

Reproductive biology of spiny lobster *Panulirus regius* from the north-western Cape Verde Islands

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Green (spiny) lobsters *Panulirus regius* were obtained by diving at Cape Verde, West Africa, during three sampling periods: May–November 2001, April–December 2002 and April–June 2003. Totals of 429 male lobsters and 423 females (852 in all) were caught. Half the females were ovigerous throughout the sampling periods. Female estimated size-at-50% maturity was 87.9mm carapace length (CL). Brood size and egg

developmental stage were examined in 68 ovigerous females. The relationship between brood size (BS, thousands of eggs) and CL (mm) was $BS = 1.59CL^{2.77}$. Females in the size-class 100–105mm and 115–120mm CL produced half the eggs in the population. Based on these results, an increase in the minimum landing size is proposed. The potential implementation of a maximum landing size is discussed.

Keywords: Cape Verde, lobster fecundity, *Panulirus regius*, reproductive biology

Introduction

Panulirus regius De Brito Capello 1864 (the royal spiny lobster) is a tropical species found in the eastern Atlantic, from approximately 28°N and 15°S (Africa), between Cape Juby (Morocco) and Namibe (Angola), including the Cape Verde Islands, as well as in the western Mediterranean (east coast of Spain, south coast of France) (Fischer *et al.* 1981, Holthuis 1991). Clotilde-Ba *et al.* (1997) considered *P. regius* to be an Atlantic–Mediterranean species of spiny lobster with one of the greatest geographical ranges among the palinurids of commercial importance. From an economic perspective, it is the most important crustacean species found in West Africa.

In Cape Verde, *P. regius* is referred to as 'lagosta verde' (green lobster), and it is heavily fished at most of the islands (Foueré 1981, Dias 1993, Reis 1997). At present, it accounts for 71% of the catch of shallow-water lobster species in the north-west islands (Figure 1). Lobsters are caught down to depths of 55m, either by divers (using a gaff to extract lobsters from their dens) or with traps (among the reefs and around islands with a narrow shelf). At Cape Verde, *P. regius* is one of four species of lobsters of commercial interest. The other three are *Scyllarides latus* (Latreille 1802), *Panulirus echinatus* Smith 1869 (a shallow-water species) and *Palinurus charlestoni* Forest and Postel 1964 (an endemic deep-water species) (Holthuis 1991, Dias 1992).

Despite earlier contributions (Marchal and Barro 1964, Postel 1966, as cited by Dias 1993, Giudicelli 1971, Maignet 1978, as cited by Dias 1993), little is known about the basic

biology, reproduction and fecundity of *P. regius* off West Africa (Dias 1993, Reis 1997). The reproductive seasons of the species vary with latitude: from June to September in the Northern Hemisphere and from January to March in the Southern Hemisphere, although in both areas the animals require temperatures of 23°–25°C for egg maturation and 26°C for spawning (Giudicelli 1971). That author reported reproductive migrations in adult *P. regius* females on the Senegal shelf, with lobsters moving from 2–20m to 20–55m deep from June to August, the period of reproductive activity (copulation), following cooler water. Like other tropical *Panulirus* species (Fonseca-Larios and Briones-Fourzán 1998), *P. regius* spawns year-round, with a spawning peak from June to September at Cape Verde (Dias 1993).

The fecundity of a palinurid lobster is usually evaluated by counting the number of external eggs carried on the pleopods of a female (Chubb 2000); the term 'brood size' is also used, specifically for decapod species that spawn repetitively during a breeding season (Pollock and Goosen 1991). Other measures of fecundity are potential fecundity (the number of oocytes in the ovary), actual fecundity (number of eggs on the pleopods at the time of capture) and effective fecundity (estimated number of eggs on the pleopods at the time of hatching) (Tuck *et al.* 2000). Palinurid lobsters are relatively fecund, with usually up to 700 000 eggs per spawning (Morgan 1980). These values are achieved through large broods of small eggs produced over a relatively short adult lifespan (Pollock and Melville-Smith 1993); the smaller the egg size, the greater the fecundity (Pollock 1995).

