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Reproductive potential of the lithodids *Lithodes santolla* and *Paralomis granulosa* (Anomura, Decapoda) in the Beagle Channel, Argentina*

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SUMMARY: Lithodidae is the only group of reptant decapods that occurs in Antarctic waters and has been particularly abundant in the Beagle Channel, Straits of Magellan and south to 50º S. Because of their abundance in coastal waters, the sympatric *Lithodes santolla* and *Paralomis granulosa* have constituted a mixed fishery since the 1930s. The two species differ markedly in their reproductive potential. *Lithodes santolla* is large (maximum size of 190 mm carapace length, CL, and 8 kg weight), has a generation time of 6 yrs., the reproductive cycle is annual and females carry between 5,000-60,000 eggs per female per clutch. In their life span, *L. santolla* females produce 6 times more eggs than *P. granulosa* females. *Paralomis granulosa* is smaller than its relative (maximum 115 mm CL and 1.5 kg weight), and has a slower growth rate, resulting in a generation time of 12 yrs. The reproductive cycle is biennial and females carry between 800-10,000 eggs per female per clutch. Moreover, the reproductive potential of *P. granulosa* is reduced because an important proportion of the largest and more prolific females of the population do not carry eggs. In other terms, in one generation time of *P. granulosa*, two complete generations of *L. santolla* are produced, and compared to other Subantarctic lithodids *L. santolla* is the most prolific species. The higher reproductive potential of *L. santolla* probably confers to this species the ability to recover more rapidly from an overfishing situation.

Key words: crab, fecundity, growth, life history traits, southwestern Atlantic, southeastern Pacific, Tierra del Fuego.

RESUMEN: POTENCIAL REPRODUCTIVO DE LOS LITODIDOS *LITHODES SANTOLLA* Y *PARALOMIS GRANULOSA* (ANOMURA, DECAPODA) EN EL CANAL DEL BEAGLE, ARGENTINA. Lithodidae es el único grupo de crustáceos reptantes presente en aguas antárticas y ha sido particularmente abundante en el Estrecho de Magallanes, Canal del Beagle y al sur de los 50º de latitud. Debido a su abundancia en aguas costeras, las especies simpátricas *Lithodes santolla* y *Paralomis granulosa* han constituído una pesquería mixta desde la década de 1930. Ambas especies difieren en su potencial reproductivo. *Lithodes santolla* es más grande (tamaño máximo de 190 mm de largo de caparazón, LC, y 8 kg de peso), su tiempo de generacion es de 6 años, el ciclo reproductivo es anual y las hembras llevan entre 5.000-60.000 huevos por puesta. Durante su vida reproductiva, las hembras de *L. santolla* producen 6 veces más huevos que las hembras de *P. granulosa*. Los individuos de esta especie son más pequeños (tamaño máximo 115 mm LC y 1,5 kg de peso), y tienen una tasa de crecimiento más lenta, que resulta en un tiempo de generacion de aproximadamente 12 años. El ciclo reproductivo es bienal y las hembras llevan entre 800-10.000 huevos por puesta. Además, el potencial reproductivo de *P. granulosa* está reducido porque una proporción importante de las hembras más grandes, y consecuentemente más prolíficas, no portan huevos. En otros términos, en el transcurso de un tiempo de generacion de *P. granulosa* se producen dos generaciones completas de *L. santolla*. Asimismo, comparada con otros litódidos subantárticos *L. santolla* es la especie más prolífica, y comparativamente con *P. granulosa,* su potencial reproductivo más alto la capacitaría para recuperarse más rapidamente de una situación de sobrepesca.

Palabras clave: Cangrejo, fecundidad, crecimiento, ciclo de vida, Atlántico suroeste, Pacífico sureste, Tierra del Fuego.

