Reproductive biology of the false southern king crab (*Paralomis granulosa*, Lithodidae) in the Beagle Channel, Argentina

Gustavo A. Lovrich
Consejo Nacional de Investigationes Cientificas y Tecnicas (CONICET)
Centro Austral de Investigaciones Cientificas (CADIC)
CC 92, 9410 Ushuaia, Tierra del Fuego, Argentina
Present Address: Maurice Lamontagne Institute, Invertebrates and Biostatistics Division, 850 Route de la Mer, P.O. Box 1000, Mont Joli, Quebec G5H 3Z4, Canada

Julio H. Vinuesa
Consejo Nacional de Investigationes Cientificas y Tecnicas (CONICET)
Centro Austral de Investigaciones Cientificas (CADIC)
CC 92, 9410 Ushuaia, Tierra del Fuego, Argentina

Abstract.—Reproduction of the false southern king crab (*Paralomis granulosa*) in two localities of the Beagle Channel, Argentina, was studied by monthly trap sampling during 1989 and 1990. Size at gonadal maturity in males (50.2-mm cephalothoracic length, CL) and females (60.6-mm CL) was significantly less than size at morphometric maturity (57.0-mm CL in males; 66.5-mm CL in females). Embryonic development lasted 18–22 months. During this period, there was apparently a 10–12 month diapause. In one of the two localities, development of eggs in a given clutch was very heterogeneous, suggesting simultaneous occurrence of eggs with 12- and 22-month development periods. Larval hatching took place mainly during winter. Female *P. granulosa* molted during November and mated immediately after. Biennial reproduction was detected on the basis of ovarian and embryonic development, and on the basis of shell condition. Thus, two different female groups occur in the population of the Beagle Channel. Fecundity increases with size (1,441 to 8,110 eggs per female) and is significantly less at the end than at the start of embryogenesis. Ovaries and brood each represented at most 6–7% of body weight. *Paralomis granulosa* is the only representative of its genus that inhabits shallow water and apparently retains some reproductive features of its deep-water relatives.

Manuscript accepted: 11 May 1993.
Fishery Bulletin: 91:664–675 (1993).

Crabs of the genus *Paralomis* are lithodids that inhabit the Atlantic, Indian, and Pacific Oceans, ranging in depth from 5 to 4152 m. The false southern king crab, or centollón in Spanish, *Paralomis granulosa* (Jacquinot, 1847), inhabits the Pacific Ocean from Paso Tenaún (Chile; 40°S) to Cape Horn, and the Atlantic Ocean from 56°S to the Golfo San Jorge (Argentina; 47°S) including the Islas Malvinas (Falkland Islands) at depths of up to 50 m (Macpherson, 1988).

Paralomis granulosa and the southern king crab (*Lithodes santolla*) constitute the main crustacean fisheries off the southern tip of South America. Commercial exploitation of *P. granulosa* started in the early 1970's. The largest catches were recorded in 1986 and amounted to 1,300 metric tons for Argentina and Chile. In Argentina, during the last three years, the yield of *P. granulosa* was at least twice as great as that of *L. santolla*. Although commercial fishing for *P. granulosa* began more than 15 years ago, studies on the life history of this species are few. Management studies were conducted in Chile which resulted in fishing regulations, such as a minimum legal size and gear restrictions (Campodónico et al., 1983). There is virtually no information on the life cycle of *P. granulosa* in South America, except for reports on larval development (Campodónico and Guzmán, 1981), larval ecophysiology (Vinuesa et al., 1989), and diets of juveniles and adults (Comoglio et al., 1990).

In this study we document aspects of the reproductive biology of *P. granulosa*, from data collected during monthly sampling in the Beagle Channel during 1989 and 1990. Data on the reproductive cycle, fecundity, embryogenesis, and other life history traits were examined to acquire basic information on the biology of this commercially valuable species.

Materials and methods

The fishing area was located along the Beagle Channel between Lapataia Bay (west) and the Moat Channel (east) (Fig. 1): fishing depths ranged from 10 to 60 m. The Beagle