To understand the relationship between stock and recruitment, parameters other than fecundity need to be considered (Chubb 2000); examples are the average reproductive potential (Correia-Ivo and Vasconcelos-Gesteira 1995) and the index of reproductive potential (Kanciruk and Herrnkind 1976). These indices combine size-specific fecundity with the size structure of the population of reproducing females.

The present work aims to obtain information on the biology and reproductive cycle of *P. regius* at Cape Verde as well as to estimate fecundity, brood size, egg size, size at the onset of maturity and an index of reproductive potential. These parameters are then used to recommend a minimum landing size for the fishery.

Material and Methods

Study area and data collection

Cape Verde is located in the central eastern Atlantic (14°50'–17°20'N, 22°40'–25°30'W) about 750km west of Senegal. It has 10 islands and several islets, totalling a land area of 4 033km². The coastline is 965km long and the island shelf (depths <200m) is 5 934km² (Bravo de Laguna 1985, DGMP 1998, Menezes *et al.* 2004). The climate is tropical, with two seasons: a moderate cold season (December–June, with an average seawater temperature of 22°–23°C) and a warm season (26°–27°C) (Almada 1993).

Lobsters were obtained by scientists accompanying commercial divers off the north-west islands of the Archipelago: Santo Antão, São Vicente and Santa Luzia (Figure 1), from May to November 2001, from April to December 2002 and from April to June 2003. Additional ovigerous females used in the fecundity study were collected from lobsters landed at Mindelo's Fish Market. The lobster fishery is closed from 1 July to 30 September, so during those months a research permit was obtained and lobsters were caught by divers at depths of 13–22m.

Carapace length (CL), from the rostral horns to the posterior dorsal edge of the carapace, was recorded to 0.1mm below using callipers. Other measurements obtained were total length (TL) and abdominal width at the fifth abdominal somite

(AW). Sex and the presence or absence of external eggs were also recorded. When external eggs were present, the development stage of the embryos was recorded according to the scale proposed by Franca *et al.* (1959), based on the presence of visible eye spots and the colour of the egg mass: 1 — newly excluded eggs (orange eggs and no eye spots); 2 — intermediate (dark orange eggs with vestigial eye spots); and 3 — about to hatch (brown eggs with clearly visible eye spots).

Estimation of brood size

The method to estimate brood size was according to the gravimetric methods of Morgan (1972), Gracia (1985) and Chubb (2000). The pleopods of ovigerous females containing the egg mass were cut and removed from the abdomen and fixed in 70% ethanol. Later, they were rinsed and air-dried until the eggs could be easily stripped from the pleopodal setae and the egg mass weighed ($\pm 0.001g$). Two methods were used to separate the eggs: (1) further drying at 45°C for 48h using an oven; and (2) soaking the egg mass in a bleach solution (1:4 parts of water). From each egg mass three subsamples of 0.01g (dried eggs) or 0.03g (bleach solution) were obtained. The number of eggs in each subsample was counted using a 10x stereo microscope and extrapolated to the total egg mass to obtain the individual brood size. The potential effect of the different egg separation methods used was compared by applying both methods to the same brood ($n = 12$, t-test for paired samples).

Very late embryonic developmental stages, observed in three females bearing brown eggs with degrading egg masses, were not included in the study. The relationship $BS = f(CL)$ used (Somers 1991, DeMartini *et al.* 2003) was:

$$\log (BS) = a + b [\log (CL)] \quad (1)$$

where BS is the number of eggs (10^{-3}), CL the carapace length (mm), and a and b are the regression parameters.

Two reproductive seasons were compared (August–September 2001, $n = 35$; and October 2002–April 2003, $n = 30$), using analysis of covariance (ANCOVA). Because there were no differences between sampling periods, a regression for the total data was obtained.

For all statistical tests, the differences were considered significant if $p < 0.05$.

Relative egg weight

The relative egg weight (REW) was obtained using the formula:

$$REW = \frac{\sum_{k=1}^{k=3} w_k}{\sum_{k=1}^{k=3} n_k} 10^5 \quad (2)$$

where w is the individual weight of each of the three subsamples and n the number of eggs counted in each subsample. This index is directly related to egg weight: the greater the index, the heavier the individual eggs.

