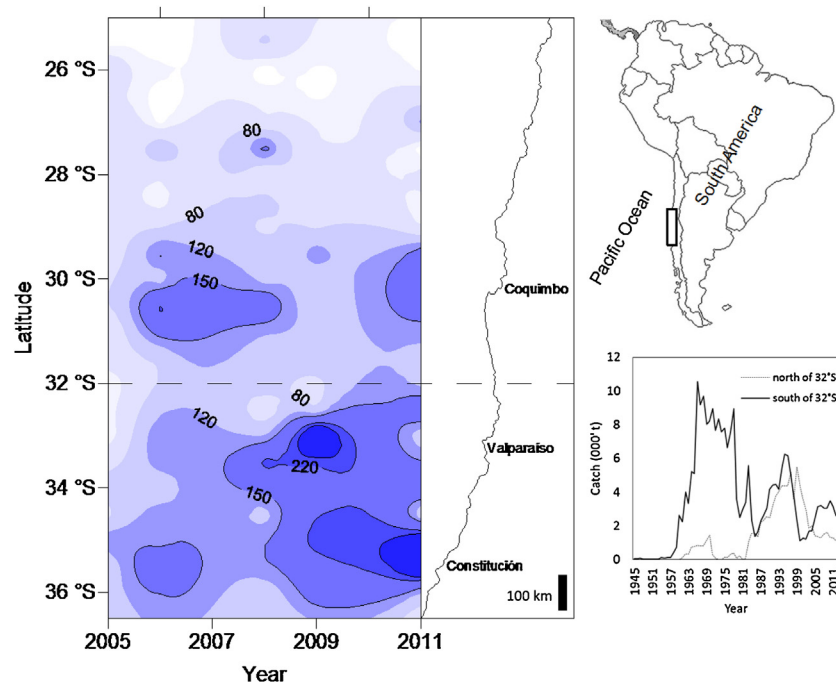
The spatial attributes of populations are not often explicitly considered in the classical approach to stock assessment used for marine invertebrates. Instead, the discussion focuses on the size of the spatial scales of analysis, presuming that the principal biological processes (e.g., spawning and larval 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 ( $\text{kg km}^{-1}$ ) estimated from scientific survey data (source: Canales et al. (2016a,b)). The horizontal dashed line ( $32^{\circ}\text{S}$ ) represents the hypothetical spatial separation of the population.

and one south of  $32^{\circ}\text{S}$ . 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  $32^{\circ}10'\text{S}$ . 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  $32^{\circ}\text{S}$  (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 ( $\text{kg km}^{-1}$ ) 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 <sup>a</sup>		
$l_{\infty}$ (mm)	41.1	42.3
$k$ (yrs <sup>-1</sup> )	0.14	0.15
$L_0$ (mm) <sup>b</sup>	20.1	18.2
$Sr^c$	2.0	1.8

<sup>a</sup> Estimated outside the model.  
<sup>b</sup> Mean carapace size of the first modal-group.  
<sup>c</sup> 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:

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

$$R_{y,z} = r_{y,z} \varphi_z \tag{2}$$

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

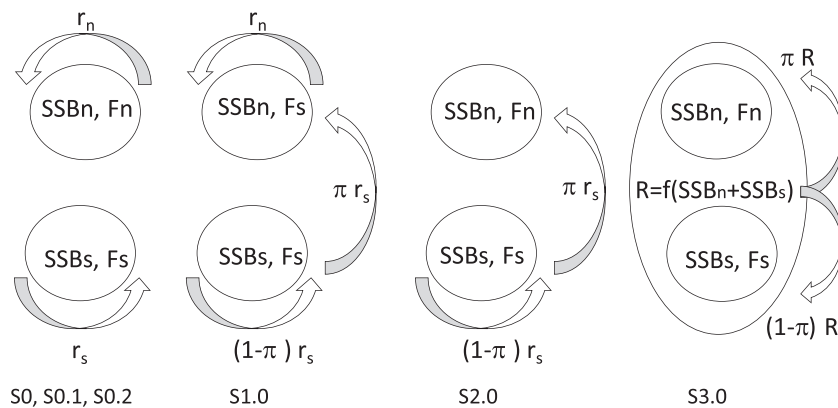
$$0 \leq \pi \leq 1 \tag{4}$$

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

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, 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 ( $\varphi_z$ ) 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  $\pi$ , 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 number 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,  $\tau$  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  $\alpha$  and  $\beta$  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-indices for ‘north’ and ‘south’, respectively,  $r$  is recruitment,  $F$  is the zone-specific fishing mortality and  $\pi$  is the proportion of south recruitment that migrated to the north (S0, S0.1, 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.  $\sigma_x$  represents deviates the standard error (log scale) of recruitments between zones ( $z$ ),  $\pi$  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	$\sigma_x$	$\pi$	$R_{0,z=n}$	$R_{0,z=s}$	$R_0$	$\varepsilon_{y,z=n}$	$\varepsilon_{y,z=s}$	$\varepsilon_y$	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

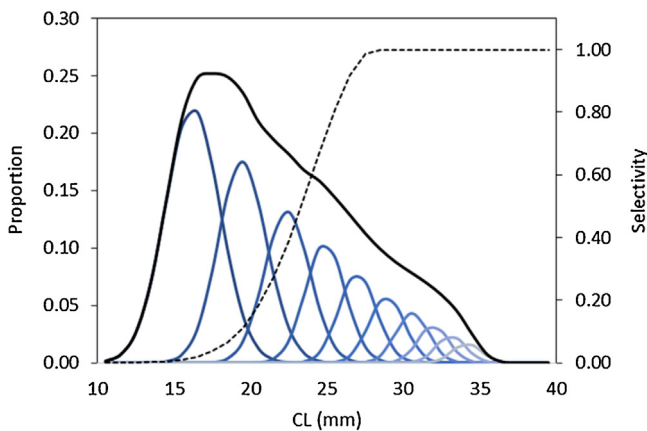
(3) allow us to evaluate different levels of correlation for recruitment between zones, with values of  $cv$  equal to 1.0, 0.5, and 0.2, given low, medium, and high cross-correlation scenarios (Appendix C, C.3.2)

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 priori* 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 theoretical 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 ( $\pi$ ) 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.



**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.

**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.

Parameter	Source	name	stock	Hypothesis (scenario)					
				S0	S0.1	S0.2	S1.0	S2.0	S3.0
Selectivity	fleet	log ( $\mu$ )	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 ( $\theta_1$ )		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 ( $\mu$ )	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)
	survey	log ( $\theta_1$ )		1.47 (0.04)	1.47 (0.04)	1.48 (0.04)	1.47 (0.04)	1.47 (0.04)	1.50 (0.05)
		log ( $\mu$ )	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 ( $\theta_1$ )		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 ( $\mu$ )	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)
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 Catchability	fleet	log ( $\pi$ )		–	–	–	–1.24 (0.16)	–0.97 (0.11)	–0.71 (0.05)
		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)
	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 ( $\omega$ )	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	<b>15,476.6</b>	15,527.6
	BIC <sup>a</sup>			17,912.4	17,930.8	17,982.2	17,332.9	<b>17,324.2</b>	17,367.2

