

# Cohorts in space: geostatistical mapping of the age structure of the squat lobster *Pleuroncodes monodon* population off central Chile

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**ABSTRACT:** Animal populations are spatial objects in the sense that their structure and functioning depend on the spatial context they inhabit. However, most population dynamics models ignore the spatial context and set populations 'in the air'. This paper is focused on the squat lobster *Pleuroncodes monodon* population inhabiting the narrow continental shelf off central Chile, and encompassing 3 degrees of latitude. We tested the hypothesis that the spatial functioning of this population is driven by annual cohorts that enter the population through a nursery ground, and then radiate away from the nursery to the north and south by individual dispersal, thus creating a spatial pattern where age and distance from the nursery are correlated. To test the hypothesis we performed an extensive survey from 34 to 37° S along the continental shelf, collecting data on individual mean size by sex and spatial location. The data gathered was analysed using a combination of mixture distribution analysis on size frequency data and geostatistical mapping on size and location data. Isotropic and anisotropic variogram models were fitted to size data for both sexes. Selection of the appropriate models and kriging parameters was done by cross validation. The hypothesis posed was fully corroborated by the data and the analysis, with 6 adult cohorts identified for both sexes radiating away from the nursery ground in waves at an average distance of one fifth the latitudinal range of the population. Geostatistical mapping of size data for juveniles in the nursery ground, collected with a higher resolution in previous years, showed that recruitment can occur as several relatively small patches interspersed through the nursery area or as a large patch in the middle of the nursery. The corroborated model of spatial population functioning explains the history of commercial over-exploitation and recolonisation of this population. It also suggests that this 350 km long population is renewed by recruits from nearby cohorts, both to the south and north of the nursery area, while cohorts farther north can be exporting recruits to prime nursery habitat. These insights into the functioning of this large population could only be gained by a fully spatially explicit analysis.

**KEY WORDS:** Population dynamics · Cohort dispersal · Geostatistical mapping · Spatially explicit · Habitat features · Crustacean biology · Chile

## INTRODUCTION

Animal populations are spatial objects in the sense that their structure and functioning depend on the spatial context they inhabit. This point of view has been emphasised during the last decade (Dunning et al. 1995, Hanski & Simberloff 1997) because it allows a more complete understanding of populations than the

pure temporal analysis. Consequently, current population modelling is increasingly being formulated in a spatially explicit context (Holmes et al. 1994, Dunning et al. 1995), an effort that should be accompanied by sampling and analysing real populations in space. The squat lobster *Pleuroncodes monodon* population, extends from 34 to 37° S (Roa & Tapia 1998), on the continental shelf off central Chile. Back in 1988 this population was reduced to its southern range (36 to 37° S) by intense fishing exploitation, but grew and expanded to the north after 3 yr of fishery closure, from 1989 to 1991 (Roa & Bahamonde 1993). It was later discovered that the southern range of the population

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harbours its nursery ground (Roa et al. 1995), from which 2 branches extend, the small southern and the large northern branches. The functioning of the 2 branches differ (Roa & Tapia 1998), a result that we attributed to differences in habitat physiognomy (Dunning et al. 1995). In our view, cohorts radiate northwards and southwards from the nursery ground in annual waves, a process that is physically constrained by (1) a narrow range of bathymetric distribution for this species in the Chilean continental shelf, and (2) several topographic obstacles—mainly in the southern branch—like canyons and bottom type changes. According to this view, these crustaceans perform a life-long migration away from their nursery area, so that annual cohorts would be stratified in latitude, and located at distances from the nursery ground that are correlated with age. Therefore our central hypothesis was that the population functions in space in the form of waves of recruits entering through the nursery ground and radiating away, to the north and south, over the continental shelf. In this work we report results from an extensive sampling of the complete population done in 1996, identifying cohorts in space by using a combination of size frequency analysis and geostatistical mapping techniques. We conclude that cohorts in this population do radiate away from the nursery ground, during a 1-way lifelong migration. This finding has interesting implications for the understanding of population functioning and its exploitation.

## MATERIALS AND METHODS

**The population and its habitat.** The squat lobster population is distributed along ca 330 km on the continental shelf off central Chile, between Topocalma (34°S) and the Gulf of Arauco (37°S), at depths of 100 to 200 m (Fig. 1). Throughout this range there are 2 major types of benthic habitats: clean muddy bottoms (soft bottoms) and rocky-muddy bottoms (hard bottoms), the latter not being accessible for trawl sampling or fishing due to the presence of abundant interspersed rocks lying on the sediments. These rocks are often heavily excavated and

may vary in diameter from a few centimetres to several meters (authors' pers. obs.). At some points in the latitudinal range, the continental shelf is partially or completely covered by hard bottoms (Fig. 1).

A single nursery ground has been observed in this population, located near its southern end, between Point Achira and Concepcion Bay (Roa et al. 1995), where each year a new cohort enters the adult-benthic population in March-April, after 4 to 5 mo of pelagic-larval life (Gallardo et al. 1994). The location of this nursery ground coincides with the widest part of the continental shelf in central Chile (Fig. 1). Two population branches of different sizes and functioning (Roa & Tapia 1998) extend to the north and south of this

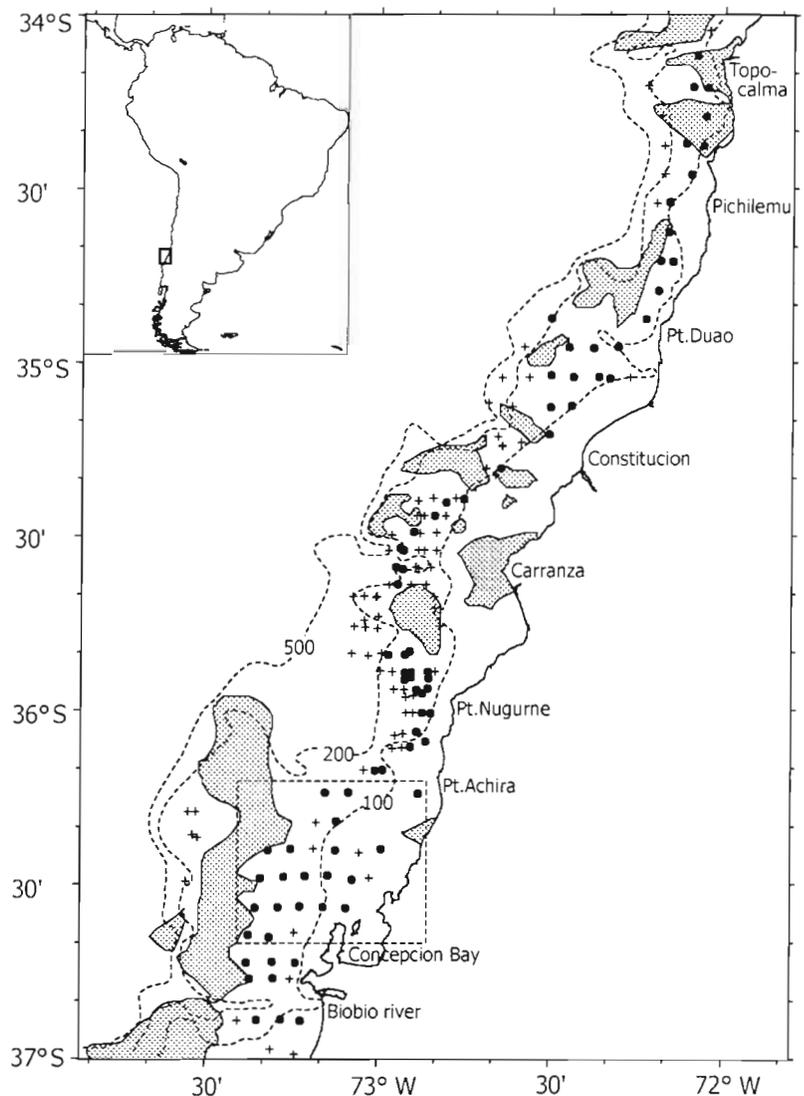


Fig. 1. Sampling scheme of the *Pleuroncodes monodon* trawling survey carried out in 1996, along the soft bottoms of the Chilean continental shelf. Fishing activities were done onboard the RV 'Kay-Kay' (dashed square), and the commercial trawler 'Antares' (remaining stations). (▨) Hard untrawlable bottoms; (+) unsuccessful hauls; (●) hauls with catch