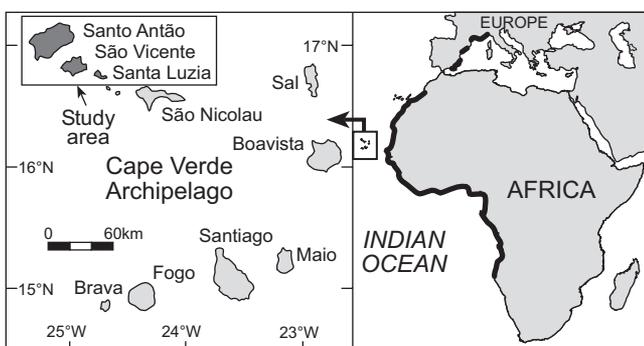


Figure 1: Map showing the geographical distribution of *P. regius* in the eastern Atlantic (thick coastline) and the area where the samples were obtained in the north-west islands of the Cape Verde Archipelago (shaded islands) (adapted from Holthuis 1991)

Because some eggs were counted on dry egg masses and others on wet egg masses, all weights were converted to dry weight. For 12 broods, both dry and wet egg weights were obtained, and the regression of wet weight (w_w) on dry weight (w_d) was estimated to be $w_d = 0.0005 + 0.2944w_w$ ($n = 12$, $r^2 = 0.985$). REW was compared among different embryo stages (newly extruded eggs, intermediate, and about to hatch) and female size (three CL classes: $<80\text{mm}$, $80\text{mm} \leq \text{CL} < 100\text{mm}$, and $\geq 100\text{mm}$), using Kruskal-Wallis tests.

Reproductive potential

Data from 423 females grouped into 5mm CL classes, representing the population structure across the study period, were used in fecundity estimates.

The index of reproductive potential (IRP; Kanciruk and Herrnkind 1976) was used to establish the size-classes of breeding females contributing most to the egg production of the population:

$$IRP_i = \frac{A_i B_i C_i}{D} \tag{3}$$

where A_i is the percentage of females in size-class i , B_i the proportion of ovigerous females in class i , and C_i the estimated mean brood (number of eggs 10^{-3}) for size-class i . D is a constant obtained by setting a standard $IRP = 100$ for the size-class with the greatest egg production.

The total egg production per size-class was calculated as

$$e_i = ov_i C_i \tag{4}$$

where ov_i is the number of ovigerous females in size-class i , and transformed to a percentage of total egg production (E_i) using the equation

$$E_i = \frac{e_i}{\sum_{i=1}^p e_i} \cdot 100 \tag{5}$$

where p is the total number of size-classes in the population. An index of individual contribution of a female in size-class i , F_i , was also estimated:

$$F_i = \frac{E_i}{A_i} \tag{6}$$

Size at onset of sexual maturity

The size at onset of maturity (SOM) in female *P. regius* was considered to be the size at which 50% of females are mature, estimated by fitting a logistic model to the proportion of egg-bearing females per size-class (Groeneveld and Melville-Smith 1994, Tuck *et al.* 2000).

Results

In all, 852 *P. regius* were sampled, 429 males (50.4%) and 423 females (49.6%). Females ranged in size from 47.1 to 137.3mm CL (mean \pm SD = $87.3 \pm 17.2\text{mm}$), and males from 42.5 to 185.0mm CL ($95.8 \pm 27.3\text{mm}$). Of the females, 212 (50.1%) were ovigerous. The size range of ovigerous females was 61.9–137.3mm CL ($95.8 \pm 15.4\text{mm}$), with CL classes 85–110mm dominating (51.9%). Males attained a larger size than females (Figure 2). The estimated size-at-50% maturity was 87.9mm CL (Figure 3).