<sup>a</sup> 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

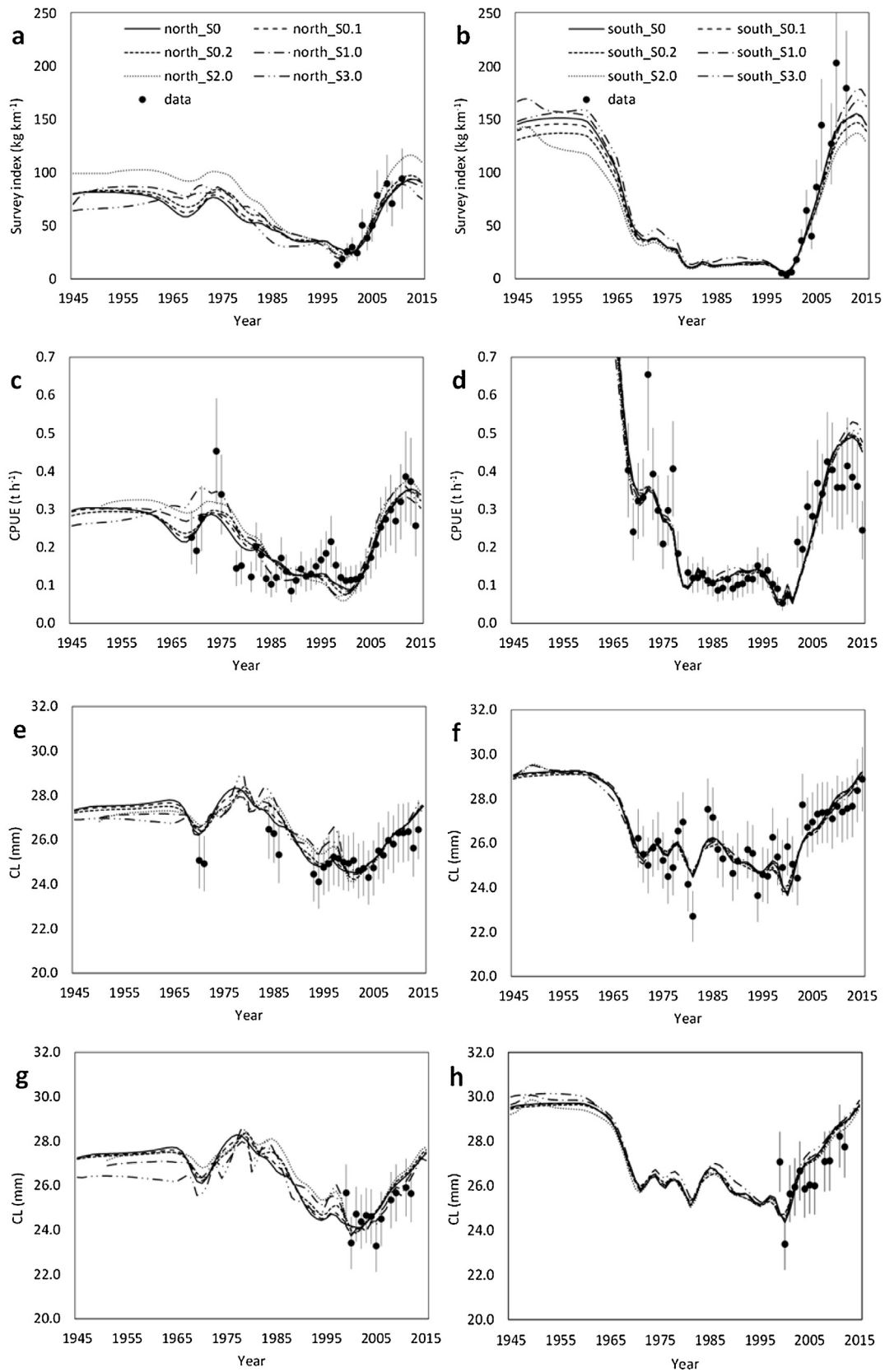
#### 3.1. Overall model fit

In all considered cases the model converges on a feasible solution with maximum gradient values that are lower than  $2.58 \times 10^{-4}$  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,