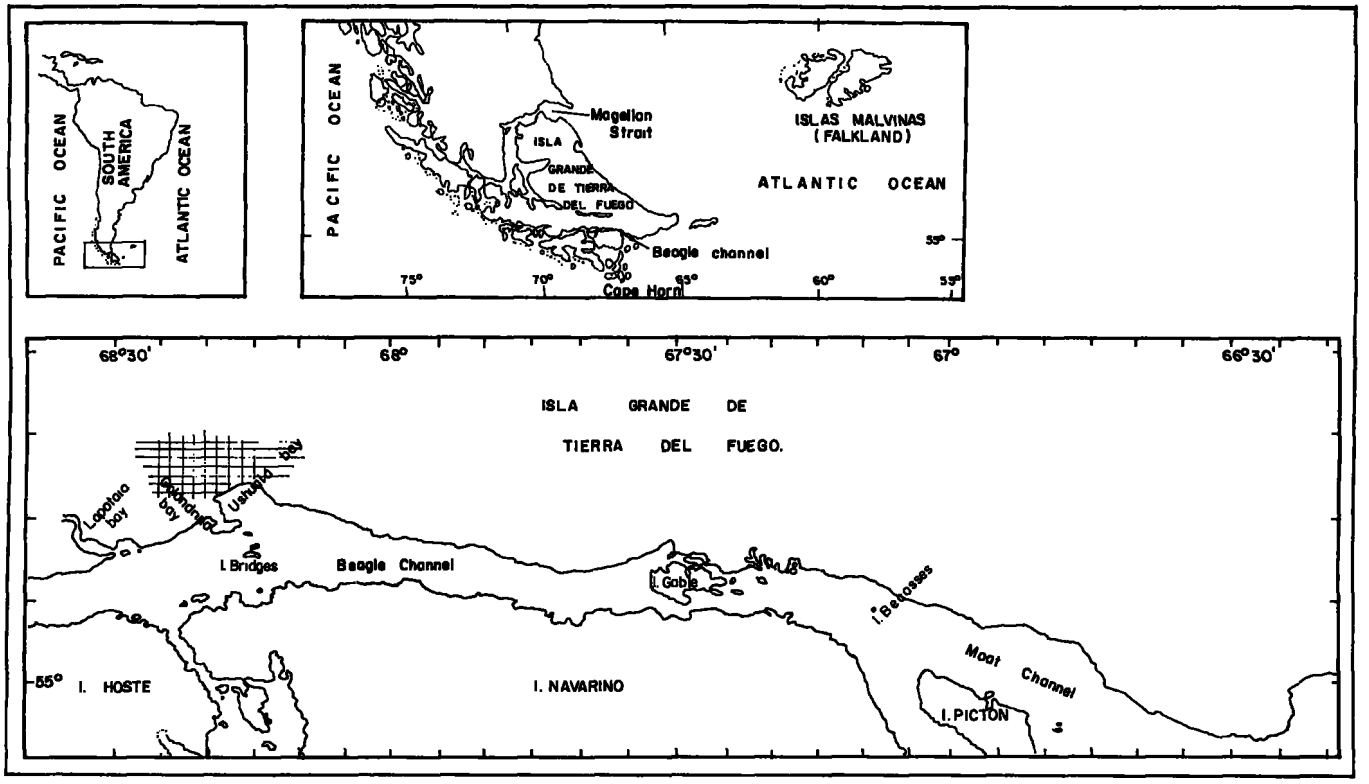

Figure 1
Location of sampling area.

Channel is an elongate glacial valley which stretches east-west, extending between the Isla Grande de Tierra del Fuego, and Navarino and Hoste Islands (Rabassa et al., 1986). It is 210 km long and on average 4 km wide and has a maximum depth of 160 m. Surface seawater temperatures range from 4.2 to 4.3°C in August and from 8.9 to 9.8°C in January; the annual mean temperature varies from 6.5 to 6.8°C. Salinity ranges from 26.7‰ in November–December to 31.3‰ during July and is highly variable during October and November because of ice melt.

Monthly samples were obtained from commercial catches from January 1989 to December 1990. Crabs were captured in traps deployed on bottom lines with 10 traps each. Traps were fished for 48 hours and usually baited with chicken, fish, horse, pig, cow, or lamb meat and bones. Each month 30–40 females and 10 males were randomly selected from the catch of a single line, placed in tanks with circulating seawater and transported alive to the laboratory. Carapace length (CL, midline distance between posterior orbital margin, excluding the rostral spine, and the posterior median margin) and right chela height (CH, measured at the anterior dorsal margin of the propodus, between the two anterior spines) of each crab were measured to the nearest 0.1 mm with a vernier caliper. Live body weight was measured to the nearest 0.01 g. The carapace of each crab was aged according to the following subjective scale:

1 Postmolt (POM): Shell soft, bright red, membranous and non-calcified, without epibiota.

2 Early Intermolt (EIM): Shell hard but brittle, bright red, without epibiota.

3 Median Intermolt (MIM): Shell hard, red to brown, variably covered with epibiota such as serpulids.

4 Advanced Intermolt (AIM): Shell hard, dark red, with numerous epibionts including balanids (6–8 mm maximum basal diameter), bivalves (*Mytilus edulis, Aulacomya ater*, 4–6 mm length), serpulids, and other calcareous polychaetes, bryozoans, and brown algae.

5 Premolt (PRM): Similar to AIM but the old shell is partially raised, revealing the new shell.

For both sexes, we used two methods to determine the size at which 50% of individuals were mature:

- Analysis of reproductive features. Females were considered to be mature if they had eggs or empty egg cases attached to the pleopods; males were considered to be mature if spermatophores were found in their vas deferens. The proportion of mature individuals was calculated for each 5-mm-CL interval and a logistic function was adjusted to provide 50% maturity.
- Allometric growth of the right chela. This method is based on the relative change in chela height at sexual

maturity (Hartnoll, 1978). We used MATURE1, the computer method described by Somerton (1980) to fit a pair of intersecting straight lines to plots of chela height on carapace length. The method determines the regression lines for crabs that are assumed to be immature and mature, based on minimum observed size at gonadal maturity and maximum size at gonadal immaturity, respectively. Then it extends the lines to the central area of the plot, where immature and mature crab are mixed, by iteratively assigning each point to either line, then recalculating lines, until no points switch lines on two successive iterations. On the basis of this classification, the proportion of mature individuals was calculated for CL-size intervals of 5 mm in males and of 4 mm in females and a logistic function was adjusted to provide 50% maturity (Wenner et al., 1974). Measurements of partially regenerated chelae were excluded from this analysis. Data for crabs <50 mm CL were obtained from a study of juvenile growth (Lovrich, 1991).

Fecundity was defined as the number of eggs per clutch. In the laboratory, pleopods with attached eggs were removed from each female and preserved in buffered 10% formalin in seawater. Later the eggs were detached from the pleopods and the clutch was blotted and weighed to the nearest 0.01 g (*WC*). Three subsamples were then weighed to the nearest 0.01 g (*ws*) and eggs in each subsample were counted (*ns*). Fecundity (*F*) was calculated as:

$$F = \sum_{i=1}^{3} [(WC * ns)/ws] / 3 .$$

Estimates of fecundity based on counts of three subsamples did not vary by more than 5%.

Egg characteristics, color, developmental stage, presence of chromatophores and appendage development were determined monthly with the aid of a stereoscopic microscope. Fifteen *P. granulosa* females were kept in a 600-L and 250-L tank in a controlled-environment room with photoperiod, temperature, and salinity adjusted to natural environmental variations from April 1990 to May 1991. Crabs were fed *ad libitum* with limpets, mussels, and fish 2–3 times a week. A subsample of 15–20 eggs was taken from each egg mass at weekly intervals at the beginning of the study and at monthly intervals thereafter. Eggs from females kept in the laboratory and eggs preserved in formalin were separated, and the maximum diameter of each egg was measured to the nearest 0.01 mm with an ocular micrometer.