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INTRODUCTION

Lithodidae is the only group of reptant decapods that occurs in Antarctic waters. Only one species, *Lithodes murrayi* Henderson, 1888 was found in the Bellingshausen Sea (Klages *et al.,* 1995) and in the Subantarctic waters off the Crozet Islands (Arnaud, 1971). By contrast, lithodids -stone or king crabs- were very abundant in the Subantarctic benthos, especially in the Magellan region. Among the 11 species of lithodid crabs that occur on Antarctic and Subantarctic waters, 7 species occur in the southern tip of South America. *Lithodes santolla* (Molina, 1782) and *Paralomis granulosa* Jacquinot, 1847 occurred at high densities between 2 and 50 m deep in the Straits of Magellan, Beagle Channel, and the Pacific channels south to 50º S. Such high densities have encouraged the development of a fishery since the 1930s, which affected negatively the populations (Campodonico *et al.*, 1983; Campodonico and Hernández, 1983; Bertuche *et al.,* 1990; Lovrich, 1997a and references therein). *Lithodes turkayi* Macpherson, 1988 is the third species that rarely occurs in the Magellan Straits and the Beagle Channel, at >70 m depth (identified as *L. murrayi* by Campodonico and Guzmán, 1972; Vinuesa *et al.*, this issue). *Lithodes confundens*, Macpherson 1988 occurs on the Atlantic continental shelf near the eastern entrance of the Straits of Magellan (Lovrich *et al.,* 1998b) and off the Islas Malvinas (Falkland Is.), and in the Straits of Magellan near Punta Arenas (Macpherson, 1988). *Paralomis spinosissima* Birstein and Vinogradov, 1972, *P. formosa* Henderson, 1888, and *Neolithodes diomedeae* (Benedict, 1894) occur south of the Antarctic Convergence, off South Georgia Islands (Macpherson, 1988; Otto and MacIntosh, 1996). However, *N. diomedae* is the only one of these species that occurs further north off the Pacific coast up to 5º S, and has been landed and sold in Puerto Montt at about 42º S (Vinuesa pers. obs.).

Knowledge on the biology of lithodids has arisen from the interest in their fishing and with the purpose of an efficient management of the populations. Therefore, most of the available information is related with the reproduction and life history of the current or potentially exploited species. By contrast, only the occurrences of less abundant or smaller species with no commercial interest were reported, as for example the other Subantarctic lithodids *Paralomis birsteini* Macpherson, 1988, *P. aculeata* Henderson, 1888 or *P. anamerae* Macpherson, 1988.

In this article, we summarize the available information on the life history and reproductive potential of *Lithodes santolla* and *Paralomis granulosa* in the Beagle Channel, Argentina.

RESULTS

The biology of the lithodids in the Beagle Channel

Both species are very different in their morphology. The body of *Lithodes santolla* is covered with spines and males may attain a maximum size of 190 mm of carapace length (CL) and 8 kg weight (Vinuesa, 1990). By contrast, *P. granulosa* is smaller, its body is covered by clusters of granules and males reach a maximum size of 115 mm CL and 1.5 kg weight (unpublished data). In the following, we summarize the main life history traits for both species. Literature sources from where the information proceeds are detailed in Table 1.

The biology of *Lithodes santolla*

In late November-early December, the reproductive cycle of *L. santolla* begins with female molting (Vinuesa, 1990). The precopulatory embrace and mating occur between a male with an old shell and a female recently molted and slightly smaller than her couple. Mating pairs may be found in the population for approximately a month (unpubl. data). As in other lithodids (Powell and Nickerson, 1965), fertilization is external and occurs immediately after female oviposition. Eggs are carried by females and the embryogenesis lasts approximately 9-10 mo. Fecundity (number of eggs per brood) increases with female size, between 5,500 and 60,000 eggs (Table 1). Larval hatching occurs between mid September and October, without significant annual variation (unpubl. data). Larvae are lecithotrophic (Oyarzún, 1992) or facultative lecithotrophic (Comoglio and Vinuesa, 1991), pass through three zoeal and one glaucothoe -or megalopal- stages (Campodonico, 1971), and metamorphose to the first benthic crab stage, which is about 1.5 mm CL (Oyarzún, 1992). The entire larval period lasts about 35-55 days at 7-8ºC (Vinuesa *et al.*, 1985; Oyarzún, 1992). At temperatures <7ºC, the glaucothoe does not succeed in molting to the juvenile stage (Oyarzún, 1992).

Molt frequency of *L. santolla* decreases with age: during the first year, crabs molt 6-7 times, during the second year, 4-5 times, and during the third

TABLE 1. – Summary of life-history traits of the sympatric *Lithodes santolla* and *Paralomis granulosa* mainly in the Beagle Channel, Argentina. Numbers in superscript indicate bibliographic references: 1: Bertuche *et al*., 1990; 2: Boschi *et al*., 1984; 3: Campodonico, 1971; 4: Campodonico and Guzmán, 1981; 5: Campodonico *et al*., 1983; 6: González, 1971, 7: Guzmán and Ríos, 1986; 8: Lovrich, 1997a; 9-10 Lovrich and Vinuesa, 1993; 1995, respectively; 11: Lovrich *et al*., 1998; 12: Oyarzún, 1992; 13-15 Vinuesa, 1982; 1984; 1987, respectively; 16: Vinuesa and Labal, in press; 17-20: Vinuesa *et al*. 1985; 1989; 1990 and 1991, respectively. (?) indicates uncertain information. CL: carapace length.