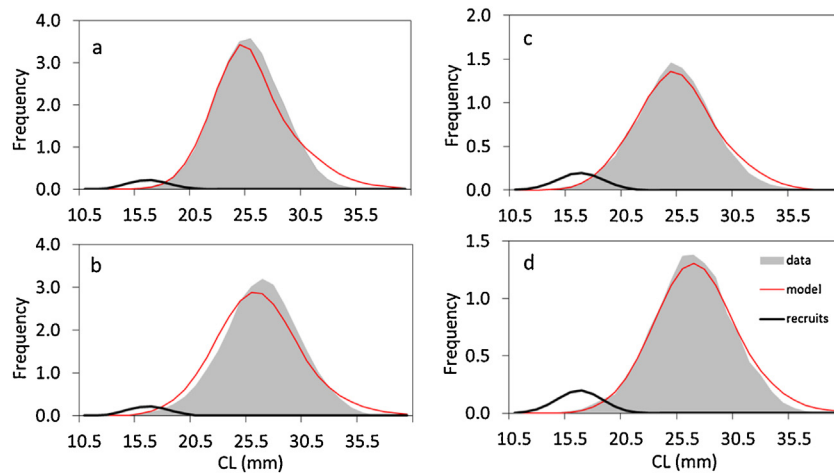
size compositions), particularly for the growing trend of the indicators beginning in 2000, is also worthy of note. Similarly and as an example, the fit of the length compositions under the hypothesis of independent populations (S0) is notable, first, for the slight tendency of the model to over-estimate 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 due to selectivity in this zone being focused on larger shrimps (see the estimates of  $\log(\mu)$  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 posteriori*) 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).

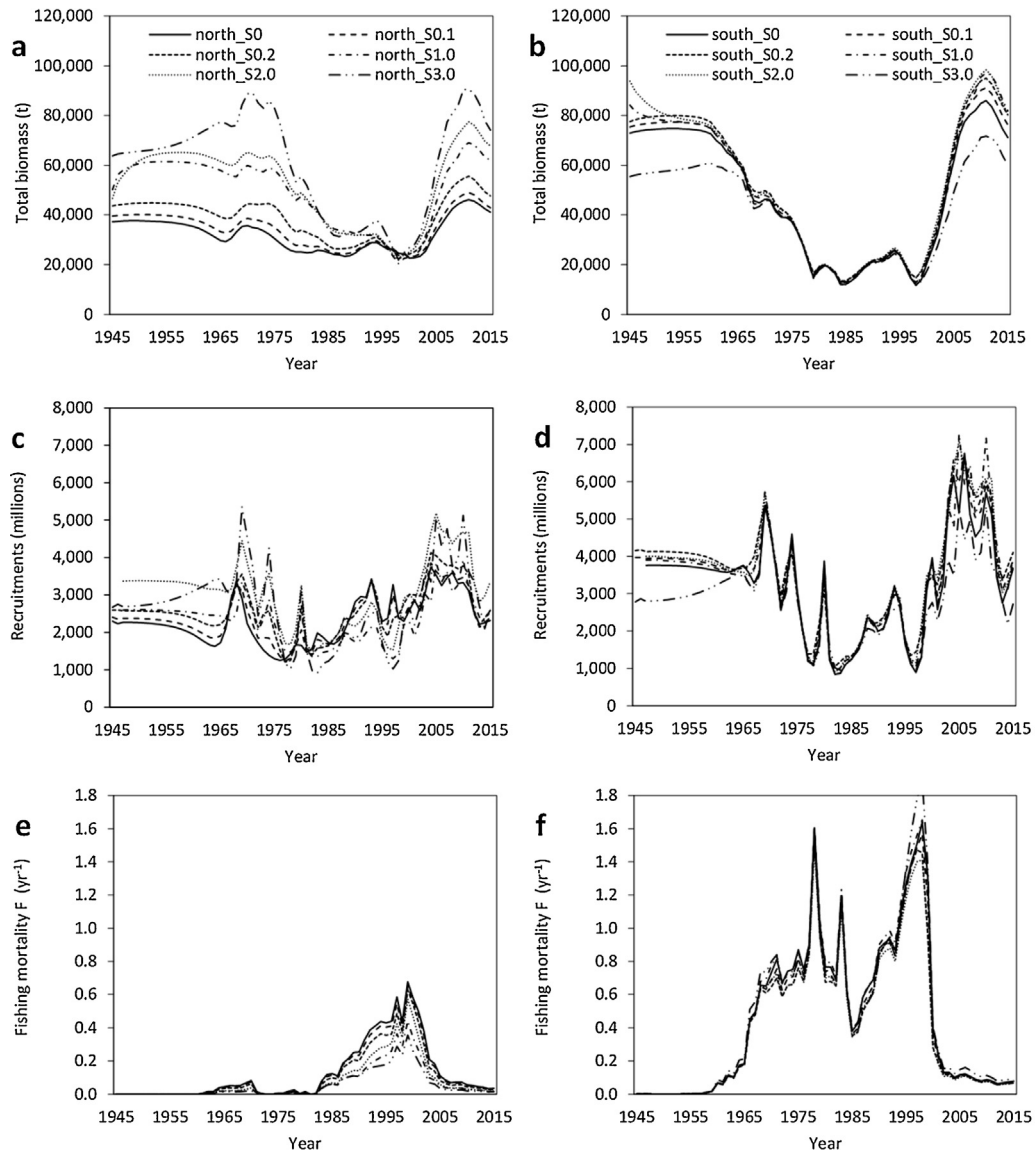
As for the hypothesis of spatial connectivity, the value of the parameter that measures the proportion of migrant recruits ( $\pi$ ) in the two metapopulation scenarios (in natural scale) is estimated to be 0.28 (S1.0) and 0.37 (S2.0) (Table 3). This means that, under the hypothesis of a metapopulation 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 ( $\Delta \log-l > 2$ ) 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  $\log-l$  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 <sup>(1)</sup>	Initial values	Prior (in log scale)
Selectivity (fleet and survey by zone) (mm)	$\mu$	4	25.0	U[−∞,+∞]
	$\theta_1$	4	4.0	U[−∞,+∞]
	$\theta_2$	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	$\pi$	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 <sup>(2)</sup>	$L_0^{(3)}$	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 <sup>(2)</sup>	$l_{oo}$	2	[41.1; 42.3] (F)	
	$K$	2	[0.14; 0.15] (F)	
	$\omega$	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)**