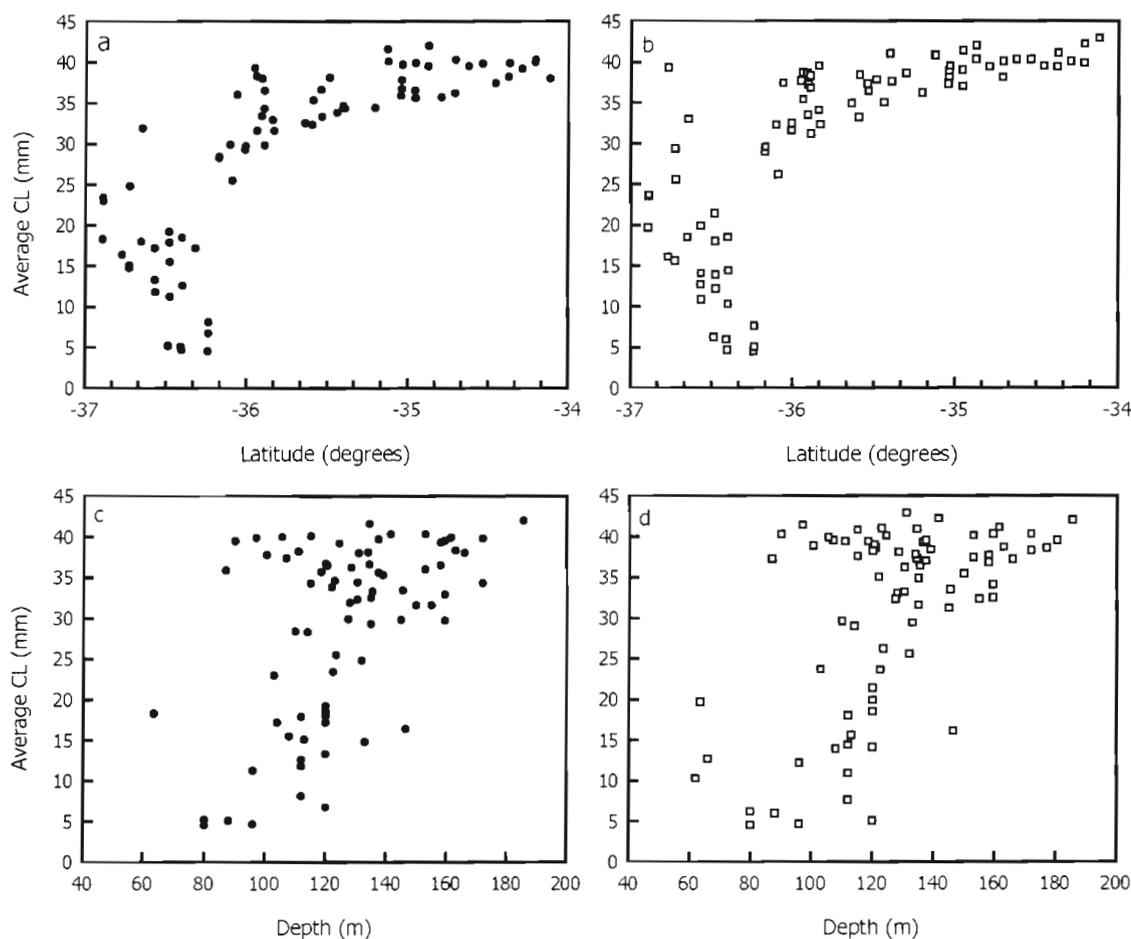


Fig. 2. *Pleuroncodes monodon*. Variation of average size per tow for female (●) and male (□) squat lobsters versus (a,b) latitude and (c,d) depth. Depth was used instead of longitude (c,d) because of the positive correlation observed between latitude and longitude (see Fig. 1)

nursery area. The northern branch, which makes up the largest portion of the adult population, is distributed along ca 240 km from Topocalma to Point Achira; the southern branch, distributed at both sides of the Biobío river canyon, is much smaller than the northern one and is surrounded to the west and south by hard bottoms (Fig. 1).

**Sampling.** A trawling survey was carried out between 34 and 37°S, from October 29 to December 9, 1996, on soft bottoms at depths of 50 to 400 m (Fig. 1). Sampling over the adult branches was done on board the commercial trawler 'Antares' (Camanchaca Fishing Company, Tomé, Chile) using a modified Otter-Trawl gear with a mesh size of 50 mm at the codend (hauls standardised at 20 min length), whereas the nursery ground was surveyed by the RV 'Kay-Kay' (University of Concepción, Chile), using an Aggasiz trawl with a mesh size of 4 mm at the codend (hauls standardised at 10 to 15 min length). A total number of 137 and 25 hauls were done over the adult branches

and the nursery ground, respectively. Additional data, gathered from the nursery ground during research surveys carried out in April 1993 (28 hauls) and March 1994 (43 hauls), were also analysed and used for mapping juvenile sizes with a better spatial resolution than in 1996.

From each haul with catch, a sample of ca 300 individuals was taken at random. Individuals were classified as males, females and juveniles, and their size was measured as carapace length (i.e. ocular cavity to posterior tip of the cephalothorax) to the nearest 0.1 mm.

**Analysis of length-frequency data.** Length-frequency data (LFD) were analysed separately for males, females and juveniles, using unconstrained mixture distribution analysis (for details see Roa 1993, Roa & Ernst 1996, Roa & Tapia 1998) implemented in the MIX algorithm (MacDonald & Pitcher 1979). This analysis considers each LFD as the sampling realisation of a mixture of probability distributions. Parameter estimates for the distribution mixture are obtained by maximum

likelihood. In this particular case, the mixture is a collection of normal distributions corresponding to squat lobster's year classes (i.e. annual cohorts). This assumption is supported by previous findings: in 1991–1992, a single peak of recruitment in the nursery ground was observed during the southern hemisphere autumn (Gallardo et al. 1994), and in 1993 the recruiting year class showed a normal size distribution (Roa et al. 1995). The parameters to be estimated in this analysis were the mean, standard deviation, and proportional representation for each cohort within each LFD.