Trait	*Lithodes santolla*	*Paralomis granulosa*
Mating frequency	annual, December [14]	biennial, October[9]
Fecundity (eggs/female)	5,500-60,000 [7,13]	800-10,000 [5,9]
Embryogenesis	9-10 mo [15]	18-22 mo [9]
Maximum egg size (diameter)	2.1 mm [15]	1.9 mm [9]
Zoeal size at hatching	2.0 mm CL[3]	2.1 mm CL[4]
Number of zoeal stages	3 [3]	2 [4]
Larval development (zoeal + megalopal)	23-26[17] + 30 d [12]	18-21[18] + ?
Larval hatching	September-October[14]	June-August [9]
Size at morphometric maturity (males)	90-99 mm CL[2]	57 mm CL[9]
Size at gonadic maturity (females)	75 mm CL [14]	61 mm CL[9]
Age at gonadic maturity	5 yrs [19, 20]	9-10 yrs (?)[10]
Duration of the oogenesis	2 yrs[14,16]	>3 yrs (?)[9]
Legal size	110 mm CL	82 mm CL
Age at legal size	8-9 yrs[8]	15 yrs (?)[8]
Relative abundance (crabs per trap)	1.8 in 1996 [8]- 11.6 in 1975 [1]	38 in 1970[6]- 105 in 1997[11]

year, 3 times. Three years old crabs are about 50 mm CL (Vinuesa *et al*., 1990). Thereafter, males molt twice a year until they reach morphometric maturity (defined as the change in the allometric relationship between carapace and claw size), i.e., at 5 yrs. age, and 90-99 mm CL (Table 1). In the fourth year, females begin the ovarian maturation and thus, molt annually (Vinuesa *et al*., 1991). Gonadal maturity (in males defined as the presence of spermatozoa in the deferent ducts, and in females as the presence of embryos attached to pleopods) is reached at 60-75 mm CL in males, and at 66-87 mm CL in females (Table 1; Vinuesa, 1984). In females, oogenesis lasts *ca*. 24 mo (Vinuesa and Labal, in press). After gonadal maturity, females continue to molt annually (Vinuesa *et al.,* 1991), and after morphometric maturity males apparently continue molting biannually until they reach 110 mm CL (pers. obs.). Males enter the fishery at 110 mm CL and males >150 mm CL probably molt biennially (Geaghan, 1973).

The biology of *Paralomis granulosa*

During October-November, the reproductive cycle begins with courtship and mating, between an old-shelled male and a recently molted female that is smaller than her couple (unpubl. data). The fertilization is external and the female broods the embryos attached to pleopods between 18 and 22 mo (Table 1). Fecundity varies between 800 and 10,000 eggs, increasing with female size. However, *ca*. 50% of the females >80 mm CL do not carry eggs although their ovaries are well developed (Hoggarth, 1993; Lovrich, 1997a). In the Beagle Channel, larval hatching occurs mainly during winter (June to August), almost two years after mating (Lovrich and Vinuesa, 1993). Larval development seems to be shorter than in *L. santolla*, since the 2 zoeal stages last 18-21 days at 8 or 5ºC, respectively (Table 1). However, there is no information about the duration of the glaucothoe stage, the entire larval development in the natural environment, and growth from the first crab stage to the stage of *ca*. 10 mm CL. During the immature phase, growth is slow. The smaller crabs (10-40 mm CL) molt twice a year: in winter and summer, while crabs >40 mm CL molt only in summer. During the immature phase, percentage of growth per molt is constant and 12.4 % irrespective of crab size (Lovrich and Vinuesa, 1995). At this rate of growth, we suspect that gonadal maturity would be reached at *ca*. 10 yrs age (Lovrich, 1997a).

Males attain gonadal maturity at 50.2 mm CL, and females at 60.6 mm CL. Morphometric maturity is reached at 57 mm CL in males and at 66.5 mm CL in females (Table 1; Lovrich and Vinuesa, 1993). By molting once after gonadal maturity, males attain morphometric maturity (Lovrich and Vinuesa, 1995). Males enter the fishery attaining the legal size of 82 mm CL at an approximate age of 15 yrs (Lovrich, 1997a). Male molting is supposed to be annual and probably biennial when males are >80 mm CL (Hoggarth, 1993; Lovrich, 1997a).

