

# Growth and expansion of an exploited population of the squat lobster (*Pleuroncodes monodon*) after 3 years without harvesting

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## Abstract

In 1991, after 3 years of fishery prohibition, the most important surviving population of squat lobster (*Pleuroncodes monodon*, Galatheididae, Decapoda) on the continental shelf of central Chile, the Achira population (36°S, 73°W), reached the highest biomass recorded since the start of population assessments in 1979 (34 084–43 910 t, 95% confidence interval), and expanded its distribution by 56 km to the north. The age composition of the population was characterised by two strong year-classes (1988 and 1989, born at the end of the previous fishing period and at the start of the prohibition respectively) and a mixture of older year-classes, less important in terms of numerical abundance. Population expansion had a clear spatial structure. The 1989 year class (mean size 23.5 mm carapace length) populated the traditional southern population area, while the 1988 and older year-classes (mean carapace length 33.5 mm and 39.5 mm, respectively) populated the areas to the north which were vacant prior to the fishery closure in 1989. We interpret this spatial structure as the result of size-dependent dispersal capacity, with recruitment of the 1989 year-class providing the impetus for expansion of the individuals of the 1988 and older year-classes. Using the simple age structure of the Achira population, we estimated an average rate of population increase of 10 323 t year<sup>-1</sup> during the period without harvesting, and a rate of expansion of 20 km year<sup>-1</sup>. Most of the reproductive potential (eggs km<sup>-2</sup>) was transported into the expansion zone, which may create new nursery grounds towards the north. This in turn may alter the spatial distribution of size, if recruitment is successful in the northern areas, with a potential effect on expansion dynamics.

## Introduction

The dynamics of population expansion is a subject that has interested ecologists for a long time. Most documented cases refer to community invasion by introduced species (e.g. Drake and Williamson, 1986; Herbold and Moyle, 1986). The alternative case, where a species whose distributional range has been reduced by human exploitation re-establishes itself in its former habitat, has not received similar attention (but see Lubina and Levin, 1988), perhaps

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because this occurs less frequently. In this paper we describe such a process for the squat lobster *Pleuroncodes monodon* (Galatheidae, Decapoda) on the continental shelf of central Chile.

The squat lobster has been the target of a fishery since the 1960s. The species has been subject to overfishing which led to a severe contraction of its latitudinal range (Bahamonde et al., 1986). The pre-fishery distribution of the populations was from 33 to 37°S, comprising most of the continental shelf of central Chile. The fishery began in the north of this range and moved southwards, driving local populations to extinction. This overfishing process lasted for almost 15 years and ended in a total closure of the fishery in 1979. Only three remnant populations survived between 36 and 37°S (Bahamonde et al., 1986). The northernmost surviving population, the Achira population, was the biggest in terms of both area and biomass, and most fishing effort was concentrated on this when the fishery re-opened in 1982. New evidence from the fishery and other sources led to a second closure in 1989, which lasted for 3 years. The purpose of this paper is to describe the situation following those 3 years of fishery closure.

## Materials and methods

During September–October 1991, the R/V 'Abate Molina' was used to carry out a survey of the Achira population. At this time of the year the whole population is distributed between 50 and 150 m, and the adult females are starting to release larvae into the plankton (Bahamonde et al., 1986).

Sampling was performed using a bottom trawl with a 30.1 m head rope and 36.4 m foot rope. The height of the mouth varied between 2.2 and 2.5 m and the wing tips had a mean separation of 19.3 m. Mesh size was 50 mm at the codend and trawl velocity varied between 2.5 and 3.0 knots. Each haul lasted 30 min. The distance covered by the trawl was measured with a Doppler log.

Simple random sampling was employed and estimates of total biomass of the Achira population were derived using the swept area method (Alverson and Pereyra, 1969; see below). The sampling procedure was as follows. Using historical evidence, the likely limits of the population were estimated. Twenty hauls were allocated to determine the limits of the population, and 54 were distributed at random inside these limits. Unexpectedly, we found that the population had expanded northwards, and 22 additional hauls were carried out to determine the limits of the expansion zone and to sample the new area. The total number of hauls was 96, of which 27 were used to describe population distribution, and 71 were randomly allocated into quadrats of 2.6 km × 1.3 km which divided the distribution area into 387 equiprobable sampling units. We assumed that a single haul was sufficient to characterise each sampling unit. The information from randomly allocated hauls only was used for biomass estimation and statistical analyses. The spatial distribution of hauls, the

form of the Achira population, and the characteristics of the sea bottom (taken from Fishery Map No. CP-500 of the Instituto Hidrográfico de la Armada de Chile and the Instituto de Fomento Pesquero) can be seen in Fig. 1 (a).