**Geostatistical mapping.** Geostatistics is a collection of techniques aimed at modelling spatially correlated data, and using the selected model for estimating values in localities not visited during the sampling (Journel & Huijbregts 1978, Isaaks & Srivastava 1989, Rossi et al. 1992, Petitgas 1996). The population is viewed as a stochastic process in space, and the data gathered is regarded as 1 sampling realisation of that process, which is then used to estimate it. As implied in the definition above, geostatistical analysis generally proceeds in 2 steps. First, in the structural analysis the spatial correlation between observations is modelled using a measure of spatial continuity like the variogram. Then, in the next phase the model is used for interpolating values over a regular grid, generally by using an optimisation algorithm known as *kriging*. This technique has been employed for mapping densities of benthic and pelagic species (Pelletier & Parma 1994, Maravelias et al. 1996) and/or to estimate biomass or abundance over a given area (Simard et al. 1992, Maynou et al. 1998). In this study, geostatistical analysis was applied to size/age and sex specific data in order to (1) identify cohorts in space, and (2) infer their movement and dispersal pattern away from the nursery ground.

**Structural analysis:** Average size per haul data showed a spatial trend along the North-South axis (Fig. 2). Therefore, the assumption of second-order stationarity (i.e. mean is constant over the study area, and covariance exists and depends only on sampling interval) was limited to a local scale (i.e. quasi-stationarity), to which comparisons between pairs of observations were restricted (Journel & Huijbregts 1978). Since a proportional effect (i.e. positive correlation between local means and standard deviations; Isaaks & Srivastava 1989) was not observed (Fig. 3), the quantitative tool used for characterising the spatial correlation of size data was the variogram function  $2\gamma(x, \mathbf{h})$ , which is the mathematical expectation of the random variable  $[Z(x) - Z(x + \mathbf{h})]^2$  (Journel & Huijbregts 1978), where  $Z$  is average size,  $x$  is spatial (2-dimensional) location, and  $\mathbf{h}$  is a distance vector composed of magnitude and direction. Under second-order stationarity, the variogram only depends on the separation vector  $\mathbf{h}$  and not

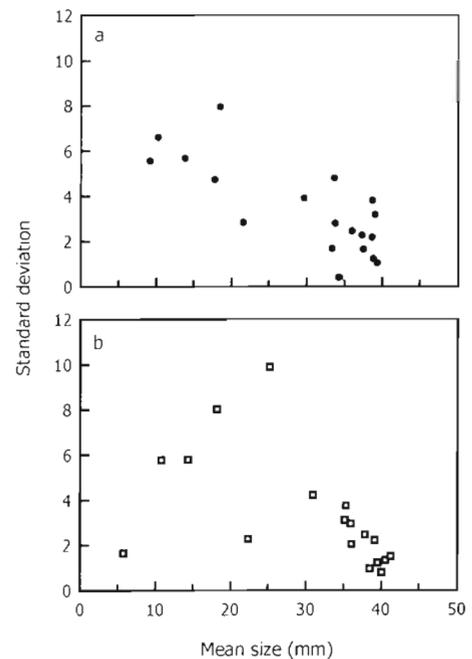


Fig. 3. *Pleuroncodes monodon*. Plots of local mean versus local standard deviation of average size per tow in (a) female and (b) male squat lobsters

on the location  $x$ . Then, it is possible to estimate the variogram  $2\gamma(\mathbf{h})$  from the available data through the experimental variogram

$$2\gamma^*(\mathbf{h}) = \frac{1}{N(\mathbf{h})} \sum_{i=1}^{N(\mathbf{h})} [Z(X_i) - Z(x_i + \mathbf{h})]^2 \quad (1)$$

where  $N(\mathbf{h})$  is the number of pairs  $Z(x_i) - Z(x_i + \mathbf{h})$ , at any 2 points separated by the vector  $\mathbf{h}$ . When variograms are computed as an average over all directions, the vector  $\mathbf{h}$  becomes a scalar and variograms are called omnidirectional. Omnidirectional variograms are appropriate when the stochastic process is isotropic (i.e. the same spatial structure exists in all directions). However, in the presence of anisotropy (i.e. different structures for different directions), the main axes of spatial continuity have to be identified and directional variograms calculated for each particular direction. The computation of variogram surfaces (Isaaks & Srivastava 1989) indicated that, for both sexes, major and minor axes of spatial continuity were located in the north-south and east-west directions, respectively. Therefore, directional variograms were computed in those directions and modelled with anisotropic nested models (Isaaks & Srivastava 1989).

**Variogram model fitting:** In fitting the omnidirectional and directional variograms, 2 basic transition models plus a nugget effect were used: (1) the Gaussian model, which is often used to model extremely continuous phenomena (Isaaks & Srivastava 1989), and

(2) the spherical model, the most common model used so far in earth and marine sciences. These models are given by

$$\gamma(\mathbf{h}) = \begin{cases} 0 & \text{for } \mathbf{h} = 0 \\ c_0 + c \left[ 1 - \exp\left(-\frac{3|\mathbf{h}|^2}{a^2}\right) \right] & \text{for } \mathbf{h} \neq 0 \end{cases} \quad (2)$$

for the Gaussian model (Pannatier 1996), and

$$\gamma(\mathbf{h}) = \begin{cases} 0 & \text{for } \mathbf{h} = 0 \\ c_0 + c \left[ \frac{3}{2} \left(\frac{|\mathbf{h}|}{a}\right) - \frac{1}{2} \left(\frac{|\mathbf{h}|}{a}\right)^3 \right] & \text{for } 0 < |\mathbf{h}| \leq a \\ c_0 + c & \text{for } |\mathbf{h}| \geq a \end{cases} \quad (3)$$

for the spherical model (Cressie 1993), where  $c_0$  is the nugget effect or microscale variability not resolved by the current sampling resolution,  $c$  is the sill or maximum level of variability, and  $a$  is the range of the variogram (i.e. the distance beyond which no correlation between data pairs is observable). Both Gaussian and spherical isotropic models plus a nugget effect were used to model the omnidirectional variograms computed for both sexes, whereas anisotropic nested models composed of a nugget effect plus a Gaussian and a spherical structure were fitted to directional variograms computed along north-south and east-west directions. Model parameters were estimated using the approximate weighted least squares procedure described by Cressie (1993), and applied by Pelletier & Parma (1994) and Maravelias et al. (1996). The objective function was

$$\min \sum_{i=1}^H N(\mathbf{h}_i) \left( \frac{\hat{\gamma}(\mathbf{h}_i)}{\gamma(\mathbf{h}_i)} - 1 \right) \quad (4)$$

where  $H$  is the number of distance lags for which the experimental variogram ( $\hat{\gamma}$ ) was computed, and  $N$  is the number of pairs for each lag. This criterion has the advantage of giving more weight to points with a high number of pairs and near the origin, which is the most important part in estimating variogram parameters (Cressie 1993). The estimation was done iteratively using a quasi-Newton algorithm, with initial values obtained from the interactive variogram modelling utility of the package Variowin 2.2 (Pannatier 1996).

