

REPRODUCTIVE BIOLOGY OF FEMALE SPINY LOBSTER

PALINURUS DELAGOAE

IN TWO AREAS OFF EASTERN SOUTH AFRICA

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INTRODUCTION

Spiny lobsters (Crustacea: Decapoda: Palinuridae) have a wide distribution throughout the world's oceans, occurring in both tropical and temperate waters (Pollock *et al* 2000). They inhabit both shallow and deep water, over a wide range of habitats including rocky substrata, mud and sand flats, and vegetated beds (Holthuis 1991) where they are key predators in the biological community – feeding on a variety of smaller benthic organisms (Griffiths and Seiderer 1980). The dominance of spiny lobsters in biological communities can be attributed to their large size and abundance, characteristics that also underlie their success as a fishery species (both ecologically and economically). Of the 49 palinurid species, 33 are commercially important and sustain large fisheries around the world (Lipcius and Cobb 2000).

Two commercially important deep-sea palinurid species occur in the temperate waters along the south and east coasts of South Africa at depths exceeding 50 m (Pollock *et al* 2000). The South Coast spiny lobster, *Palinurus gilchristii*, inhabits rocky substrata on the coastal shelf (up to 200 m deep) between Cape Point (18°20'E) and the Eastern Cape Province (28°E) (Berry 1971, Lipcius and Cobb 2000, Groeneveld in press). The East Coast spiny lobster, *Palinurus delagoae*, has a larger depth range (50 - 600 m) and generally prefers sandy substrata (Groeneveld 2000, Pollock *et al* 2000). Its range along the African coastline extends from northern Mozambique (17°S) to southern Kwa-Zulu Natal in South Africa (32°S) (Pollock *et al* 2000).

Both species have reasonably long-standing histories of exploitation by trap and trawl fisheries. The trap fishery for *P. gilchristii* (established in 1974) is South Africa's second largest lobster fishery and is almost entirely an export fishery. Management of this fishery is by limiting the Total Allowable Catch and number of fishing days of quota holders (Groeneveld in press). The trawl fishery for *P. delagoae* began in the 1960s, followed by the emergence of the trap fishery in the 1980s, after which catches declined rapidly from 200 – 300 tons to 81 tons by 1997 (Pollock *et al* 2000). Following stock assessments (Groeneveld 2000) and research for the commercial fishery for *P. delagoae* (Pollock *et al* 2000) the fishery was limited to trawling only, as the best way to meet both economic and ecological management aims. It was however suggested that pulse fishing might be a better way to meet management aims (Groeneveld *et al* 2000).

A one-year experimental fishery for *P. delagoae* was established in April 2004 to determine the frequency and magnitude at which pulse fishing may be sustainable (Government Gazette 2004). Determining the extent of recovery after fishing is one aim of the experimental fishery. Assessments of the growth rate, size at sex maturity and natural mortality of *P. delagoae* were performed in 2000 (Groeneveld *et al*) and can be supplemented by the results of this study, which assess the reproductive biology of the East Coast spiny lobster in order to address this aim. A recent study (Groeneveld in press) assessed fecundity, egg loss during gestation, relative reproductive potential and lifetime egg production per recruit for *P. gilchristii* from three areas along the South African south coast. A general east-west trend of increasing fecundity, size at sexual maturity, and lifetime egg production per recruit was found for *P. gilchristii*. Examining egg-loss

through the first four (of six) developmental stages of gestation showed significant loss of around 15 % by stage four, irrespective of lobster size (Groeneveld in press). The study of fecundity in *P. gilchristii* (Groeneveld in press) was used as a framework for assessing the fecundity of *P. delagoae* in this study.

Juvenile *P. delagoae* lobsters recruit to the deeper depths of the range (>350 m) for the species and migrate inshore as they mature (50 – 59 mm CL) where they are known to form dense aggregations (Berry 1973, Pollock *et al*/2000). This spatial division between small and large lobsters is possibly due to different dietary requirements (both type and quantity) between the size-classes (Berry 1973). East Coast spiny lobsters, like most palinurid lobsters, demonstrate life-history characteristics of both r- and K-selection – they are slow growing and long lived (Berry 1973) and have a delayed maturity (K-selection), yet they produce large numbers of offspring, and, since offspring is spawned, demonstrate no parental care (r-selection) (Lipcius and Cobb 2000). ok ?