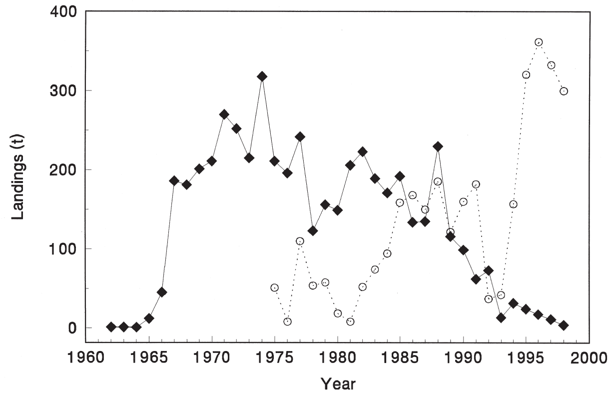

FIG. 1. – Landings of *Lithodes santolla* (u) and *Paralomis granulosa* (m) in Ushuaia, Argentina. Landings for 1998 were forecasted with the available data until July 1998, i.e., 6 out of 10 mo of the fishing season. Source: Dirección de Recursos Naturales, Province of Tierra del Fuego.

The fishery and fishing mortality

In the Argentinean Beagle Channel, the fishery began in the late 1950s. This fishery has contributed about 10% of the total landings from Argentina and Chile (Lovrich, 1994). Although both species were initially abundant, the target species was exclusively *L. santolla*. It was fished with tangle nets which were very selective and captured only this species (González, 1971). In 1975, with the imposition of the trap as the unique fishing gear, *P. granulosa* appeared as bycatch, and usually <50 t per year were landed (Fig. 1). When landings of *L. santolla* started to decline after 1984, the fishery for *P. granulosa* began to develop, but the magnitude of landings was constrained by the international demand for *P. granulosa*. In the last 4 years, the scenario of the fishery has inverted: the target species has been *P. granulosa* and landings peaked in 1996, whereas *L. santolla* has been so scarce that it became the bycatch of the fishery.

Several indirect evidences indicate that fishing has been the main factor of mortality and the cause of the density reduction in the populations of lithodid crabs of the Beagle Channel (Campodonico and Hernández, 1983; Bertuche *et al*., 1990; Vinuesa, 1990; Lovrich, 1997a). Since *L. santolla* has been continuously fished, the effects of the fishery on its population were more evident than on *P. granulosa*. Between 1975 and 1996 the population of *L. santolla* underwent significant decreases in (1) the relative abundance (Table 1), (2) the proportion of legal males, (3) the proportion of ovigerous females, and (4) the mean size of the size frequency distributions of males and females. The only stock assessment of the population of the Beagle Channel was done in 1980-1981 after 14 yrs of annual landings of ≥ 200 t (Boschi *et al.,* 1984), and was roughly coincident with the start of the decline of landings. Hence in 1980-81, crabs were probably less abundant than before the fishery developed, i.e., in the 1950s. On average, the density of *L. santolla* ≥ 60 mm CL was 3.1 crab · 100 m^{-2} and the relative abundance was 9.3 crabs per trap (Boschi *et al.,* 1984).

Density estimations of *P. granulosa* are still needed, and reported relative abundances are scarce. In 1970, the relative abundance in the Beagle Channel was 38 crabs per trap (González, 1971), whereas in 1996 and 1997 it was 66 and 105 crabs ≥55 mm CL per trap, and 19 and 16 legal crabs per trap, respectively (Table 1; Lovrich 1997b; Lovrich *et al.*, 1998a). However, there is some evidence of the negative influence of the fishery on the population. In the Straits of Magellan between 1979 and 1984-86, after intensive fishing, there were decreases in (1) the ~60% of the biomass of legal sized-crabs, (2) the relative abundance of landed crabs (probably > 75 cm CL) from 9.5 to 4 kg per trap, and (3) the mode of male size distributions from 92 to 74 mm CL (Campodonico *et al.*, 1983; Díaz and Alvarado, 1986).