**Cross validation:** Previous to the second phase of interpolation by ordinary point kriging, one of the fitted models, along with a set of kriging parameters, had to be selected. The selection was done by a procedure known as cross validation (Isaaks & Srivastava 1989). This procedure is based on a systematic removal of observations from the data set, one by one, which are then estimated by interpolation using the fitted model of spatial continuity being validated and the observations located in a pre-defined search neighbourhood. The result of this procedure is a vector of  $n$  estimates for each model being validated, where  $n$  is

the number of observations in the raw data set. Thus, a vector of  $n$  residuals ( $Z - Z^*$ ) can be calculated and used for comparing the performance of different models fitted to the experimental variogram. Since the main goal of this validation was to select a model giving unbiased estimates with a distribution resembling as much as possible that of the observations, our first decision criterion was the mean squared error (MSE), which is defined by Isaaks & Srivastava (1989) as

$$\text{MSE} = \left( \frac{1}{N} \sum_{j=1}^N [Z^{*(k)}(x_j, y_j) - Z(x_j, y_j)] \right)^2 + \frac{1}{N-1} \sum_{j=1}^N [Z^{*(k)}(x_j, y_j) - Z(x_j, y_j)]^2 \quad (5)$$

$$\text{MSE} = \text{bias}^2 + \text{var}_\gamma$$

where  $\text{var}_\gamma$  and bias are the variance and average of residuals, respectively. This selection criterion, which has been successfully used in earth and marine sciences (see Maravelias et al. 1996), is a compromise between the spread and centering of residuals around zero. Hence, the selected model and kriging parameters should be those giving the minimum MSE. However, not only the univariate distribution of residuals should be considered when selecting an appropriate model of spatial continuity. As suggested by Isaaks & Srivastava (1989), conditional unbiasedness (i.e. no correlation between the magnitude of estimates and residuals) and a good correlation between observations and kriged estimates were also checked, restricting the selection of minimum MSE to only those combinations of parameters that met these conditions. The spatial distribution of residuals was also incorporated as an additional criterion, so as to ensure that estimates were not only conditionally unbiased with respect to any range of values, but also with respect to their location (Isaaks & Srivastava 1989).

**Mapping:** Mapping was done by ordinary point kriging on a regular grid with an internodal distance of 2.8 km. At each node of the grid, the average size ( $Z^*$ ) was estimated as the weighted average

$$Z^* = \sum_{i=1}^N \lambda_i Z(x_i) \quad (6)$$

of the  $N$  observations  $Z(x_i)$  falling within a pre-defined search neighbourhood. The weights  $\lambda_i$  were calculated using the selected variogram model and the observations by solving a system of linear equations where the kriging variance was minimised under the constraint that  $\sum \lambda_i = 1$ , which insured and unbiased estimation of  $Z^*$  (Journel & Huijbregts 1978).

When interpolation by kriging was done, cohort mean sizes estimated from the distribution mixture analysis were mapped and smoothed by their standard

deviations, thus tracing the spatial distribution of cohorts as convex-upward curves whose height is proportional to the probability of encountering a given cohort in space in the population.

## RESULTS

### Analysis of length-frequency data

Carapace length was measured in 11 745, 7038 and 49 male, female and juvenile squat lobsters, respectively, in the research survey of 1996, while 3184 juveniles were measured in 1994. Length data of juveniles in 1993 was analysed by Roa et al. (1995). Observed ranges of carapace lengths were 10 to 50 mm for males, 10 to 47 mm for females, and 2 to 12 mm for juveniles (Fig. 4). Results of the distribution mixture analysis are shown in Fig. 4 and Table 1. Six adult cohorts were identified for females and males, the latter being larger at specific ages than females as size increased (Table 1). Estimated mean size for juveniles in 1996 and 1994 (Table 1) agreed with the value estimated by Roa et al. (1995) for individuals sampled in 1993.

### Structural geostatistical analysis

As already mentioned, a relationship was observed in 1996 between average size per tow and latitude, with size increasing northwards and southwards from

the nursery ground, located around 36° 30' S (Fig. 2a,b). In an east-west direction, no relationship between average size and depth was observed (Fig. 2c,d).

Omnidirectional and directional variograms computed for both sexes in the north-south and east-west directions (Fig. 5) showed a clearer structure for females, with lower sills (less variability) but similar ranges to those computed for males. Ranges of ca 65 km and 37 km were observed for north-south and east-west variograms, respectively. Omnidirectional and north-south variograms computed for both sexes were almost identical (Fig. 5), suggesting that most of the variability in the data occurs along a latitudinal axis. However, east-west variograms revealed that spatial structure is also detectable in that direction, though with less variability and a shorter range of correlation (Fig. 5), indicating the presence of a combination of geometric and zonal anisotropy (Isaaks & Srivastava 1989, Pannatier 1996).

Gaussian and spherical models were used to fit isotropic and anisotropic nested models to omnidirectional and directional variograms, respectively (Fig. 6, Table 2). The fitting of isotropic models, in addition to anisotropic ones, was justified by the resemblance between omnidirectional and north-south variograms. This fact, along with the almost linear shape of the population at larger scales, suggested that most of the total variability could be well explained by a simpler isotropic model.

Cross validation showed that, for both sexes, isotropic Gaussian models with a nugget effect (Table 2)

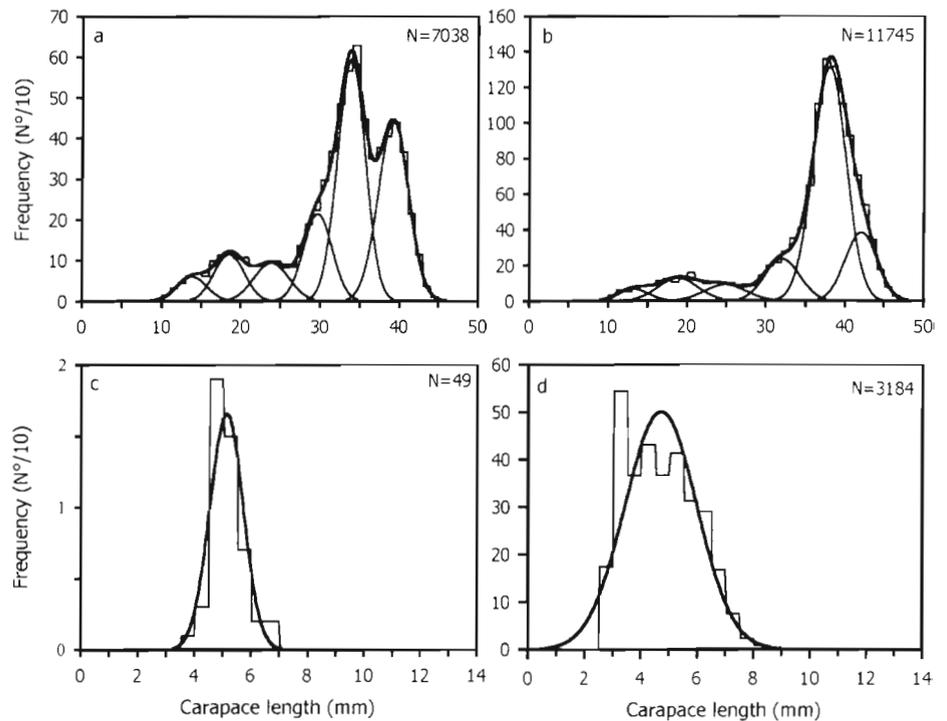


Fig. 4. *Pleuroncodes monodon*. Cohorts identified by the distribution mixture analysis of length-frequency data of (a) female and (b) male squat lobsters, and normal distributions fitted to juvenile size data in (c) 1996 and (d) 1994. Histograms: raw data; lines: estimated normal components and fitted distribution mixture

Table 1. *Pleuroncodes monodon*. Results from the distribution mixture analysis of length data for adult squat lobsters in 1996, and for juveniles in 1996, 1994 and 1993. SD: standard deviation; P: proportion of participation in the distribution mixture. Standard errors are given in parentheses