The total catch of squat lobster in terms of biomass and the bycatch of each haul were estimated by putting the whole catch of each species into identical boxes, counting the number of boxes occupied by each species, and weighing all or a random sample of boxes. The error associated with this procedure was not taken into account in estimating total biomass, since it was relatively small

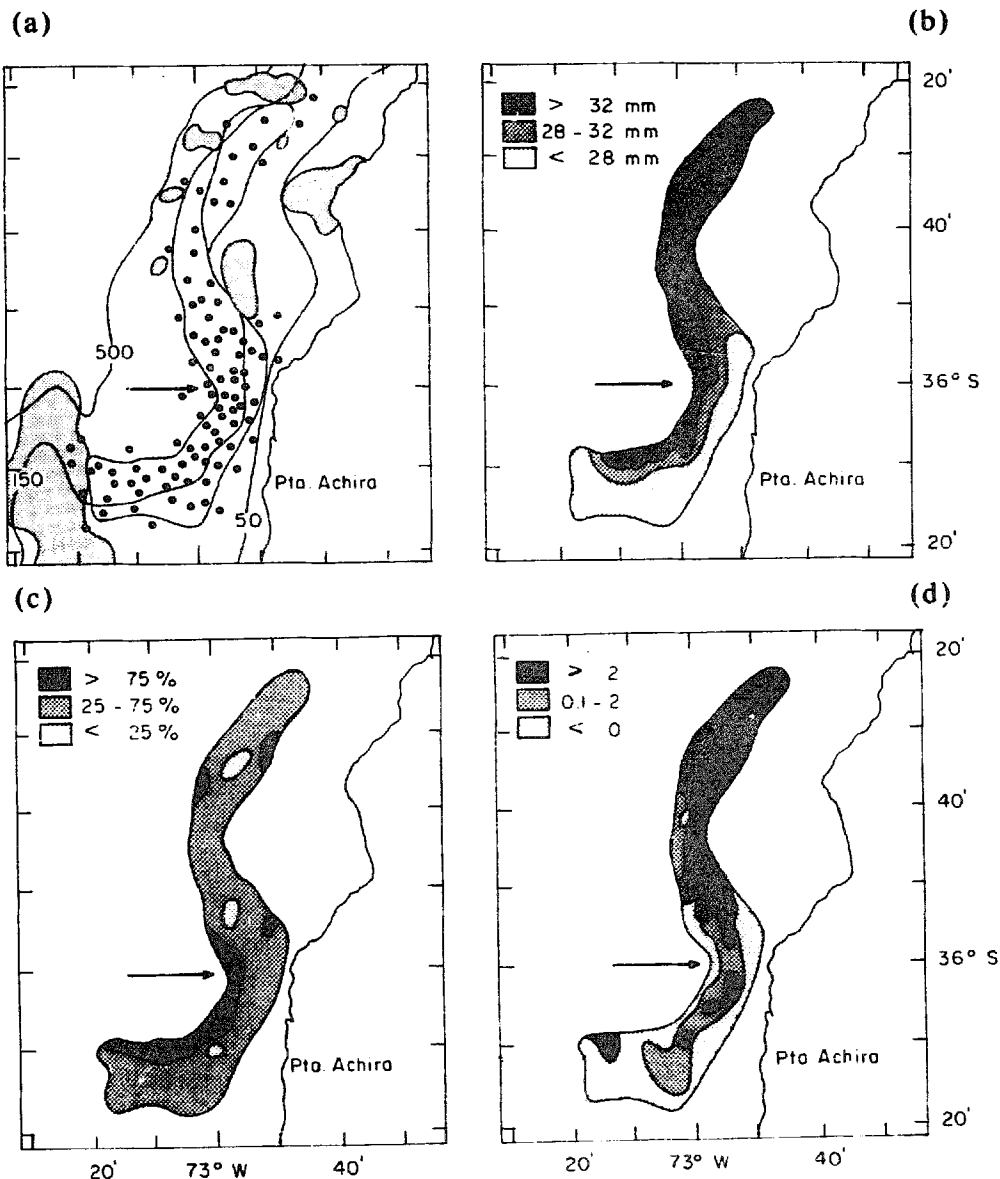


Fig. 1. Sampling and spatial characteristics of the Achira population of squat lobster. The arrow indicates the historical northern limit of the population. (a) Distribution of hauls (dots), mapping of the population, zones of hard bottom (shaded areas), and depth (m). (b) Spatial distribution of mean length (CL). (c) Spatial distribution of the proportion of males. (d) Spatial distribution of reproductive potential ( $10^{12}$  eggs  $\text{km}^{-2}$ ); the black region in the centre of the population indicates a single patch with an estimated egg density of  $17 \times 10^{12}$  eggs  $\text{km}^{-2}$ .

in most cases, owing to the rather uniform size structure of squat lobster on each haul.