Ovaries were removed and weighed to the nearest 0.01 g. Two portions of the ovary were sampled: one was stored in buffered 10% formalin in seawater and the other was fixed in Bouin's solution and later transferred to 70% ethanol. The latter portion was then embedded in paraffin, sectioned at 8–10 μm and stained with "one time" trichrome (Gabe, 1958). Ovarian development was described in two ways: 1) the gonadosomatic index was the ratio weight of ovaries : total body weight, multiplied by 100; 2) mean diameter of oocytes was determined from measurements of 30 to 40 of the roundest oocytes from the periphery of the formalin-preserved ovary by using an eyepiece micrometer on a compound microscope.

Ten to 12 males were dissected bimonthly to check for the presence of spermatophores in the vas deferens. The right vas deferens was stored in 10% formalin and later pressed between a slide and coverslip to detect spermatophores under a microscope.

Data were $\log_{10}$-transformed to obtain normality and to reduce heteroscedasticity. Simple correlations and predictive regressions were then calculated for selected life history traits. Outliers were detected by comparing the values of the standardized residuals from the regression line to Student-*t* tabulated values. Slopes and elevations of regressions were compared by analyses of variance (ANOVA) and of covariance (ANCOVA), respectively (Sokal and Rohlf, 1981).

Discriminant analysis was used to determine the existence of two groups in ovarian development data. We then classified each crab into either group on the basis of an objective decision rule (Morrison, 1976). Variation in oocyte diameter and gonadosomatic index were positively correlated with ovary size. Thus, one of the assumptions of discriminant analysis was not met since variance-covariance matrices were not statistically equal even though data were transformed. The discriminant function was used to score individual females. The Games and Howell test (Sokal and Rohlf, 1981) was then used to contrast groups identified by the discriminant analysis.

Results

Gonadal and morphometric maturity

Fifty percent gonadal maturity occurred at 50.2-mm CL in males and at 60.6-mm CL (95% confidence limits: 58.3–62.9) in females (Fig. 2A). Even though the largest females did not carry eggs, we assumed they were mature because their ovaries were normally developed. The smallest male with spermatophores was 49.1 mm CL, whereas the largest one without spermatophores was 70.2 mm CL. The smallest female carrying eggs was 59.7 mm CL and the largest one without eggs and without developed ovaries was 75.1 mm CL.

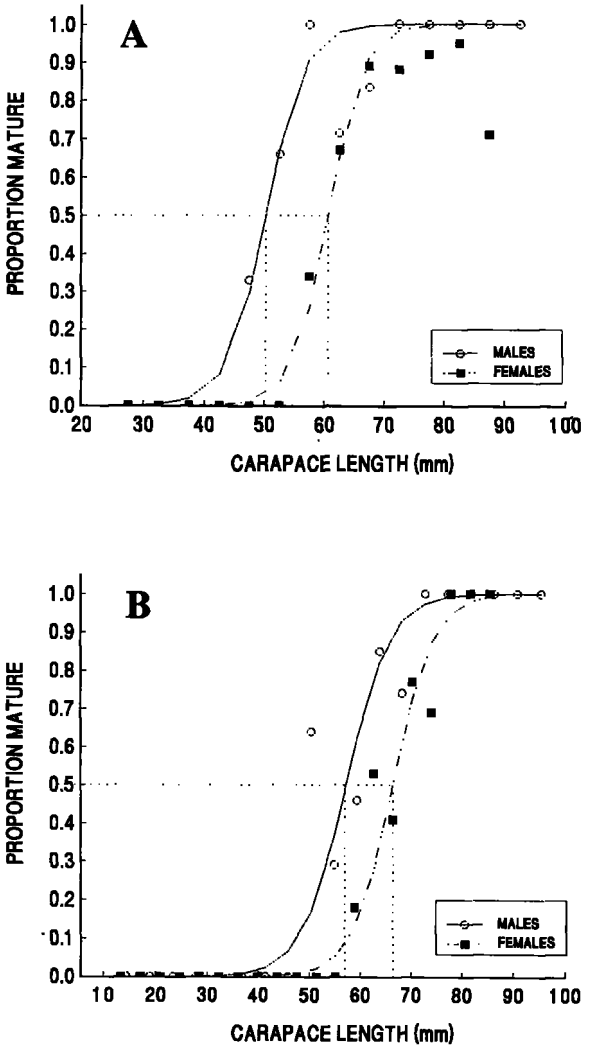

Figure 2

Gonadal and morphometric maturity in *Paralomis granulosa*. Size at 50% maturity is given by the intersection between the calculated logistic function and 0.5 ordinate. (**A**) Proportion of mature *P. granulosa* on the basis of presence of spermatophores in 137 males and presence of eggs or empty egg capsules in 732 females. (**B**) Proportion of mature *P. granulosa* on the basis of allometric growth of chelae.

Size at morphometric maturity was calculated for 851 females (11–88.8 mm CL) and 759 males (6.5–115.1 mm CL). The slope of the regression of chela height on carapace length for juvenile males (<49.1 mm CL; slope=1.012) was significantly less (F=385.7; P<0.001) than that for adult males (>70.2 mm CL; slope=1.473) (Fig. 3). The slope of the regression for known juvenile females (<59.7 mm CL; slope=0.96) was significantly greater (F=223.0; P<0.001) than that of adult females (>75.1 mm CL; slope=0.84). Estimated size at morphometric maturity 50% were 57.0 mm CL (95% confidence limits: 53.9–60.1) for males and 66.5 mm CL (95% confidence limits: 63.4–69.5) for females (Fig. 2B). These results indicated that the method can be applied to both sexes.

Embryogenesis

Embryogenic development was divided into five stages as follows:

Embryonic Stage I (ES I): Spherical or slightly ellipsoidal egg. Yolk bright yellow or orange. A perivitelline space present between the chorionic membrane and the yolk mass. No evidence of division.