Year class	Males			Year class	Females			Sampling year	Juveniles	
	Mean (mm)	SD (mm)	P		Mean (mm)	SD (mm)	P		Mean (mm)	SD (mm)
1	13.226 (0.173)	1.947 (0.125)	0.028	1	13.825 (0.182)	1.896 (0.133)	0.041	1996	5.139 (0.087)	0.591 (0.065)
2	18.878 (0.178)	2.548 (0.150)	0.069	2	18.549 (0.161)	1.887 (0.126)	0.078	1994	4.712 (0.023)	1.270 (0.017)
3	24.903 (0.295)	2.618 (0.211)	0.051	3	23.872 (0.258)	2.198 (0.161)	0.074	1993 <sup>a</sup>	6.51 (0.01)	1.11 (0.01)
4	32.083 (0.142)	2.173 (0.095)	0.109	4	29.701 (0.132)	1.804 (0.102)	0.138			
5	38.009 (0.037)	2.071 (0.037)	0.579	5	33.907 (0.061)	1.732 (0.050)	0.366			
6	42.048 (0.087)	1.998 (0.065)	0.163	6	39.249 (0.063)	1.933 (0.044)	0.304			

<sup>a</sup>From Roa et al. (1995)

had a better performance than spherical and even anisotropic nested ones. Selected minimum and maximum numbers of neighbours to be used during interpolation were 1 to 7 and 1 to 9 for females and males,

respectively. Results of the cross validation for the selected models and search parameters in female and male squat lobsters showed a good correlation between observed and estimated data (Fig. 7a,b). Conditional bias was not observed, though residuals were less scattered for sizes above 30 mm (Fig. 7c,d). Univariate distribution of residuals was fairly symmetric for both sexes, although less bias and a narrower distribution was observed in males (Fig. 7e,f).

### Geostatistical mapping

Mapping by ordinary kriging was done using the parameters indicated above and a circular search neighbourhood of 22 km in diameter. Adult cohorts identified from the analysis of length data appeared to be sequentially ordered in space from the nursery ground to the north and south (Fig. 8). For both sexes, the first 3 cohorts were found at both sides of the nursery ground. On the northern side, these cohorts were distributed in a small area between the nursery ground and Point Achira (Fig. 8), with the remaining 3 cohorts occupying most of the northern branch of the population. The largest spatial coverage was observed for Cohorts 6 and 5 in females and males, respectively.

Ordinary kriging maps of juvenile size on the nursery ground in April 1993 and March 1994 (Fig. 9) indicate that settlement had different spatial features in the 2 years. In 1993 (Fig. 9a) several patches were distributed around a larger patch of larger, and presumably previously settled, individuals. In 1994 a single large patch of recruits was observed, with smaller individuals located near its centre and larger ones towards the periphery (Fig. 9b).

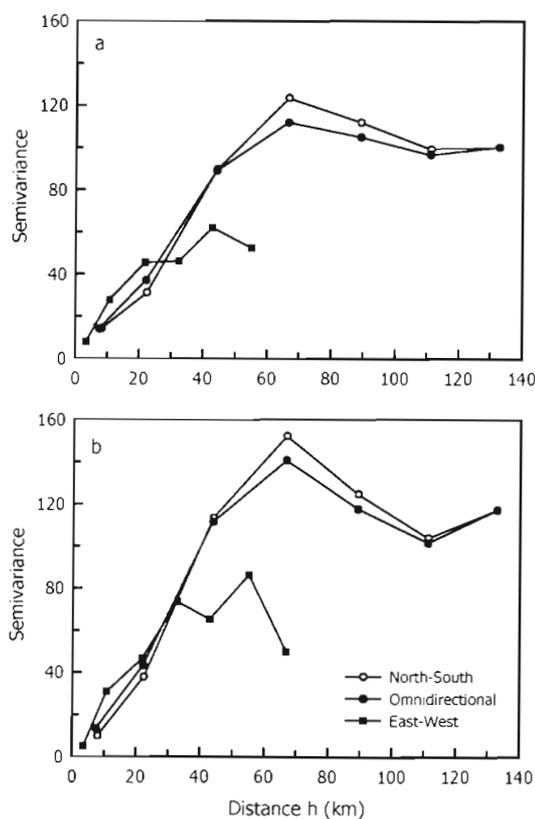


Fig. 5. *Pleuroncodes monodon*. Experimental variograms computed for average size per tow data in (a) female and (b) male squat lobsters

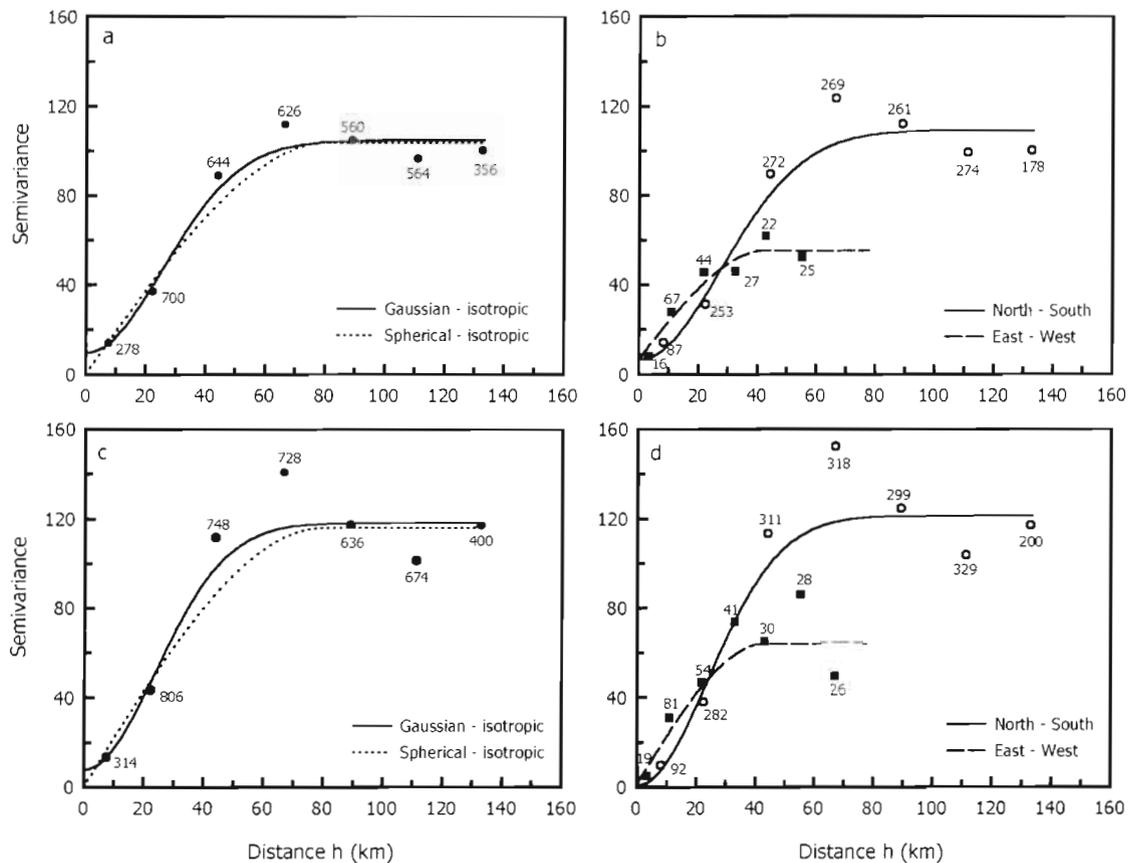


Fig. 6. *Pleuroncodes monodon*. Models fitted to omnidirectional (left panels) and directional (right panels) variograms computed for size data of (a,b) female and (c,d) male squat lobsters. Gaussian and spherical isotropic models were fitted to omnidirectional variograms, while anisotropic nested models of Gaussian and spherical structures plus a nugget effect were used for directional ones. Number of pairs compared for each lag distance is indicated