To describe the total area occupied by the population, we marked the mid-point between those hauls with zero catches at the edge of the distribution and the neighbouring hauls with positive catches. In this way, we outlined the perimeter of the area occupied by the population (see Fig. 1(a)). The area was quantified by means of a digital planimeter.

The expression for total biomass was (Alverson and Pereyra, 1969)

$$B = (AC) / (aq) \quad (1)$$

where  $A$  is the total area ( $\text{km}^2$ ) occupied by the population,  $a$  is the average area swept by the trawl ( $\text{km}^2$  per linear km covered by the trawl),  $q$  is a dimensionless term representing the fraction of the stock within the swept area which is actually caught by the trawl (catchability coefficient), and  $C$  is the average catch per unit of effort (kg per linear km covered by the trawl). In the absence of specific information, the catchability coefficient  $q$  was set at 1.0. Thus, biomass estimated using Eq. (1) relates only to size groups that are retained by the net. The variance of the total biomass estimation was calculated using the expression for the variance of the product of a constant and a random variable (Lindgren, 1976)

$$\text{Var}(B) = (A/a)^2 \text{Var}(C)$$

where we assumed that the ratio  $A/a$  had a sufficiently low variance to be considered negligible. To calculate a confidence interval for the estimated total biomass  $B$  we assumed that estimation errors came from a normal random distribution whose variance was unknown but whose unbiased estimate was given by the expression above.

To evaluate the magnitude of the error in biomass estimation we used the expression for the relative amplitude ( $RA$ ) of the confidence interval

$$RA = (B - IL) / B$$

where  $B$  is the central value of the confidence interval of the total biomass estimation, and  $IL$  is the lower limit of the confidence interval.

From each haul, a random sample of about 4 kg of lobster was used to obtain the distributions of size by sex. Size (carapace length,  $CL$ ) was measured to the nearest millimetre, measuring from the base of the eye socket dorsally, along a line parallel to the mid-line, to the posterior edge of the carapace. Additionally, the number of ovigerous females in the sample was recorded. A separate random sample was taken on a daily basis, transported to land, and used to obtain the length–weight relationship, measuring weight to the nearest 0.01 g.

From the size distribution, year-classes were identified using the maximum likelihood procedure of MacDonald and Pitcher (1979). For this, the com-

puter software MIX Version 2.3 (MacDonald and Green, 1988) was used, and size was assumed to be a normal random function of age. The analysis was done without imposing constraints on parameter estimation. The age structure of the population was estimated using the inverse Von Bertalanffy equation, with parameters according to Arana (1990), i.e.  $CL_{\infty} = 59.9$  mm,  $k = 0.245 \text{ year}^{-1}$ ,  $t_0 = -0.06$ .

To evaluate partial biomasses of male and female lobsters of three year-classes (see Results) we used the expression

$$B_i = Bp_i \quad (2a)$$

where  $B_i$  is the partial biomass of the sex–size category  $i$ ,  $B$  is the total biomass of squat lobster, and

$$p_i = (N_i m_i) / (\sum_i N_i m_i) \quad (2b)$$

where  $N_i$  is the number of individuals in category  $i$  from the total sample, and  $m_i$  is the average weight of category  $i$  calculated from the length–weight relationship.

To estimate the reproductive potential we used a model similar to that of Restrepo and Watson (1991), but indexed by spatial position instead of time

$$E_y = N_y P_y G_y \quad (3)$$

where  $y$  represents haul (spatial position),  $E$  is the average number of eggs per unit area in the sea,  $N$  is the number of females per unit area,  $P$  is the fraction of females carrying eggs (berried females), and  $G$  is the number of eggs per female. The term  $N_y P_y$  in Eq. (3) was obtained using an expression similar to that used to compute partial biomass (Eqs. (2a) and (2b)) but using three different categories of individuals: males, non-ovigerous females, and ovigerous females. We then calculated the biomass density of ovigerous females per unit area, and number density from the average weight of ovigerous females in the haul. The term  $G_y$  in Eq. (3) was obtained from the equation

$$G_y = 0.015 (CL_y)^{3.844}$$

where  $CL$  is the average size of ovigerous females, and parameters are according to Palma and Arana (1990).