Eggs from 65 females were counted (35 in 2001 and 30 in 2002 and 2003). Size of these females ranged from 66.4 to 125.8mm CL. Fecundity data based on external egg numbers are listed in Table 1. No significant differences in BS–CL regression were found between 2001 and 2002 or 2003. The partial ANCOVA results showed that both regressions had similar slopes ($p = 0.173$) and elevations ($p = 0.962$). Therefore, data for the 65 females

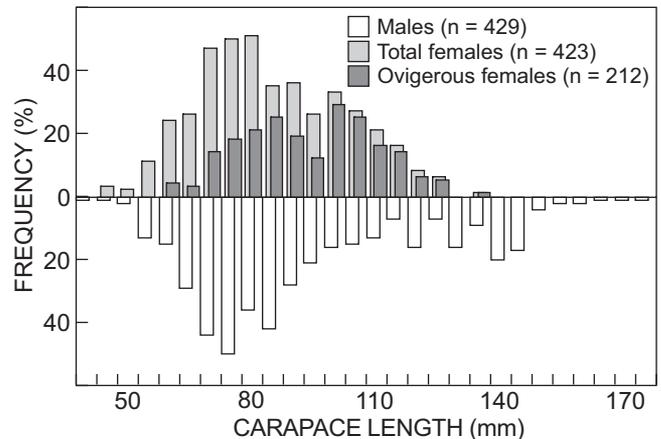


Figure 2: Size distribution of males, ovigerous females, and all females of *P. regius* during the sampling period (May 2001–June 2003)

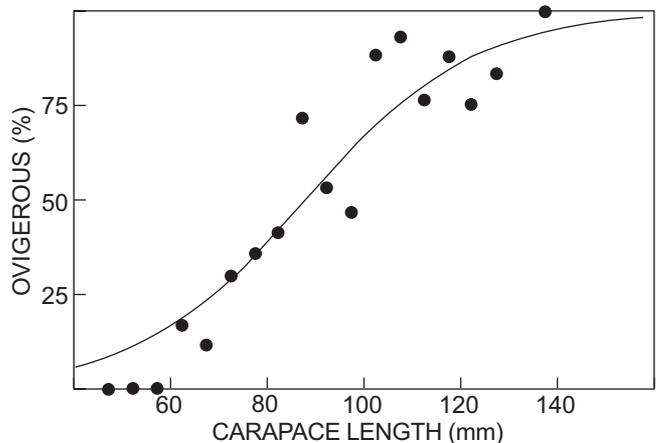


Figure 3: Relationship between proportion of ovigerous females and carapace length (mm) of *P. regius* at the Cape Verde Archipelago

Table 1: Range in carapace length (CL), mean size, sample size, regression equation of log of brood size (BS) as a function of log (CL), coefficients of determination (r^2) and p-value of the ANOVA regression (H_0 : slope = 0) for each sampling period and overall

Period	Size range (CL, mm)	Mean size (CL, mm)	n	Regression equation	r^2	p-value
2001	66.4–115.8	84.9	35	$\text{Log BS} = 3.0759(\text{log CL}) - 0.3913$	0.78	<0.001
2002–2003	73.5–125.8	95.1	30	$\text{Log BS} = 2.5287(\text{log CL}) + 0.6726$	0.74	<0.001
Overall	66.4–125.8	89.6	65	$\text{Log BS} = 2.7683(\text{log CL}) + 0.2003$	0.78	<0.001

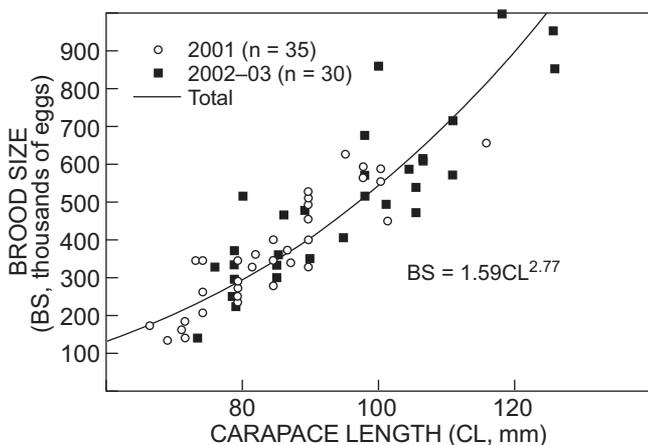


Figure 4: Relationship between carapace length and brood size for female *P. regius*

from all sampling periods were combined to obtain a single regression (Table 1, Figure 4). Brood size ranged from 134 000 eggs for a 69mm CL female to 995 000 for a 118mm CL female.