## DISCUSSION

With the remarkable exception of the theory of biological dispersion (Skellam 1951, Okubo 1980), population theory has traditionally ignored the spatial dimension of population dynamics, focusing instead on total abundance change through time, like in the well-known logistic differential (MacArthur & Levins 1967, Levins 1968) and difference (May 1973) models, the fishery version of the logistic model (Schaefer 1954), the stock recruitment models (Ricker 1954, Beverton & Holt 1993), and the age-structured models of fisheries science (Megrey 1989). These models, with populations 'in the air', have been shown to be very useful from both heuristic and applied points of view. Nevertheless, specific populations inhabit a given region, which has its own nontrivial structure full of contingencies. Therefore, a more complete modelling framework of theoretical and real populations should be spatially explicit, in the sense that abundance should be a function of both temporal and spatial co-ordinates, and

spatial contingencies like canyons, slope changes, and different ground types should be represented. In the terrestrial realm, the emergent field of landscape ecology (Dunning et al. 1992, 1995) and the new theory of metapopulations (Hanski & Simberloff 1997) are conceptually based on spatial descriptions of populations, although the latter theory is still not spatially explicit (i.e. populations form patches 'in the air'). In this work we have laid the empirical foundations for a spatially explicit modelling of the squat lobster population off central Chile. This is not a metapopulation; it is a single spatial entity which is asymmetrically branched. Our central hypothesis was that the population functions in space in the form of waves of recruits entering through the nursery ground and radiating away to the north and south over the continental shelf. This hypothesis was tested by mapping the cohorts in space and was corroborated by the evidence (Fig. 8). Cohorts recruit to the benthos into a single and large nursery area, located in the widest region of the continental shelf off central Chile, and then start radiating away from the

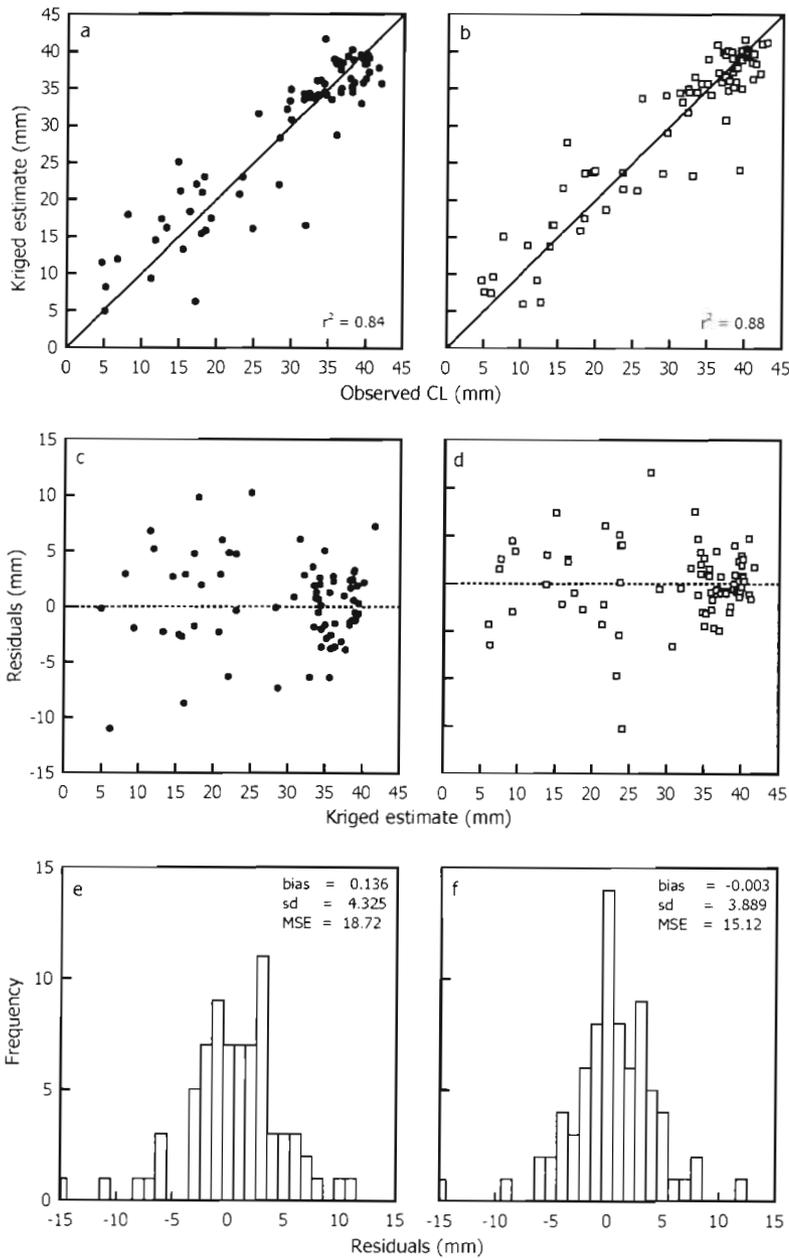


Fig. 7 *Pleuroncodes monodon*. Results of cross validation for the selected models of spatial continuity (see Table 2) in female (left-hand panels) and male (right-hand panels) squat lobsters

area of recruitment in a lifelong migration. Those individuals that happen to move south appear to be constrained by physical barriers in later life, namely, a canyon, emerged land, and a vast region of hard bottoms (Fig. 1). This physical constraint acting through unknown physiological processes was the main mechanism that Roa & Tapia (1998) offered to explain the faster growth rate and earlier age at maturity of the southern squat lobsters compared to individuals from

the northern branch. The mapping of the cohorts of this larger branch clearly shows the process of age-dependent dispersion in a large region where squat lobsters do not seem to be physically constrained to disperse, except probably in some regions of hard bottoms that cross the continental shelf between 36° 10' S and 36° 50' S (Fig. 1). However, the extent to which hard bottoms affect squat lobster dispersal has not yet been fully assessed. Population modelling can now be undertaken to simulate this process of cohort radiation, with the spatial layout of the habitat explicitly incorporated. An interesting approach would be to model cohort dispersal by some form of the diffusion-reaction model in a spatially explicit grid of 2 types of habitat: soft and hard bottoms.