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

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

$$F_{l,y,z} = F_{cr,y,z} O_{l,z}^f \tag{9}$$

F<sub>cr</sub> is the fully recruited fishing mortality and O<sub>l,z</sub><sup>f</sup> 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**

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

μ is the fully recruited size and θ is the dispersion parameter for each normal distribution. θ<sub>2,z</sub><sup>f,s</sup> = 1000 (fixed to produce a logistic model).

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

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

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

$$\hat{Y}_{y,z} = \sum_l \hat{c}_{l,y,z}^f w_{l,z} \tag{12}$$

w<sub>l,z</sub> 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))**

$$\hat{p}_{l,y,z}^{f,s} = \hat{c}_{l,y,z}^{f,s} / \sum_l \hat{c}_{l,y,z}^{f,s} \tag{13}$$

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

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

q<sub>z</sub><sup>f,s</sup> 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<sub>l,z</sub> 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:

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

where Δ(l) = (l<sub>00</sub> - l)(1 - e<sup>-k</sup>) which reflects the marginal increment in a year of individuals with size l. The variance of this increment is given by δ<sub>l</sub> = ωΔ(l), ω being a scale factor to be estimated, while l<sub>00</sub> and k are parameters of Von Bertalanffy growth model.

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

**C.1 Catch at-size proportions**

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

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<sup>f</sup> = 0.3, σ<sup>s</sup> = 0.15, σ<sup>y</sup> = 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<sub>R</sub> = 0.6

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

$$p_2 = \frac{0.5}{\sigma_x^2} \sum_y (\varepsilon_{y,z=n} - \varepsilon_{y,z=s})^2 \tag{20}$$

σ<sub>x</sub> = [1.0; 0.5; 0.2]

**C.3.3 Surveys catchability deviates between zones**

$$p_3 = \frac{0.5}{\sigma_q^2} (\log(q_{z=n}^s) - \log(q_{z=s}^s))^2 \tag{21}$$

σ<sub>q</sub> = 0.05

**C.3.4 Size of recruitment deviates by zone**

$$p_4^z = \frac{0.5}{\sigma_{Lo}^2} (\log(Lr_z) - \log(Lo_z))^2 \tag{22}$$

σ<sub>Lo</sub> = 0.10

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