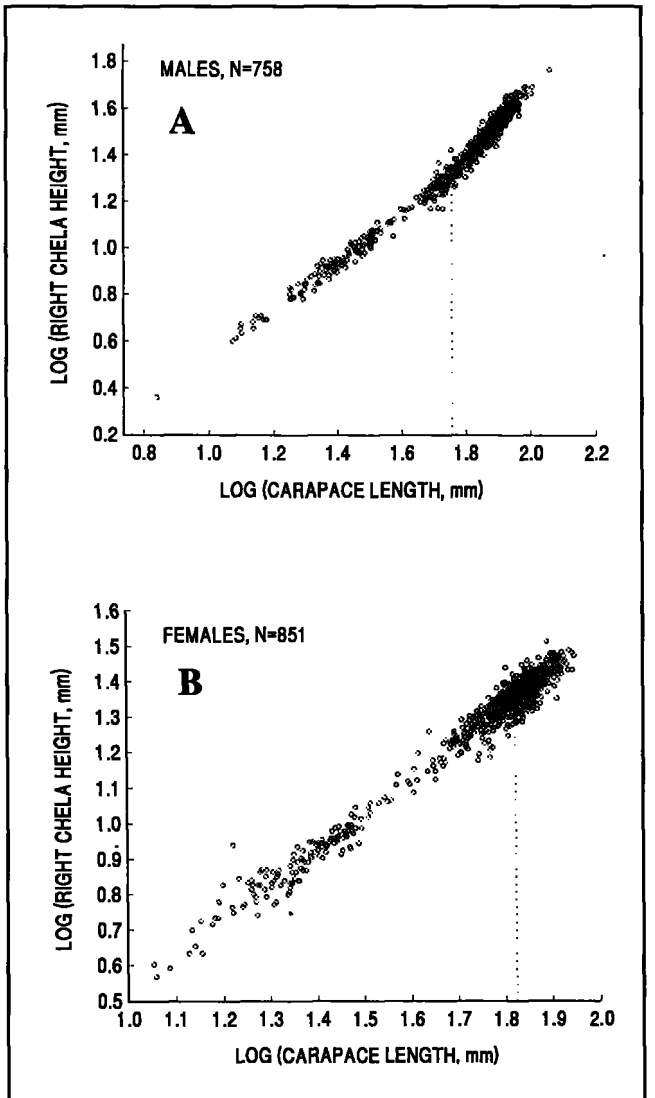

Figure 3

Scattergrams of log right chela height on log carapace length for 758 males (**A**) and 851 females (**B**) of *Paralomis granulosa*. Data for regenerated chelae were removed. Dotted line shows the intersection of juvenile and mature regressions and represents size at maturity: CL = 57 mm for males; CL = 66.5 mm for females.

Embryonic Stage II (ES II): Similar to stage I but a whitish mass of cells visible on yolk surface. This mass is associated with a slight depression in the yolk where the perivitelline space is deeper.

Embryonic Stage III (ES III): A whitish embryo without pigmentation clearly visible, occupying approximately 20% of egg volume. Eye spots clearly outlined. A dorsal organ is present at opposite of embryo (cf. ectodermal thickening of other malacostracan and peracaridan embryos; Anderson, 1982). Abdomen is segmented (5 somites+telson). Telson with 5–7 setae on each of the two lobes. Antennulae and antennae have setae-like projections. Three pairs of appendages are formed posterior to the antennae: mandible, maxillula, and maxilla.

Embryonic Stage IV (ES IV): Egg ellipsoidal; embryo occupies up to 50% of egg volume. Eye spots with ocular pigments. Up to 200 red chromatophores present on carapace. Dorsal organ no longer found.

Embryonic Stage V (ES V): Egg ellipsoidal, pale brown to pale orange. Fully developed zoea clearly visible. Embryo occupying from 50% to almost all of egg volume. Yolk masses reduced and restricted to two dorsal areas in the anterior third of the cephalothorax. All post-mandibular cephalothoracic appendages are differentiated into 3 pairs of maxillipeds and 5 pairs of pereopods, the last one reduced. Telson with 9 setae on each lobe. Heart beat evident.

Duration of embryogenesis and molt stages

Females held in the laboratory were divided into two groups on the basis of embryonic development. One group of females had eggs in ES II from April 1990 up to September 1990 through February 1991, when ES III appeared. ES III did not last longer than two months (in each egg mass) and in May 1991 all eggs were in stage IV. Therefore, these eggs spent autumn and winter in stage II, which suggests an arrest in embryonic development or diapause. The second group of females had clutches with eggs in ES IV in April 1990, which hatched into larvae in October 1990. Post-ovigerous females molted in November 1990, and then extruded and attached eggs in the absence of males. These eggs were unfertile since females have no receptacle to store male gametes (cf. spermathecae in majids). The unfertilized eggs were lost within the next 20 days.

Females collected from the Beagle Channel at any time during the year had egg masses with eggs either in early (I or II) or late (III, IV, or V) stages of development (Table 1; Fig. 4A). ES I and ES II were generally >40% in frequency during the two sampled years. ES III never exceeded 5% in frequency and was observed in February and August 1989, and in April, July, and October 1990. These findings suggest that diapause ends between early winter and late summer, as observed in the laboratory. ES IV and ES V occurred mainly from late autumn to early spring. Post-ovigerous females appeared from late autumn to early spring.

Samples of *P. granulosa* taken from the study area at any given time comprised females in at least two different molt stages: either EIM or AIM occurred with MIM (Table 1, Fig. 4B). PRM females occurred in October and POM females were found in October and November 1989.

Asynchronous embryonic development

A portion of the females (21%; n=100) from the Bécasses Islands, and some from the area near Ushuaia (2%; n=395) carried clutches with eggs at different stages of development: ES II and ES IV or V were found in the same egg mass. This was observed around the Bécasses Islands in August 1990, where 7 females carried eggs in ES II (at least 50% frequency in each clutch) and in ES IV. In October 1990, 12 females had eggs in ES II (at least 50% frequency) and ES V. Two other clutches had eggs in ES II and ES IV. The more advanced eggs would probably hatch earlier than those that were less developed. We could not determine when hatching occurred because commercial fishing around the Bécasses Islands was suspended in October 1990 and the females were not held for further observation.