We were also interested in calculating the rate of advance of the expansion front, the rate of biomass increase, and the ratio between these to estimate biomass gain due to expansion. To calculate the average annual rate of expansion and biomass increase we need data only on spatial position and biomass at the start and the end of the period without harvest. To calculate the trajectories of biomass increase and expansion during the period without harvest we further need data on biomass and spatial position during the period without harvest. We have data on total and partial biomass and latitudinal posi-

tion of the northern front in 1991, and can make reasonable guesses about the initial northern limit of the population (at the end of the last fishing period in 1988, see Fig. 1). However, we lack reliable data on the initial biomass and its increase, and on the northern position of the expansion front during the years of the fishery closure (1989–1991). To partially fill this gap we used a basic model of biomass change of a cohort as a function of age and the current estimated age structure of the population. The model is

$$B(t) = w(t)N(t) \quad (4)$$

where for each cohort,  $B$  is biomass,  $w$  is the mean weight of each individual, and  $N$  is the number of individuals, all functions of age (or time)  $t$ . The function  $w(t)$  can be given explicit form by assuming Von Bertalanffy growth. The function  $N(t)$  can be modelled using the exponential decay model with constant natural mortality. In this way the model in Eq. (4) can be written

$$B(t) = w_{\infty} (1 - \exp(-kt))^b N_0 \exp(-Mt) \quad (5)$$

where  $w_{\infty}$  is asymptotic weight,  $k$  is the Von Bertalanffy coefficient of growth,  $t$  is age (or time),  $b$  is the exponent of the exponential relationship between length and weight,  $N_0$  is the number of recruits to the cohort, and  $M$  is natural mortality. With model (5), the fraction of biomass that a cohort of age  $t$  had or will have at age  $t'$  is

$$F(t, t') = \frac{B(t')}{B(t)} = \left[ \frac{1 - \exp(-kt')}{1 - \exp(-kt)} \right]^b \exp(-M(t' - t)) \quad (6)$$

By using Eq. (6) with parameters of growth according to Arana (1990, see above), natural mortality estimated by Peñailillo and Henríquez (1990), i.e.  $M=0.63$ , the exponent of the length–weight relationship estimated by us ( $b=3.177$ ,  $SD=0.663$ ) using least squares regression of the natural logarithms of length and weight, and the estimated age structure of the population in Table 2 (approximate integer average between males and females of each year-class), we were able to back-calculate biomasses of the two younger year-classes at the start and during the period without harvest.

## Results

### *Biomass, size and age structure*

The total area occupied by the population was estimated as 1301.5 km<sup>2</sup> (Fig. 1). The mean ( $\pm 1$  SD) catch per unit of effort was  $578.3 \pm 50$  kg km<sup>-1</sup>, while the mean area swept was 0.0193 km<sup>2</sup> km<sup>-1</sup>. These results yielded a 95% confidence interval for total biomass with limits of 34 084 and 43 910 t, with a relative amplitude of 12.6%. The central value was 38 997 t. It must be emphasised that this estimation takes into account only those size groups

which are retained by the sampling gear. Individuals with *CL* values less than 17 mm were absent from the catch. In addition, our central value is probably an underestimate of the biomass of the size range caught by the net (17–45 mm *CL*), since an undetermined fraction of the smallest individuals of those caught by the net may have escaped through the mesh.

Table 1 shows estimates of total biomass of the Achira population made during the period 1982–1986 using the same methodology. The biomass estimated after the fishery closure of 1989 was 75% higher than the average biomass estimated in four surveys carried out before the closure of the fishery.

The size structure of the Achira population showed a simple pattern which could be broken down into three size groups for each sex (Fig. 2). Normal curves were fitted to the observed distributions using the method of MacDonald and Pitcher (1979). The first two distributions for both sexes are the most important in terms of numerical abundance (Fig. 2). Assuming normal random stochasticity in size as a function of age, we may consider that the first and second age groups represent the youngest adjacent year-classes in the catches, and the remaining curves represent a mixture of older year-classes of uncertain age (MacDonald and Pitcher, 1979). Using parameters of growth according to Arana (1990; see Materials and Methods section) and the estimated mean size of males and females from each frequency distribution in Fig. 2, we estimated the average age of individuals in each cohort (Table 2). We concluded that the oldest individuals (4+ years) are survivors from the last fishing period which ended in 1988, individuals of intermediate age (3 years) were born in 1988, just before the start of the fishery closure of 1989, and the youngest individuals (2 years) were born in 1989, during the fishery closure (Table 2).