The presence of spatial dynamics in cohort distribution is a rather common phenomenon in benthic crustaceans. For example, in all of the following species juveniles inhabit shallow bottoms and migrate to deeper bottoms to join the adult population: the rock lobster *Panulirus cignus* (Phillips 1990, Walters et al. 1993), the brown tiger shrimp *Penaeus esculentus* and the endeavour shrimp *Metapenaeus endeavouri* (Watson & Turnbull 1993), the green tiger prawn *Penaeus semi-sulcatus* (Abdulqader & Naylor 1995), and the snow crab *Chionoecetes opilio* (Comeau et al. 1998). The squat lobster population differs, however, in that the main geographical axis of migration is not inshore-offshore but parallel to the coast, within the same depth range, and therefore much more elongated. In the presence of such long distances travelled by the adult cohorts, the question arises as to what proportion of total larvae released in

the population can reach the nursery ground after ca 6 mo of pelagic life. We hypothesise that most of the annual recruitment to the nursery area is contributed by recently matured cohorts, not too far away from the nursery, in the region of hard bottoms between 35° 10' S and 35° 50' S, and from the southern adult population branch. In our view, older cohorts of the northern branch do not contribute to population renewal through the nursery ground because they are

Table 2. *Pleuroncodes monodon*. Isotropic (1, 2) and anisotropic nested (3) models fitted to the experimental variograms computed for average size per tow data. Models selected for interpolation by ordinary kriging

	Females			Males		
	(1)*	(2)	(3)	(1)*	(2)	(3)
Nugget	9.7	0	6.5	7.8	0	0.8
<b>1st structure</b>						
Type	Gaussian	Spherical	Gaussian	Gaussian	Spherical	Gaussian
Direction	–	–	0°	–	–	0°
Sill	94.9	103.6	102.3	110.4	115.9	120.3
Range (km)	63.0	81.3	68.0	58.5	79.6	59.1
<b>2nd structure</b>						
Type	–	–	Spherical	–	–	Spherical
Direction	–	–	90°	–	–	90°
Sill	–	–	48.8	–	–	63.3
Range (km)	–	–	42.8	–	–	43.2
Anisotropy coeff.	–	–	1000	–	–	1000

too far away to the north. This raises the intriguing possibility of identifying a northern portion of the population whose biomass could be commercially harvested without affecting population renewal and persistence,

a kind of spatially explicit surplus production. Alternatively, northern cohorts may export larvae advected by equatorward coastal currents (Strub et al. 1998) to not-yet-sampled prime nursery grounds further north.

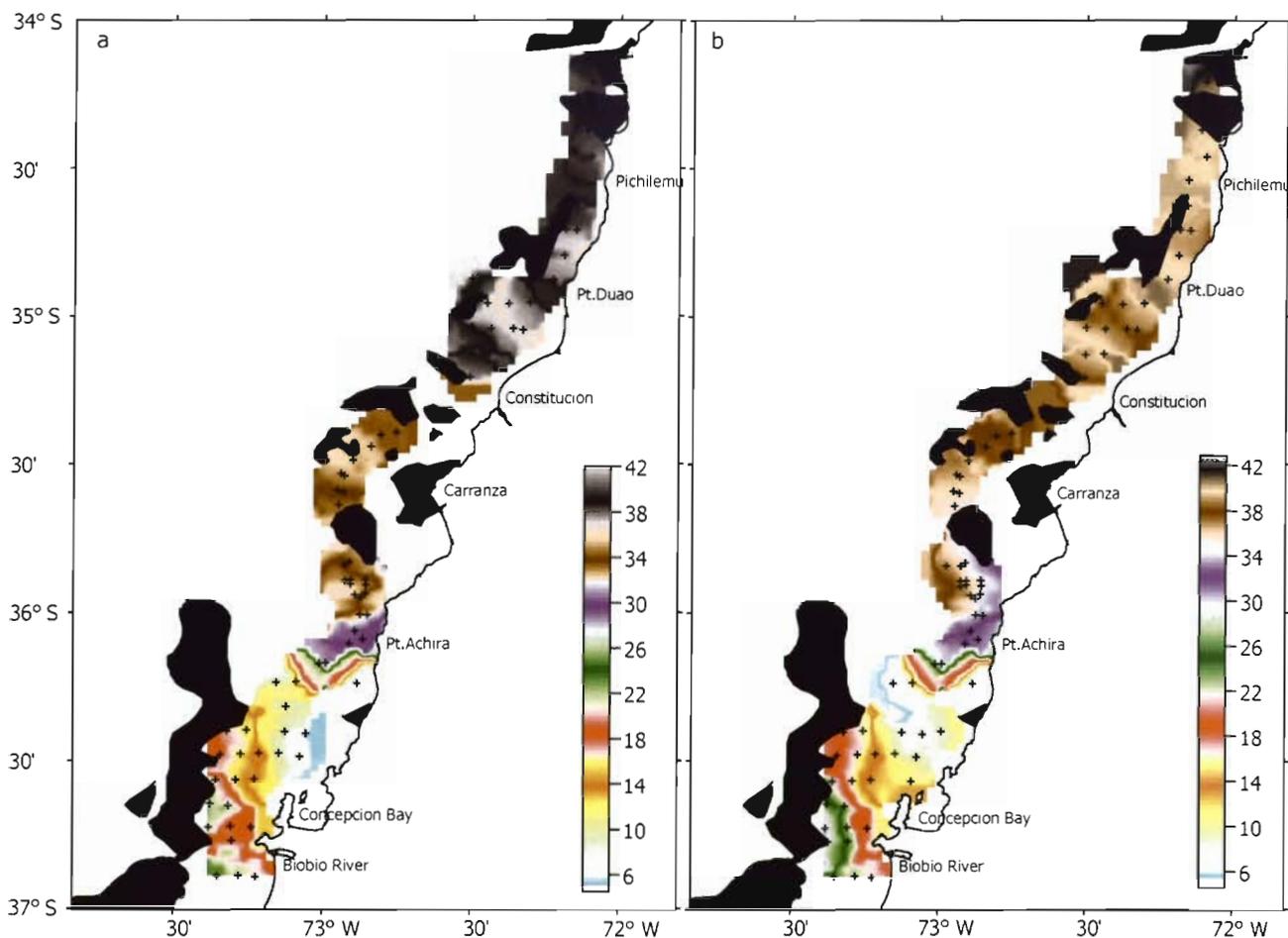


Fig. 8. *Pleuroncodes monodon*. Ordinary kriging maps of cohort spatial distribution in (a) female and (b) male squat lobsters in 1996. Each colour corresponds to an annual cohort, with its maximum intensity centred on the mean size estimated by the distribution mixture analysis, and smoothed proportionally to its standard deviation (see Table 1). (■) Hard bottoms; (+) survey design