Table 1

Embryonic development and shell condition of female *Paralomis granulosa* on 20 May 1990 in two localities, 10 km apart. ES=embryonic stages. Postovigerous females have empty egg cases and funiculi attached to the pleopodal setae. MIM=median intermolt; AIM=advanced intermolt. Frequencies for both embryonic development and shell-condition are significantly different between the two localities (G-test for homogeneity on embryonic development = 12.66; P<0.005; G-test for homogeneity on shell condition = 23.45; P<0.005).

	Embryonic development			Shell condition		
Location	ES I, II, and III	ES IV and V	Postovig. females	MIM	AIM	n
Golondrina	60	31	9	64	35	587
Bridges Is.	44	51	5	31	69	84

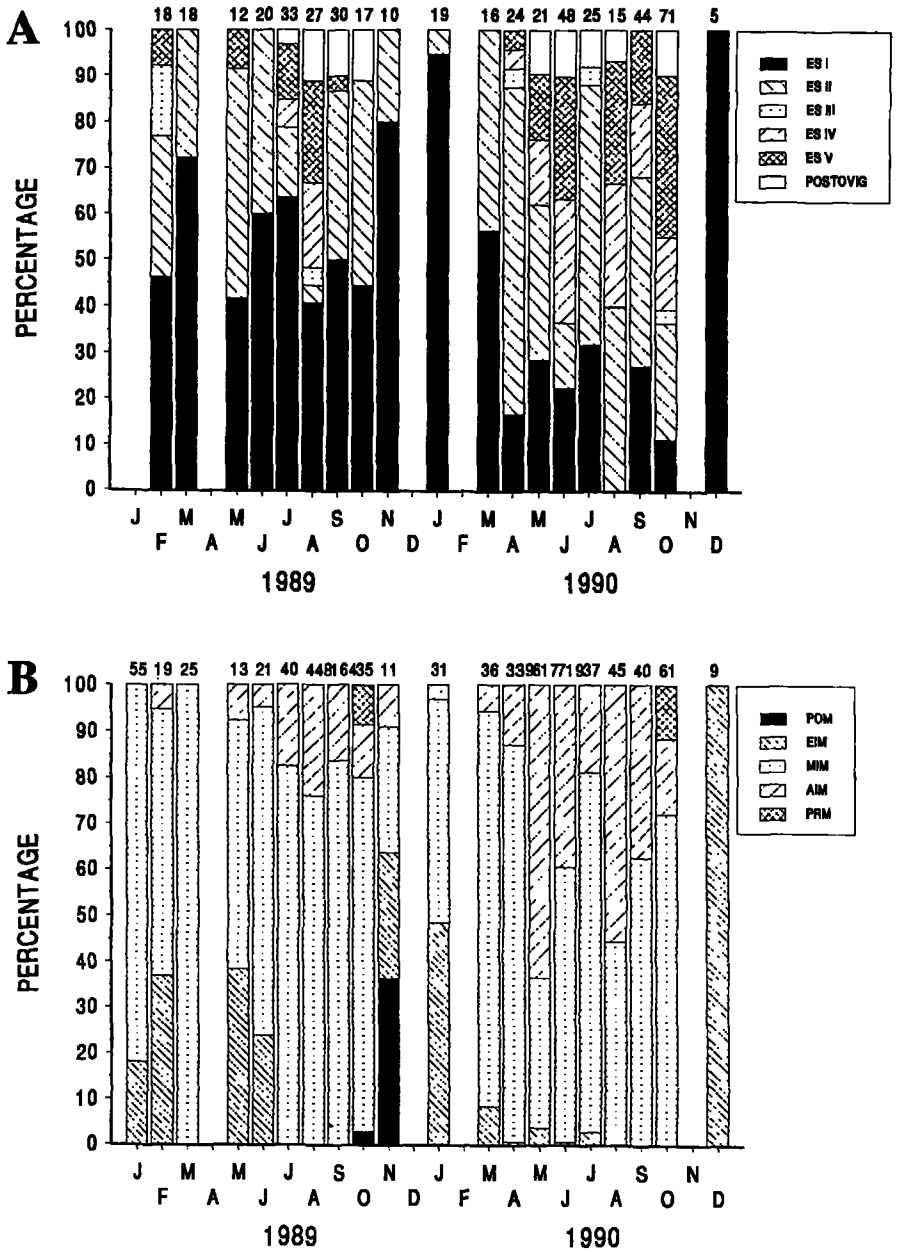

Figure 4

(**A**) Frequency of occurrence of egg stages through two years of sampling. Sample sizes are indicated above bars. Months with no samples are bare. (**B**) Frequency of occurrence of molt stages through two years of sampling. Sample size are indicated above bars. Months with no samples are bare.

Embryonic growth

Eggs from a single clutch increased significantly in size from the ES II (1.71 mm) to ES V (1.96 mm) (paired t-test: t=4.604; 3 df; P=0.02) in approximately one year of incubation in the laboratory. Within each asynchronously developing clutch, eggs in ES II (1.87 mm) were significantly smaller than those in ES IV or ES V (1.94 mm) (completely randomized ANOVA; F=22.5; 1,12 df; P<0.001). Egg size at a given stage of development varied significantly among females (F=13.28; 12,12 df; P<0.001). This demonstrates that embryonic growth cannot be generalized from eggs of individual female *P. granulosa*.

Development and maturity of ovaries

Ovarian development of *P. granulosa* was described in detail by Lovrich (1991) and is similar to that of *L. santolla* (Vinuesa, 1984). The only difference with the latter was that oocytes in the ovaries of female *P. granulosa* that had recently molted and spawned were already in an early vitellogenic phase. These oocytes were surrounded by fibrous connective tissue and radiated outwards from the germ strand.