Partial biomass calculations indicate that at the time of the survey, in terms

Table 1

Comparison of results of surveys of the Achira population of squat lobster carried out using a similar methodology to that of this study

Year	Month	Area (km <sup>2</sup> )	Biomass (t)	Global density (t km <sup>-2</sup> )	Estimation error (%)
<i>1979–1981 fishery prohibition</i>					
1982	April	775.4	23 204	29.9	39.7
1983	April	1038.3	27 004	26.0	24.3
1984	March	464.2	21 876	47.1	31.4
1986	March	859.8	17 099	19.9	22.2
Average		784.4	22 296	28.4	29.4
<i>1989–1991 fishery prohibition</i>					
1991	Sept.–Oct.	1301.5	38 997	30.0	12.6

Data from technical reports of the Instituto de Fomento Pesquero.

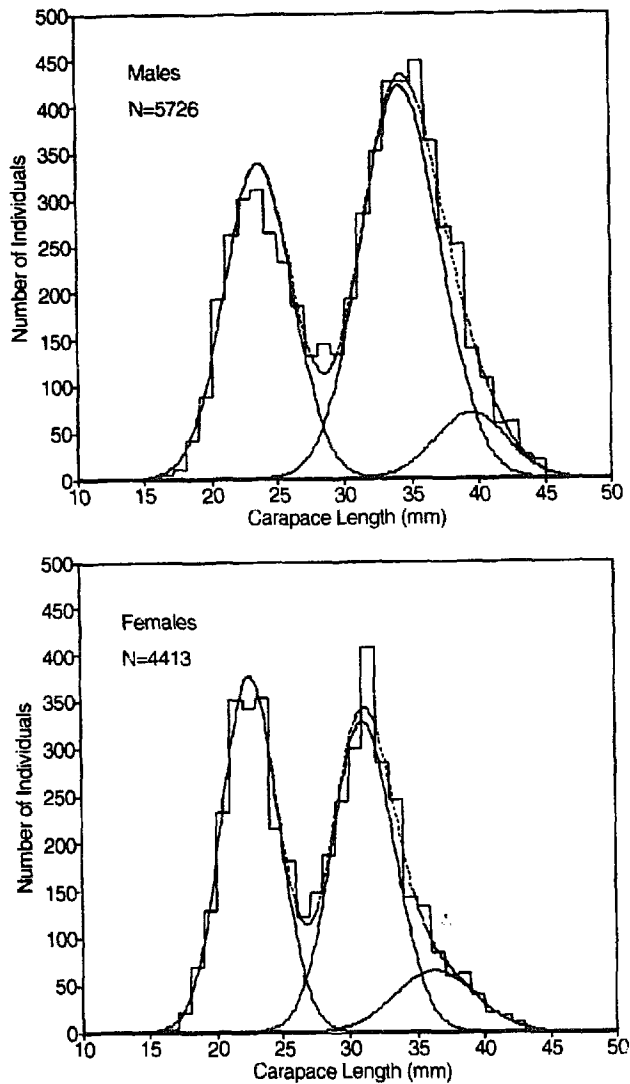


Fig. 2. Global size distribution. Curves were separated using the maximum likelihood method of Macdonald and Pitcher (1979). Dashed line, data; dotted lines, fitted distribution mixture; solid lines, component normal curves of the distribution mixture.

of biomass, the 1988 year-class was the most important both for males and females (Table 2). The 1989 and the mixture of older year-classes were of similar importance (Table 2). However, the 1988 year-class almost certainly had not reached its full growth potential, while the mixture of older cohorts must have been decaying owing to the predominance of mortality over somatic growth after a certain critical age.