A Kruskal-Wallis test revealed no significant difference in REW relative to embryonic stage ($p = 0.808$) or female size ($p = 0.514$) (Table 2).

Data used for IRP values are presented in Table 3. The constant D was 400.56, obtained by setting the IRP value of the 100–105mm class to 100. This class was chosen as standard because it had a large percentage of ovigerous females and was well represented in the population. The smallest ovigerous female in the sample was 61.9mm CL, the CL classes 70–80mm had the greatest percentage of females, and the classes >100mm CL had the highest proportions of ovigerous females. Similar to *Panulirus argus* in the Bahamas (Kanciruk and Herrnkind 1976), we assumed only one spawning event per year throughout the size range of females when estimating IRP for *P. regius*.

Females in CL class 100–115mm produced 52.5% of all the eggs and had the highest IRPs. The size-at-50% maturity (87.9mm) is included in CL class 85mm, also with a high IRP (Table 3). The relative reduction of IRP for smaller and larger females was related to poorer representation of ovigerous females and large females in the samples. The 105mm CL class had one of the highest individual productivity indices ($F = 2.38$), resulting from relatively high fecundity and a good representation of ovigerous females in the sample, making females from this class 29 times more productive than the recently mature class (65mm CL, $F = 0.08$).

Discussion

The sex ratio was well balanced in the studied population. Kanciruk (1980) reported that the sex ratio in palinurids can vary considerably. The method of capture used in the present study (diving) is highly efficient and unselective, which may explain the absence of significant deviations from a balanced sex ratio. The size distributions by sex differed, with males attaining a larger size than females. Kanciruk (1980) suggested that this could be a consequence of differential growth or moulting rate between sexes, a longer male lifespan, or an increased metabolic demand on females during egg production.

Data on fecundity of *P. regius*, including the present study and earlier ones, are presented in Table 4. As *P. regius* experiences a wide range of climatic and oceanographic conditions along the African coast (28°N–15°S; 15°–28°C) (Postel 1966, as cited by Dias 1993), variation in biological parameters for this species was expected. Data on fecundity were therefore interpreted for three regions separately: north of the Gulf of Guinea (Mauritania, Senegal and Cape Verde), the central Gulf of Guinea (Ivory Coast and Benin), and south of the Gulf of Guinea (Angola). Although samples were very small in some studies, there appear to be variations in fecundity and reproduction parameters from region to region. Considering minimum carapace size of ovigerous females (MOF) values (to the nearest mm), the Cape Verde values (62mm CL) lie between those for the Ivory Coast (57mm CL) and Senegal and Angola (67mm CL), and are considerably lower than off Benin (75mm CL), suggesting an absence of a latitudinal gradient and consequently a lack of correlation with water temperature. Apart from possible effects of small sample sizes, factors other than water temperature may explain changes in maturity parameters. These include genetic selection, food availability, fishing pressure (Leocádio 2004), density-dependent processes (Chubb 2000) and physiological adjustment to differing photoperiods (Quackenbush and Herrnkind 1981).

An important consideration in fecundity studies is the average number of spawning episodes per adult female per year. Field studies of tropical palinurids have established that rapid and repetitive brood cycles are common, with up to five broods per year (Junio 1987, for *Panulirus penicillatus* in the Philippines). Quackenbush (1993) suggested that larger females might spawn more frequently than smaller lobsters, because they may skip the annual moult. Protracted spawning seasons (Briones-Fourzán and Lozano-Alvarez 1992) and high indices of egg productivity (large number of eggs at $L_{50\%}$) (Fonseca-Larios and Briones-Fourzán 1998) may imply multiple spawning. We assumed that female *P. regius* spawn only once a year, but this should be considered an open

Table 2: Descriptive statistics for relative egg weight (weight of eggs / number of eggs $\times 10^5$) by embryonic developmental stage defined by the colour of the egg mass and carapace length-classes