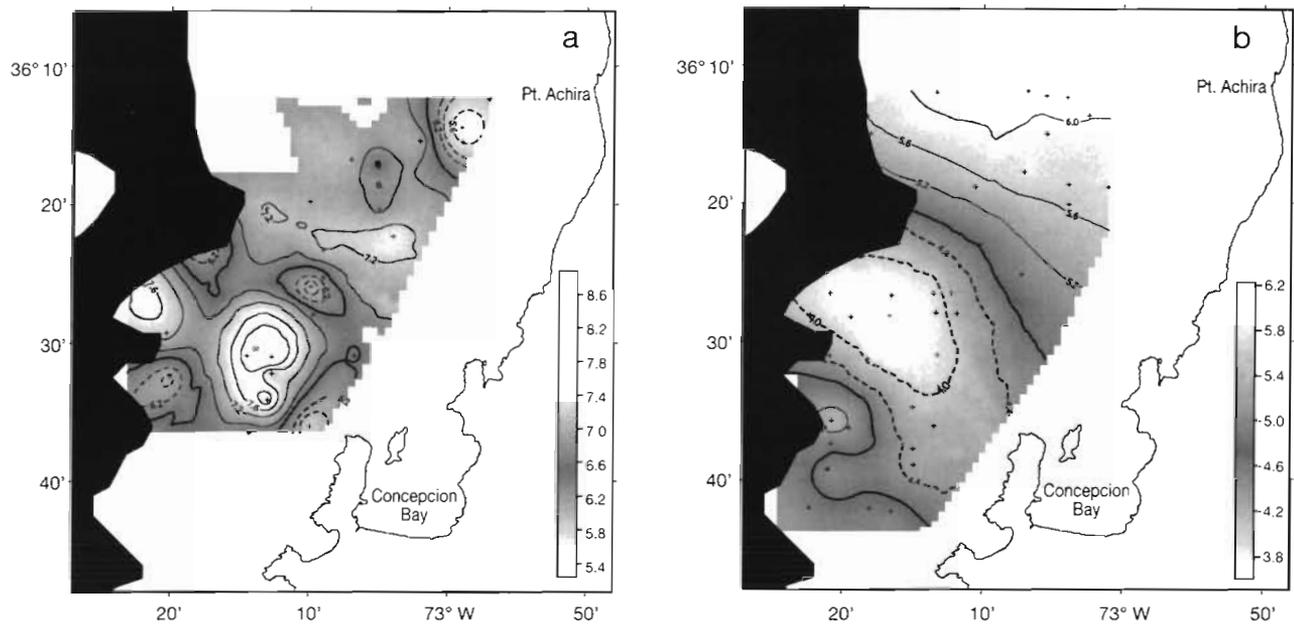


Fig. 9. *Pleuroncodes monodon*. Ordinary kriging maps of juvenile size on the nursery ground during (a) April 1993 and (b) March 1994. Darker regions correspond to mean sizes estimated each year for juveniles by fitting a normal distribution to juvenile length frequency data. Smoothing is proportional to the standard deviation (see Table 1). Isolines corresponding to sizes larger and smaller than the estimated mean (bold lines) are indicated by solid and dashed lines, respectively. (■) Hard bottoms; (+) sampling stations

Recent anecdotal evidence from the fishery for the shrimp *Heterocarpus reedi* from as far north as 25 to 30°S indicates the presence of juvenile squat lobsters in large quantities, therefore supporting this alternative scenario. The testing of these ideas requires intensive sampling of the pelagic larval population and knowledge about advective forces present during the period of larval abundance (late spring to early autumn) as well as trawling for juveniles in the suspected primary nursery habitat.

Geostatistics is not only a technique of interpolation and mapping. In the first phase of structural analysis it provides a model of spatial continuity of the variable of interest—the variogram—which is assumed to be valid over the area covered by the population (the second-order stationarity hypothesis). This model can be interpreted from a biological view point. In our case, the model selected through cross validation was isotropic Gaussian, a model frequently mentioned as appropriate for extremely continuous data (Isaaks & Srivastava 1989). This type of spatial continuity indicates a very smooth increase in size as distance from the nursery ground, mainly to the north and south, increases, which means a high variance of size at a particular age and/or a high degree of cohort overlap. The simple variogram was an appropriate tool for characterising the spatial continuity of size data because no increase in size variance with size/age was observed, which is in agreement with previous findings showing

that the variance of size at age for both sexes is a conservative measure in the squat lobster population (Roa 1993). An equivalent spatial structure of the cohorts by sex is evident in the similarity of the variogram parameters fitted for both sexes (Table 2) and in the mapping of cohorts by kriging (Fig. 8), although the oldest female cohort is widely distributed while the corresponding male cohort only occupies a small fraction of the northern tip, probably because males have reached bottoms farther north than our northernmost sample. Isotropy in the variogram models for both sexes was clearly a consequence of the overwhelming predominance of the north-south axis, which obscured any possible anisotropy in the orthogonal axis. Finally, the spatial range of correlation in the data was about one fifth of the latitudinal extension of the population. Given that this parameter is generally interpreted as the size of the patches (Maravelias et al. 1996), the range could be interpreted as the average spatial extension of the dispersing cohorts (Fig. 8), although the cohort mapping reveals that older cohorts occupy much more space than younger ones.

A close-up of the nursery ground (Fig. 9) with additional data from 2 previous sampling programs in 1993 and 1994 showed that recruitment can occur as several relatively small patches interspersed through the nursery area (1993) or as a large patch in the middle of the nursery (1994). However, these contrasting spatial patterns of settlement need not imply yearly differences,

because they may have been originated as a combination of sampling at different times during the settlement period and post-settlement mortality. In fact, judging from the smaller sizes of recruits in 1994 than in 1993, it can safely be assumed that the 1994 data was gathered earlier during the settlement period than the 1993 data. If such is the case, then post-settlement mortality of early settlers and subsequent arrival of late settlers can yield a sequence of events starting with a simple spatial pattern like in 1994 and ending with a more complex spatial pattern like in 1993. That is, the 2 contrasting spatial patterns can be the starting and end points of a typical settlement period. Of course, more complex explanations like yearly variation in the dynamical behaviour of the oceanographic processes affecting settlement cannot be ruled out with the current state of knowledge.

One consistent non-spatial pattern that has emerged from our research into the squat lobster population off central Chile is that of a fairly male-biased sex ratio: about 60% of the adult population appears to be composed of males (Roa 1993, Roa & Bahamonde 1993, Roa & Tapia 1998, and Fig. 4). This result has been obtained at several periods during the annual cycle and levels of population abundance (Fig. 2 of Roa & Tapia 1998). Assuming a balanced ratio at settlement, there are 2 possible explanations for this pattern: females are harder to catch than males or females suffer higher mortality than males. On average, females are smaller than males of the same age (Roa 1993), and thus they may be better able to escape the net through the mesh. However, the same size difference between sexes may render females more susceptible to predation, and thus lead to higher mortality rates on females. Probably both factors contribute to the biased sex ratio observed in this population.

The spatial functioning of the squat lobster population presented in this work explains some important facts about the history of the fishery, some of them described by Bahamonde et al. (1986). Firstly, during the 1970s the commercial fleet started to exploit the squat lobster population in their northernmost range of distribution, at 33°S, but heavy exploitation quickly led northern fishing grounds to local extinction. The fleet then started to move south to maintain high levels of yield, causing a process of north-to-south annual decimation. This process lasted throughout the 1970s and ended in 1979, when the first fishery closure, not sufficiently enforced, was decreed for 3 yr. In the light of our results, this history is evidently a consequence of heavy exploitation of a population whose fishing grounds were fully dependent on migration from the south to persist, and therefore were prone to decimation. During the 1980s the exploitation was again high, precluding the population from expanding to the north

by cohort dispersal, and probably affecting the level of recruitment into the nursery ground (Anonymous 1991). A second fishery closure, from 1988 to 1991, was much more heavily enforced than the previous one, and was followed by a very moderate level of exploitation in the 1990s. Then, and with the same ease with which the population was decimated in the 1970s, it started expanding and recolonising the northern regions in the 1990s. In the first 3 yr of expansion, from 1988 to 1991, the population advanced 56 km to the north, from 36 to 35°20'S (Roa & Bahamonde 1993). Our results from sampling in 1996 show that squat lobsters have now reached at least as far north as 34°S, and probably farther (Fig. 8). This understanding of the recent history of the squat lobster would not have been possible without a fully spatially explicit conceptualisation of population functioning.

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