Reproductive potential

In crustaceans, the reproductive potential has been quantified in terms of fecundity, age at maturity, fishing mortality, proportion of females in each size class, and growth of individuals in a population (Campbell and Robinson, 1983; Shields, 1991). In this study the reproductive potential was calculated as the cumulative fecundity of a given female along

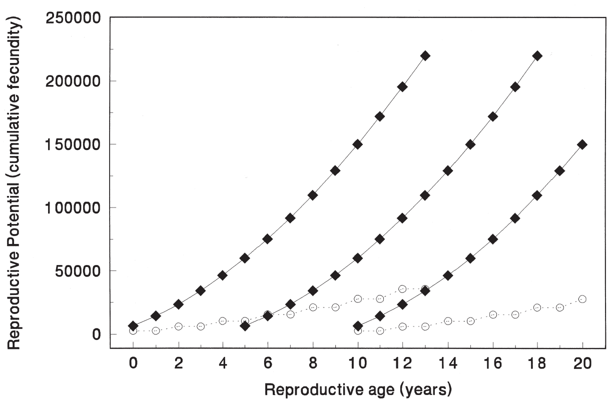

FIG. 2. – Reproductive potential as cumulative fecundity in the reproductive life span of an adult female of *Lithodes santolla* (u) and *Paralomis granulosa* (m). Maximum ages were calculated from sizes of the largest females found in the Beagle Channel.

her reproductive life-span (see Shields, 1991 p. 207). The size of each molt stage was derived from data of *L. santolla* female growth (Vinuesa and Lombardo, 1982), and the size-fecundity relationship was calculated from data of Vinuesa (1982). The size of each molt stage of *P. granulosa* was assumed to be 5 mm CL (Campodonico *et al*., 1983 and unpubl. data), and the fecundity at size was calculated according to the function reported by Lovrich and Vinuesa (1993).

For an individual female and along her life span, *L. santolla* produces 6 times more eggs than *P. granulosa* (Fig 2). This is determined by two factors: first, *L. santolla* is larger and thus may carry more eggs than *P. granulosa*. Second, the embryogenesis of *L. santolla* lasts 9-10 mo, which allows females to have an annual reproductive cycle. Thus, a single female molts every year, increases her size and the total productivity. By contrast, the biennial reproductive cycle constrains *P. granulosa* females to molt once every two years, and thus prevents the increase of productivity. Moreover, if the female becomes large, e.g., >85 mm CL, she probably does not find a male of the appropriate size to mate, does not carry eggs, and thus the reproductive potential will not increase (Lovrich 1997a; 1997b and unpubl. data). Finally, in population terms, in one generation time of *P. granulosa* (i.e., when one egg produces another egg), two generations of *L. santolla* are already produced, and the third one begins to produce eggs (Fig 2).

Compared to other Subantarctic and Antarctic lithodids, *L. santolla* is the most prolific. Although eggs of southern lithodids have similar sizes, *L. santolla* females carry more eggs (Table 1): *c.f. L. murrayi*: 2.4 mm diameter and 380-3500 eggs (Arnaud and Do-Chi, 1977), *L. turkayi* 1.7 mm (own unpubl. data), *P. granulosa* 1.9 mm and 800-10,000 eggs (Table 1), and *P. spinosissima* 2.0 mm and 2,000-14,000 eggs (Otto, 1993). As occurs in brachyuran crabs (Hines, 1982), female *L. santolla* carry more eggs, because they reach a maximum size (152 mm CL, Guzmán and Ríos, 1986) larger than that of other southern lithodids: *c.f. L. murrayi*: 82 mm CL (Arnaud and Do-Chi, 1977), *L. turkayi* ~70 mm CL and *L. confundens* 105 mm CL (own unpubl. data), *P. granulosa* 94 mm CL (Campodonico *et al*., 1983; Lovrich 1997b), and *P. spinosissima* 110 mm CL (Otto and MacIntosh, 1996).

From the preceding observations, we advance two different hypotheses. First, life history traits of *L. santolla,* such as having more eggs that are produced annually, annual molt, and reaching larger sizes, suggest that this species has more energetic requirements than its sympatric *P. granulosa*. Hence, *L. santolla* has probably occupied grounds of better quality than those used by *P. granulosa*, as occurs with king crabs of the Bering Sea *Paralithodes camtschaticus* and *P. platypus* (Jensen and Armstrong, 1989). So far, only anecdotal observations sustain that grounds formerly occupied by *L. santolla* were colonized by *P. granulosa*, once *L. santolla* was removed by fishing. Second, we suggest that the higher reproductive potential of *L. santolla* confers to this species the ability to recover more rapidly from an overfishing situation. By contrast, the longer generation time, the lower fecundity and the correspondingly lower reproductive potential of *P. granulosa* suggest that this species cannot support heavy rates of fishing for many years, as has occurred in the Islas Malvinas-Falkland Is. (Hoggarth, 1991). In the case of overfishing, the population recovery to pre-fishery levels will be relatively slow. However, much work is needed to estimate pre-fishery abundances, interactions between both species and niche overlapping, and effects of fishing on the competition between the two populations. Therefore, data acquisition from virgin stocks should be a priority for lithodid research in the Magellan region.

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