Egg colour	Parameter	Carapace length (CL, mm)			Total
		CL <80	80 \leq CL < 100	CL \geq 100	
Orange	n	10	8	5	23
	Mean	2.68	2.72	2.46	2.64
	Variance	0.284	0.329	0.253	0.277
Dark orange	n	8	17	10	35
	Mean	2.23	2.72	2.71	2.60
	Variance	0.300	0.158	0.122	0.212
Brown	n	3	3	1	7
	Mean	2.88	2.64	2.03	2.65
	Variance	0.012	0.082	–	0.122
Total	n	21	28	16	65
	Mean	2.53	2.71	2.59	2.62
	Variance	0.301	0.186	0.177	0.220

Table 3: Estimation of the index of reproductive potential (IRP). The size-class with the greatest egg production is identified in bold. The symbol n_i is the total number of females in class i ; ov_i is the number of ovigerous females in class i ; $IRP_i = (A_i \times B_i \times C_i) / D_i$, where A_i is the percentage of females in each 5mm CL class, B_i the percentage of berried females in a given CL class, C_i the estimated brood size of the midpoint of the size-class (10^{-3} eggs) and D is the constant (400.378) used to standardise the most productive CL class to 100% (Kanciruk and Herrnkind 1976), calculated by multiplying A_i , B_i and C_i from CL class 100mm and dividing this product by 100; e_i is the number of eggs produced/spawned per year (10^{-3}); E_i is the percentage of total egg production; $F_i = E_i / A_i$, a class-specific index of egg productivity

Size-class (mm)	Number of females		A_i	B_i	C_i	IRP_i	e_i	E_i	F_i
	n_i	ov_i							
<60	16	0	3.8	0.0	80	0.0	0	0.0	0.00
60	24	4	5.7	16.7	149	3.5	596	0.5	0.10
65	26	3	6.1	11.5	184	3.3	552	0.5	0.08
70	47	14	11.1	29.8	224	18.5	3 136	2.9	0.26
75	50	18	11.8	36.0	269	28.6	4 842	4.4	0.37
80	51	21	12.1	41.2	320	39.7	6 720	6.1	0.51
85	35	25	8.3	71.4	377	55.7	9 425	8.6	1.04
90	36	19	8.5	52.8	440	49.4	8 360	7.6	0.89
95	26	12	6.1	46.2	509	36.1	6 108	5.6	0.90
100	33	29	7.8	87.9	584	100.0	16 936	15.4	1.98
105	27	25	6.4	92.6	667	98.4	16 675	15.2	2.38
110	21	16	5.0	76.2	756	71.4	12 096	11.0	2.22
115	16	14	3.8	87.5	853	70.5	11 942	10.9	2.87
120	8	6	1.9	75.0	957	33.9	5 742	5.2	2.76
≥ 125	7	6	1.7	85.7	1 128	40.0	6 768	6.2	3.72
Total	423	212					109 898	100.0	

question that requires further study. Observations made at Cape Verde suggest that the reproductive season coincides with an increase in water temperature. Although the climate at Cape Verde fluctuates little throughout the year, leading Franca *et al.* (1959) to suggest that *P. regius* there do not undertake reproductive migration, there are periods of the year when the sea temperature increases, creating conditions similar to those of spring (Dias 1993). This can explain some synchrony in the reproductive cycle of Cape Verde lobsters, with a peak in ovigerous females from June to September. Mark-recapture studies need to be carried out in the population to determine whether small females only breed early in the season, and larger lobsters breed year-round, as observed in *Panulirus inflatus* and *Panulirus gracilis* (Briones-Fourzán and Lozano-Alvarez 1992).

The fecundity values estimated here are consistent with the results of other studies in geographically proximal areas. For waters off Mauritania, Maigret (1978, as cited by Dias 1993) estimated an average brood size of 1 300 000 eggs for female *P. regius* of 129–140mm CL; our estimates for similar sizes were 1 104 000 eggs (CL 129mm) and 1 385 000 eggs (CL 140mm). Greater fecundity was reported for the Ivory Coast, one female of 81mm CL carrying some 416 000 eggs (Marchal and Barro 1964), compared with our estimated value for the same CL for the Cape Verde population of 304 000. However, it should be noted that fecundity estimates for the Mauritania and Ivory Coast populations were based on small sample sizes. A review of palinurid life history patterns by Pollock (1995) gives the range of fecundity (standardised to