Two groups of females, separated by differences in oocyte diameter (OD) and gonadosomatic index (GSI), were present in virtually all of the sampled months (Figs. 5 and 6). Discriminant analysis on a matrix consisting of CL, CH, OD and GSI (n=220 females sampled during 1990) gave 2 groups. The first included POM, EIM, or MIM females with eggs in ES I and ES II, the second comprised AIM or PRM females with eggs in ES III, ES IV, or ES V. The resulting discriminant function was

$$y = 0.083\ CL + 0.08\ CH - 0.727\ OD - 0.323\ GSI,$$

where coefficients were standardized by the standard deviations within groups. The canonical correlation was 0.798. The reproductive variables OD and GSI dominated the function, whereas morphological measurements contributed negligibly (canonical loadings: CL: 0.17; CH: 0.155; OD: –0.955; GSI: –0.866).

An *a posteriori* classification was generated from the discriminant function. After applying the discriminant function to data for individual females we found that mean scores (i.e., y in function above) were significantly different for each group (Games and Howell test, t'_s=2.49; P<0.01). We thus conclude that there are two distinct groups differing in shell condition and development of ovaries and eggs. These two groups are a key feature of a biennial reproductive cycle.

Females with asynchronous embryonic development were grouped by the discriminant analysis with females in their first year of the reproductive cycle. In fact, for these females, mean GSI was 2.78% in August and 3.38% in October, representing 45 to 55% of maximum GSI (fully developed ovaries in October, Fig. 5), respectively. Their average OD was 1.24 mm in August and 1.36 mm in October, whereas the maximum expected at the end of the reproductive cycle was 1.8 mm (Fig. 6).

Fecundity and reproductive effort

Fecundity was studied in relation to carapace length in the Ushuaia (Fig. 7) and Bécasses Islands. Clutches in late stages (ES IV or ES V) were analyzed separately to avoid underestimations due to possible loss of eggs (Kuris, 1991). Regressions of fecundity on carapace length were significant (Table 2; Fig. 7) and the slopes did not differ between females carrying clutches with eggs in ES I-II, in ES V, or with asynchronously developing eggs (from Bécasses Islands) (F=1.12; P=0.33). ANCOVA indicated that females with ES V eggs or with asynchronously developing eggs had fewer eggs per clutch than those with ES-I and ES-II eggs (F=7.29; P<0.001) (Table 2). Adjusted fecundity was

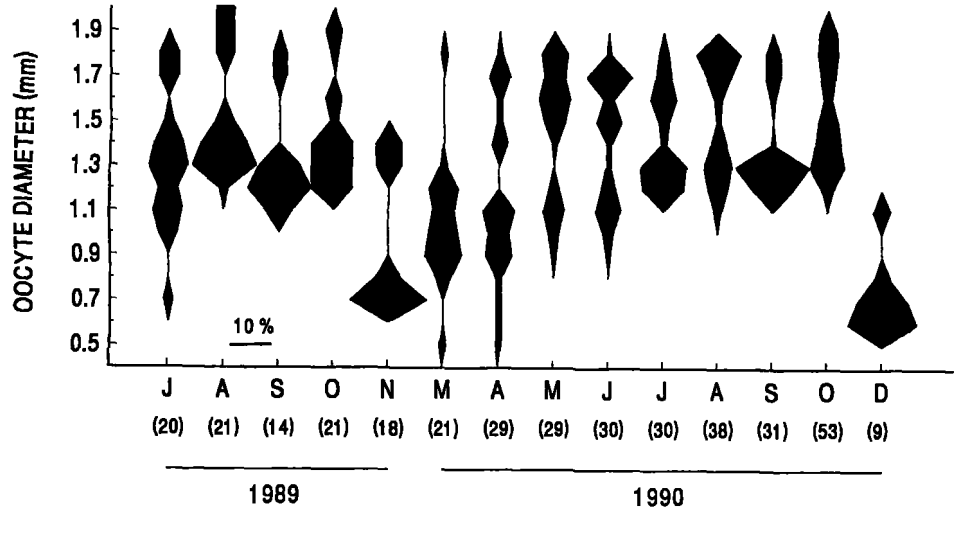

Figure 5
Relative frequency of oocyte diameter for female *Paralomis granulosa* caught in the Beagle Channel. Sample size is indicated in parentheses below each month.

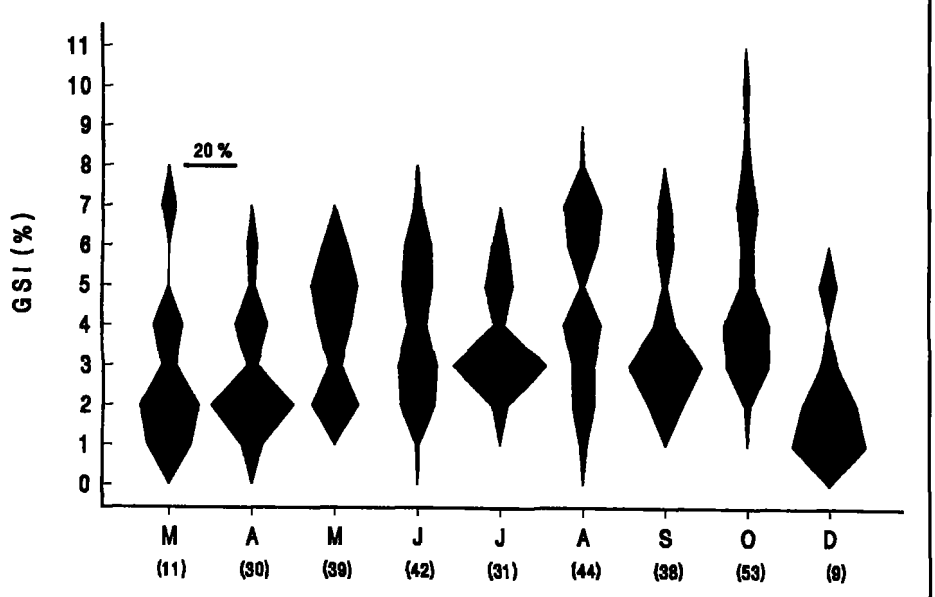

Figure 6

Relative frequency of gonadosomatic index (ratio ovaries weight : body weight * 100) of female *Paralomis granulosa* during 1990. Sample size is indicated in parentheses below each month.

3,688 eggs for females with ES-V eggs and 3,783 eggs for females with asynchronously developing eggs, representing about 88–90% of the estimated 4,201 eggs of females with ES I–II clutches for a constant carapace length (71.0 mm).