### *Spatial structure*

Compared with the area occupied by the Achira population of squat lobster prior to the fishery closure of 1989, the population has expanded northwards



Table 2

Mean length, mean individual weight, and partial biomass of each year class in the size structure of the Achira population (Fig. 2) sampled in September–October 1991

Year-class	1989		1988		Older	
	Male	Female	Male	Female	Male	Female
<i>Length</i>						
CL (mm)	24	23	35	32	40	39
N	2177	1907	2776	2216	783	290
SD (mm)	2.7	2.0	2.5	2.6	2.3	2.1
Weight (g)	10.59	7.22	23.13	19.27	34.65	34.73
N	1411	1433	1130	973	155	70
SD (g)	3.62	3.23	6.63	6.02	7.25	6.09
Age (years)	2.06	1.91	3.44	3.01	4+	4+
<i>Partial biomass</i>						
Tonnes	4976	2972	13 804	9216	5855	2174
Percentage	12.8	7.6	35.4	23.6	15.0	5.6

CL, carapace length; N, sample size; SD, standard deviation.

by almost 56 km (Fig. 1). The expansion zone spans the 150 m isobath (Fig. 1(a)), although the depth range (100–170 m) is narrower and the deep border is shallower than in the southern area (92–243 m, Fig. 1(a)). Furthermore, the expansion front seems to have advanced, avoiding patches of hard bottom.

The spatial distribution of mean size (Fig. 1(b)) shows that the 1988 and older year-classes are predominant on the northern expansion zone, while the 1989 year-class is found almost exclusively in the southern part of the distribution. There is also an effect of depth on the spatial distribution of sizes (Fig. 1(b)): larger individuals occupy the deep border, while smaller individuals tend to be distributed in shallower bottoms. The spatial distribution by sex (Fig. 1(c)) shows that over most of the distribution each sex is equally represented. However, males predominate on the deep-southern border of the population (male proportion over 75%), and females show three patches of predominance along the centre of the population distribution. Figure 1(d) indicates that most of the reproductive potential (more than  $2 \times 10^{12}$  eggs  $\text{km}^{-2}$ ) is on the expansion zone, and that it decreases south of this area and towards the edges of the population distribution. In two cases, the centres of female predominance coincide with centres of high reproductive potential (Figs. 1(c) and 1(d)). The most important is located at the base of the expansion zone, which has an estimated egg density of more than  $17 \times 10^{12}$   $\text{km}^{-2}$  (Fig. 1(d)).

### Expansion parameters

We based our calculation of expansion parameters on the two strong year-classes (1988 and 1989) only. It was considered that the mixture of older year-classes was uncertain with respect to age and probably was about to reach its full potential of growth by 1989. In addition, the mixture of older year-classes had suffered fishing mortality while the 1988 and 1989 year-classes had not. Hence our estimation of biomass gain as related to expansion included only those two cohorts which had not suffered fishing mortality and that had not reached their full growth potential. Given the ages of those cohorts in Table 2, we may consider the initial biomass of that fraction of the population as zero. The partial biomass of these two cohorts in 1991 was 30 968 t, thus the average annual rate of biomass increase during the prohibition was  $10\,323\text{ t year}^{-1}$ . According to historical evidence, the northern limit of the population before the expansion was that indicated on Fig. 1. This implies a total northwards advance of about 60 km in 1991, and an average annual rate of advance of the front of  $20\text{ km year}^{-1}$ .

The trajectories of biomass increase for the 1988 and 1989 year-classes (Fig. 3) imply that in 1991, those cohorts had not reached their full growth potential. If the rate of advance of the front is linearly related to biomass increase, the quasi-linear trajectory of the summed biomass of the 1988 and 1989 year-classes (Fig. 3) suggests that the expansion front advanced at a constant rate during the years of fishery closure.

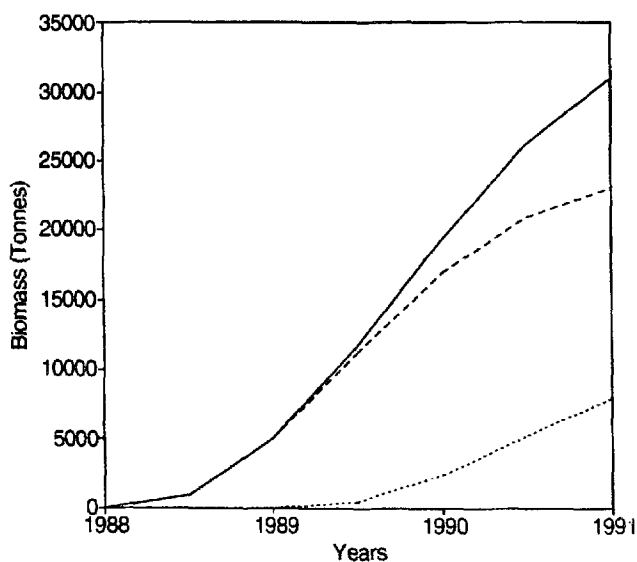


Fig. 3. Biomass trajectories of the two main year-classes at the start and during the period without harvest. Solid line, 1988 + 1989 year-classes biomass; dashed line, 1988 year-class biomass; dotted line, 1989 year-class biomass.