Table 4: Comparison of some reproductive parameters in *P. regius*: minimum carapace size of ovigerous females (MOF); size at onset of maturity for females (SOM) (criteria not defined in most cases); maximum number of eggs per female (e_{\max}) (observed)

Species	Study area	MOF (CL, mm)	SOM (CL, mm)	Brood size ($\times 10^{-3}$) 300–550 (90mm CL)	n	e_{\max} 1.2×10^6	Source
<i>Panulirus</i> spp.	Worldwide						Pollock (1995)
<i>Panulirus regius</i>	Eastern Atlantic/Gulf of Guinea						Maigret (1978), as cited by Dias (1993)
	North — Mauritania	67.2	53	1 300 (129–140mm CL)	3	1.3×10^6	Clotilde-Ba <i>et al.</i> (1997)
	North — Senegal	61.9	87.9	93–309	65	1.0×10^6	This study
	North — Cape Verde	57	58–73	BS = $1.59 \times \text{CL}^{2.77}$	1		Machal and Barro (1964)
	Centre — Ivory Coast	75		416 (81mm CL)			Giudicelli (1971)
	Centre — Benin	67					Franca (1966)
	South — Angola						

90mm CL) as 300 000–550 000 eggs. In this study, we obtained a value of 408 000 eggs.

Possible differences in egg size and/or weight are important in the evaluation of fecundity, because they may lead to different larval survival (DeMartini *et al.* 2003). The indicator of individual egg weight used in this work was modified from an earlier index presented by Fonseca-Larios and Briones-Fourzán (1998). Those authors considered the number of eggs in 0.01g of dry weight of egg mass to be an indicator of egg size, referring to it as ‘relative egg size’. The problem with this index is that its value is inversely related to individual egg size (the more the number of eggs in a standard egg mass, the smaller the eggs), making interpretation and discussion of comparative values difficult. In this study, we suggest an alternative index, designated the relative egg weight (REW). Eggs about to hatch may be significantly larger in diameter than recently oviposited eggs (Gracia 1985), but also lighter because of the consumption of the dense yolk material during embryo development (Briones-Fourzán and Contreras-Ortiz 1999). Studies on *P. argus* suggest that larger females, which may conduct multiple spawning, may produce smaller eggs in second or later egg masses (Fonseca-Larios and Briones-Fourzán 1998). Relative egg weight would therefore be expected to be lower, on average, at late developmental stages (brown eggs) or for larger females. However, the REW indices obtained here, which are directly proportional to individual egg weight, did not differ significantly with either egg stage or female size.

When determining reproductive potential, several aspects need to be considered in order to avoid biasing the estimates. Knowledge of spawning period is of relevance for estimating size–fecundity relationships when evaluating reproductive potential (Lizárraga-Cubedo *et al.* 2003). Specific fecundity can vary throughout the year, depending on variations in the number of individuals in age-groups and in food availability in the periods preceding reproduction (Correa-Ivo and Vasconcelos-Gesteira 1995). We minimised the bias in fecundity estimates by excluding egg masses in late development stages (likely to have suffered egg loss) and by estimating the population structure from intensive sampling, over three fishing seasons, in order to produce a fair representation of the population. At Cape Verde, females in the CL classes 100mm and 115mm produce half the total eggs of the population and have similar indices of productivity. Although a single spawning was assumed, multiple spawning may take place in large females, i.e. CL >115mm, resulting in underestimating the importance of those females in egg production. In such a situation, a reasonable management measure for the species would be to protect the large females by introducing a maximum landing size, in addition to the minimum landing size already in place. Such an approach has proved beneficial for other lobster species (Tully 2001).

The minimum landing size (MLS) for green lobsters at Cape Verde is 200mm TL, equivalent to 71.5mm CL. This value is close to the size-at-25% maturity estimated here (68.8mm). We suggest that the MLS should be increased to 250mm TL, equivalent to 89.3mm CL for females and 96.6 for males; for females this value would be just above the estimated $L_{50\%}$ here (87.9mm CL \approx 246mm TL), thus

protecting a large portion of effective reproductive females, about 55.6% of IRP, and is likely more realistic for a fishery partially based on SCUBA diving and traps. This measure would imply an increase in the current minimum landing weight from 500g to 600g.

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