The ovaries and clutch of female *P. granulosa* were limited to less than 6–7% of body size. Brood weight varied from 3.67 to 30.39 g and scaled isometrically with weight of body, excluding clutch. Brood weight was at most 7% of female body weight:

$$\log \text{clutch weight} = -0.94 + 0.89 \log \text{weight (body excluding clutch)}$$

(n=196; r^2= 0.303 $F_{regression}$ = 81.99, P<0.001; t-statistic for H_0 slope=1 = –1.122; P=0.26).

In addition, towards the end of the reproductive cycle in October (23rd month), GSI was about 6–7% (Fig. 6).

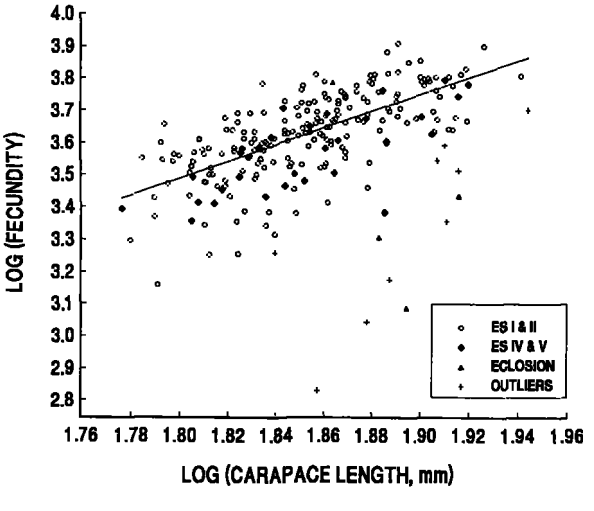

Figure 7

Scattergrams of log fecundity (eggs carried by a female) on log carapace length for *Paralomis granulosa* from Ushuaia area. ES I and II, n=192; ES IV and V, n=32; hatching eggs, n=4; outliers, n=9. The line represents the calculated equation for clutches in ES I and II.

Discussion

Our data indicate that *Paralomis granulosa* has a biennial reproductive cycle. First, female *P. granulosa* molt from late October to November, as evidenced by occurrence of PRM and POM stages (Fig. 4B). We consider that this event marks the beginning of the molt cycle and thus of the reproductive cycle. The frequencies of the different molt stages were consistent with those of the embryonic developmental stages, suggesting that embryogenesis and molting are phased. Embryogenesis lasts 18–22 months and is protracted by a 10-month diapause. Females with ES-I and ES-II eggs were always present throughout the year in the field samples and laboratory. Eggs are extruded from October through November and embryonic development stops or slows at the beginning of cell division (ES II probably representing the diapause stage). After approximately one year of incubation, embryonic development resumes between October and January, and

Table 2

Predictive regression of fecundity (F) on crab size (CL, in mm) in two different locations of the Beagle Channel, during 1989 and 1990. Regressions for different stages of embryonic development (ES) are presented for Ushuaia. R^2=coefficient of determination; F=F-statistic; ***=P<0.001.

Embryo development and location	Equation of regression	n	r^2	F	CL range (mm)
(1) ES I and II (Ushuaia)	$\log F = -1.21 + 2.61 \log CL$	192	0.459	161.3***	60.2–88.0
(2) ES V (Ushuaia)	$\log F = -1.03 + 2.48 \log CL$	32	0.501	33.2***	59.7–83.2
(3) Asynchronous (Bécasses I.)	$\log F = -2.72 + 3.41 \log CL$	43	0.528	45.9***	61.1–78.4

Average log CL = 1.851 (± 0.034)

Adjusted log F (1) = 3.633 (± 0.007)
Adjusted log F (2) = 3.567 (± 0.017)
Adjusted log F (3) = 3.578 (± 0.015)
(1) ≠ (2) & (3), P < 0.01; (2) ≠ (3), P = 0.63

continues through the next winter, when eclosion occurs. Second, females separated into two groups on the basis of brood development, shell condition, and maturity of ovaries (Table 1; Figs. 5 and 6). In general, females that carried eggs in ES IV and ES V were in advanced molt stages (AIM and PRM) and had fully developed ovaries; by contrast, females with eggs in ES I, ES II, and ES III were in EIM or MIM stages and had small ovaries. Additionally, the presence of oocytes in early vitellogenesis in the recently spawned ovary denotes that oogenesis started before spawning and thus lasts more than two years. In *Lithodes santolla*, oogenesis lasts 24 months (Vinuesa, unpubl. data) while embryogenesis lasts 11 months (Vinuesa, 1984).

The asynchronous embryonic development of *P. granulosa* is a novel feature among lithodid crabs. Our data suggest that some of the eggs within a single clutch develop in 12–14 months and hatch in early summer, while the remainder of the eggs complete their development during the next 10 months. We discount the possibility of a second mating and egg extrusion without molting because 1) there is no seminal receptacle, and chitinous plates cover the gonopores during intermolt, and 2) the ovaries of females with asynchronously developing eggs were in the first year of their cycle. There is clearly a regional effect involved in asynchronous development since females from Ushuaia had more uniformly developed broods. However, with data presently available, we cannot speculate on the causes of this phenomenon.

Since gonadal maturity (presence of gametes) does not necessarily imply morphometric maturity (crabs with differentiated secondary sexual characters), these two terms should be used to define different events in life history that may or may not occur simultaneously. We consider that these concepts are applicable to *P. granulosa* since different sizes at maturity were calculated by using different features (Figs. 2 and 3). Size at maturity for *P. granulosa* tends to increase with increasing latitude (Table 3). This relationship has been noted for *L. santolla* as well (Vinuesa, 1985). By contrast, in the Northern Pacific, size at maturity of lithodid crabs decreases with increasing latitude (Jewett et al., 1985; Somerton and Otto, 1986; Blau, 1990; Otto et al., 1990). Causes of geographical variation in size at maturity are still unknown, but environmental conditions such as bottom temperature may be a factor.