## Discussion

### *Management implications*

In describing the expansion of a population that has been reduced in spatial extension by overfishing and that re-invades its former habitat after a period without harvesting, it is useful to estimate the rate of advance of the front(s) and the rate of population increase. These results are fundamental to understanding the potential for recovery of the population and to making future management decisions, such as re-opening the fishery and establishing annual quotas.

Using a basic model of biomass change of a cohort over time and the simple age structure of the Achira population after 3 years without harvesting, we obtained an estimate of biomass increase during the period of fishery closure (Fig. 3). These results in turn yielded an estimate of the average rate of biomass increase of  $10\,323\text{ t year}^{-1}$ . From the points of view of management and conservation, it may be desirable to allow the population to continue its expansion until it reaches a stable size, age structure and geographical range. However, if the fishery is to be re-opened, a reasonable initial policy would be to set total annual quotas that correspond to some fraction of the annual average rate of biomass increase during the period without harvesting. In this way, we may expect the population to continue to expand and grow even in the presence of fishing mortality, provided that effort will not concentrate on the expansion front or on the recruiting year-class, and that annual recruitment will not fall. In fact, the fishery was re-opened in 1992, under the Individual Transferable Quota regime, allowing for a total annual catch representing 40% of the estimated average annual rate of biomass increase during the period without harvest.

Our estimates of average annual rate of biomass increase ( $10\,323\text{ t year}^{-1}$ ) and annual rate of biomass increase (trajectory of the curves in Fig. 3) completely depend on Eqs. (4), (5) and (6) and the parameters of growth (Arana, 1990) and natural mortality (Peñailillo and Henríquez, 1990) incorporated into Eq. (6). It is clear that Von Bertalanffy growth is not the most realistic approach to crustacean growth (Fogarty and Idoine, 1988), even when it can be a good approximation; nevertheless, it is often used (Campbell and Robinson, 1983; Caddy, 1984; Addison and Bennett, 1992). However, because of the interaction between growth and sexual maturity, it is common in decapod crustaceans that males and females have different growth schedules (Caddy, 1984; Fogarty and Idoine, 1988), with males attaining greater sizes. Arana's (1990) Von Bertalanffy approximation does not reflect this expected difference in growth schedules between sexes. Hence, our estimation of the annual rate of biomass increase depends on a model and parameters of growth which seem to be inappropriate for the squat lobster. In fact,

our data show that males of our 1988 year-class do have greater sizes than females of the same year-class ( $t$ -test,  $P < 0.001$ ). This produces age differences between the sexes (Table 2) which we consider anomalous, because it is very unlikely that males of the 1988 year-class were born before females of the same year-class. Consequently, to use Eq. (6) we ignored this age difference and rounded to the nearest integer, implicitly assuming different growth schedules for males and females. In this way, it is expected that we introduced a partial correction into our estimates of average annual rate of biomass increase, yielding a more realistic figure.

To explore the effect of parameter uncertainty on the trajectory of biomass increase (Fig. 3), we calculated total biomass (1988 and 1989 year-classes summed) during the period without harvest with different estimates of growth and natural mortality. We used three different values of  $k$  and  $M$ : the values estimated by Arana (1990) and Peñailillo and Henríquez (1990) and  $\pm 20\%$  of each, producing nine scenarios (Table 3). In the worst of the cases (20% increase in both  $k$  and  $M$ ), the annual rate of biomass increase deviated on average by 34% with respect to the estimations given on Fig. 3. In the second worst case (20% decrease in both  $k$  and  $M$ ), the annual rate of biomass increase decreased by 24% compared with estimations given in Fig. 3. This exercise shows that mild fluctuations in the parameters incorporated into Eq. (4) do not have a large effect on the trajectory of the curve of summed biomass for the two strong year-classes (Fig. 4).

Eventually, the population will reach some stable size, age structure, and latitudinal range, in which case management tools which have been proved useful for crustaceans, such as yield per recruit and egg per recruit analysis (Campbell and Robinson, 1983; Fogarty and Idoine, 1988), or length cohort analysis (Addison and Bennett, 1992) may be useful for establishing biological reference points.