Traps may give biased samples because 1) they select for larger animals (Miller, 1990, but see Blackburn et al., 1990), 2) small crabs and females are excluded

Table 3

Size at maturity (in mm) of *Paralomis granulosa* in different localities. Size at morphometric maturity (SMM) is presented for males and size at gonadal maturity (SGM) for females. Where available, ±95% confidence intervals are presented in parentheses.

Area	Males (SMM)	Females (SGM)
Malvinas I. (Falkland)[1] (51°30'S)	52 (2.15)	46
Seno Otway[2] (53° S)	64	52
Magellan Strait[2] (52°30'S–53°S)	71	62
Beagle Channel (1981–2)[2] (54°55'S)	75	66
Beagle Channel (this study)	57 (3.1)	60.6 (2.3)

[1]Hoggarth, D.D., National Rivers Authority, Welsh Region, Gwyneedd, UK, pers. commun. 1992.
[2]Campodónico et al. 1983.

by larger males, and 3) crabs near ecdysis and berried females are less vulnerable to trapping since they do not feed (Miller, 1990). Size at maturity of *P. granulosa* may be overestimated because the 57.5-mm-CL size class was poorly sampled; this would particularly affect size at gonadal maturity. Also, the frequency of occurrence of females with late embryonic stages, especially those in pre- and postmolt conditions, may be underestimated by trap sampling. Unfortunately, we have no way to assess these possible biases because we have no trawl surveys with which to compare data.

Compared with other shallow-dwelling lithodids, *P. granulosa* has low fecundity and large eggs, resembling in this respect the deep-water species: *Lithodes ferox* (8,000 eggs maximum, 1.97 mm egg diameter; Abelló and Macpherson, 1992); *L. couesi* (5,000, 2.3 mm; Somerton, 1981); *L. murrayi* (4,200, 2.45 mm; Miquel and Arnaud, 1987; Miquel et al., 1985). By contrast, the shallow water *Paralithodes camtschaticus* and *P. platypus* carry up to 350,000 and 280,000 eggs, respectively, with an average egg diameter of 1.2 mm (Matsuura et al., 1971, 1972; Somerton and MacIntosh, 1985). Fecundity of *P. granulosa* was less in females with ES V or with asynchronously developing clutches for a constant carapace length (Table 2), because of egg loss. At the end of embryogenesis about 10–12% of the initial brood was lost. Diseases and egg predators are frequent causes of egg loss in crab species (Kuris, 1991). However we did not find evidence of epibiosis in broods of *P. granulosa*. Exceptionally small broods, outliers in Fig. 7, may have resulted from delayed mating, lack of mates, or to small size of mating males, as occurs in other lithodids (McMullen, 1969; Powell et al., 1973; Paul and Paul, 1990). This question requires further investigation.

As the energy expended on each offspring increases, the number of offspring that parents produce decreases (Smith and Fretwell, 1974). Thus, in two related species similar energetic investment may result in many small or few large offspring. However, considering the two lithodids of the Beagle Channel, one finds that *P. granulosa* biennially produces eggs which are fewer but not larger than those of *L. santolla*, which annually produces up to 59,000 eggs (Guzmán and Campodónico, 1972) of 2.1–2.2 mm in diameter (Vinuesa, 1987).

There is no evidence that the biennial reproductive cycle of *P. granulosa* is more advantageous (i.e., an adaptative strategy) than the annual cycle of *L. santolla*. *Paralomis granulosa* larvae pass through fewer molting events (Campodónico, 1971; Campodónico and Guzmán, 1981); thus mortality due to ecdysis is reduced. Shorter larval development would also reduce predation risks in the plankton. Inhabiting the layer of water closest to bottom (Lovrich, unpubl. data) allows larvae to find refuge and thus reduces losses to predation. We speculate that the lesser fecundity of *P. granulosa* may be partially compensated for by a high survival during their development. In *Paralithodes platypus*, Jensen and Armstrong (1989) interpreted biennial reproduction as a consequence of physiological and energetic constraints incurred by the species in a harsh environment.

King crab species can be categorized into three groups on the basis of their reproductive cycles: *Paralithodes camtschaticus* and *Lithodes santolla* spawn annually, *Paralomis granulosa* and *Paralithodes platypus* (except primiparous females) spawn biennially, and finally *L. aequispina, L. couesi*, and *L. ferox* spawn asynchronously. All *Lithodes* species, with the exception of *L. santolla*, inhabit deep waters whereas *Paralithodes* species inhabit shallow waters. Otto and Cummiskey (1985) hypothesized that king crabs inhabiting shallow waters (*L. santolla, P. camtschaticus*, and *P. platypus*) spawn synchronously during spring while deep-sea king crabs (*L. aequispina* and *L. couesi*) have protracted spawning periods. These authors suggest that this pattern could be related to a dependence on food sources by shallow water species. *Paralomis granulosa* inhabits shallow waters and spawns synchronously every two years, but we suppose that in this species synchronicity is not related to food dependence because larval hatching occurs mainly during winter when neither food nor potential competitors are abundant (Lovrich, unpubl. data).

Paralomis is a deep-water genus (Takeda et al. 1984; Macpherson, 1988) and *P. granulosa* is the only species that inhabits shallow waters. This species probably colonized the Beagle Channel relatively recently, i.e., 8,500 years ago after the last deglaciation occurred (Rabassa et al., 1986). This species still retains certain features of its deep-water relatives: low fecundity, large eggs, protracted reproductive cycle, and independence of larval hatching from food availability.

Acknowledgments

This study was funded by CONICET (PID # 3154700-88). We thank the fishing companies Mar Frio S.A. and Pesquera del Beagle S.A. for allowing us to sample on board. Special thanks to José T. García, Héctor Monsalve, and the crew of the fishing boats. Beatriz González (Biological Dept., F.C.E.y N., University of Buenos Aires) supervised statistical analysis; Mercedes Cattaneo assisted in correction of the early English version; and Bernard Sainte-Marie (Dept. Fisheries and Oceans, Canada) as well as two anonymous reviewers

provided helpful comments that improved the manuscript.

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