Table 3

Mean percentage deviation of the trajectories of biomass increase for the 1988 and 1989 year-classes (summed), due to parameter uncertainty

Mortality parameter $M$ (year <sup>-1</sup> )	Growth parameter $k$ (year <sup>-1</sup> )		
	0.8 × Estimate 0.196	Estimate 0.245	1.2 × Estimate 0.294
0.8 × Estimate 0.504	-24.3	-16.9	-8.8
Estimate 0.63	-9.3	0.0	10.2
1.2 × Estimate 0.756	9.5	21.3	34.2

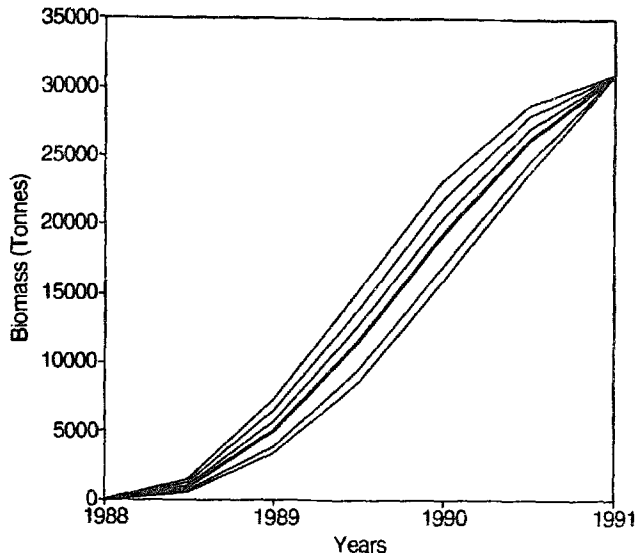


Fig. 4. Biomass trajectories of the 1988 + 1989 year-classes under mild parameter uncertainty. Heavy solid line, estimated trajectory using Arana's (1990) estimate of the Brody growth coefficient  $k$  and Peñailillo and Henríquez's (1990) estimate of natural mortality  $M$ ; light solid lines, five worst scenarios in which  $k$  and  $M$  are allowed to vary between 20% of their estimated value.

### *Mechanism of expansion*

A possible mechanism of expansion and its associated spatial size distribution is pelagic dispersal of larval stages. However, two different lines of evidence argue against it. First, the spatial size distribution shows that individuals dispersing northwards were the largest (i.e. oldest). If expansion was driven by larval dispersal we would expect the opposite, that the smallest (i.e. youngest) individuals would be located in the expansion areas. Second, the larvae hatch at the beginning of summer (Palma and Arana, 1990) in an environment dominated by the Peru–Chile Subsurface Countercurrent (Gallardo, 1977). Since this subsurface current flows southwards (Brockmann et al., 1980; Huyer et al., 1991), larval advection cannot explain a northwards expansion of the population.

Consequently, the mechanism of expansion must be looked for in population processes at the level of the benthic adult life. Specifically, we interpret our results on the expansion of the Achira population of squat lobster and the pattern of spatial distribution of size as evidence of a particular form of expansion pressure. The recruitment of the 1989 year-class into the population area provided the impetus for population expansion, but it was the 1988 and the mixture of older cohorts, free from fishing mortality, which dispersed into the vacant areas to the north (Fig. 1(b)). Expansion to the south could have been impeded by a bottom not suitable for squat lobster (see Fig. 1(a)) and/or the presence of recruits entering from the south (see Fig. 1(b)). Previous

to the closure, expansion could have been precluded by the removal of the potential dispersers by the fishery.

The proposed mechanism contrasts with what was found in a comparable case of re-invasion of habitats by the California sea otter (Lubina and Levin, 1988). In that case, data on population size and latitudinal range from several years since 1914, allowed the authors to show that range expansion of the California sea otter is described by a classical model of population diffusion (Skellam, 1951). In the classical model without advection and with homogeneous habitat, asymptotic rate of advance is proportional to the intrinsic rate of population increase and a diffusion coefficient calculated from individual movement or from distributional data (Okubo, 1980; Kareiva, 1983). Skellam's (1951) model assumes that all individuals are equal with respect to dispersal capacity. We have already noted that individual squat lobsters that dispersed to the northern vacant areas were not a random sample of individuals from the population but were those of greatest size (Fig. 1(b)), represented by the 1988 and older year-classes. Hence, size-dependent dispersal capacity seems to be a fundamental difference between population expansion of the California sea otter and the squat lobster.

### *Reproductive considerations*

Another important feature of the spatial distribution of population variables is the apparent transport of reproductive potential by large-sized females (Fig. 1(d)). A possible consequence of this spatial pattern of reproductive effort is the appearance of new nursery grounds towards the north. This in turn may alter the pattern of spatial size distribution, if recruitment is successful in the northern areas, with a potential effect on expansion dynamics.

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