Mature *P. delagoae* females reproduce once a year (Berry 1973). A small proportion of lobsters are in berry throughout the year, but the frequency of berried females begins to increase in September, peaks between February and April and declines rapidly in May (Pollock *et al*/2000). As females reach sexual maturity the first two pairs of pleopods (ovigerous setae) become setose to cover the externally carried eggs, which are attached to endopods (stalks) that develop on each. Setae are never lost, thus sexual maturity can be established by the presence of setae, irrespective of the presence or absence of eggs / on the pleopod (Berry 1973, Lipcius and Cobb 2000). *P. delagoae* has a lower fecundity than

most other palinurid species – producing fewer but larger eggs, with a higher yolk content (Berry 1973). They also have a prolonged gestation, compared to other crustaceans, whereby larvae are retained in the eggs until the end of the nauplius stage and hatch as phyllosome larvae. Most other crustaceans emerge from eggs as nauplius larvae (Berry 1973, Lipcius and Cobb 2000). The larger eggs-sizes and longer gestation period for *P. delagoae* enhances the probability of larval survival, increasing the proportion of the initial egg-stock that will survive until recruitment (Lipcius and Cobb 2000).

The following elements of the reproductive biology of female *P. delagoae* were assessed for two regions off the east coast of South Africa: 1) the relationship between CL and wet lobster mass; 2) the relationship between lobster size and fecundity; 3) size at sexual maturity; 4) relative reproductive potential and 5) lifetime egg production per recruit. Results were compared to those of previous studies for *P. delagoae* (Berry 1973, Groeneveld *et al* 2000) and *P. gilchristii* (Groeneveld in press).

METHODS

Data collection

Egg-bearing females were caught by experimental fishing vessel in two regions off the South African East Coast (southern east-coast region and central east-coast region).

Specimens were frozen at sea and returned to Marine and Coastal Management in Cape Town for processing. Carapace length (CL), measured along the dorsal mid-line from the

anterior edge of the rostrum to the posterior edge of the carapace, and wet lobster mass were measured for each lobster. Egg masses were then removed and weighed (wet berry mass). Samples were dried overnight (~ 18 hours) in an oven at 80 °C.

Dry egg samples were cleaned by removing any foreign (non-egg) material, such as fragments of endopods and pleopods, and weighed (= W_t , dry berry mass). A small sub-sample of eggs from each dry berry mass was removed and weighed (= W_s , sub-sample berry mass) and the exact number of eggs in the sub-sample counted (E). The fecundity, or number of eggs carried externally on the abdomen (F), was calculated for each lobster using the following equation (Groeneveld in press):

$$F = (W_t / W_s) E,$$

Six stages of egg development have been identified by Berry (1973) of which only the first three were represented in the sample. The developmental stage of each egg sample was classified using the following visual classification system (Berry 1973, Groeneveld 2000):

Stage 1: bright orange egg mass, no macroscopically visible embryonic development,

Stage 2: orange egg mass, embryonic development visible in form of eye-spots,

Stage 3: brown egg mass, eye-spots visible and slightly larger than in stage 2.

Catch data collected from the southern and central regions included CL and sexual status (mature female (F), immature female (I) or male) for each lobster caught. Mature females were recognised by the presence of ovigerous setae. Data for females were formatted into frequency data for the number of females in each sexual class per 1-mm CL size-class and per 5-mm CL size-class.

Data analysis

Regression analyses were performed to examine the relationship between CL and wet lobster mass for individuals collected from the southern region (S-R) and central region (C-R) separately, as well as for both regions collectively (all – 2004). A logarithmic transformation was performed on the data and a linear regression analysis conducted (where $x = \log(\text{CL})$ and $y = \log(\text{wet lobster mass})$). The full range of CLs from the catch data were logarithmically transformed (x) and the linear equations (for south, central and all) used to estimate y for each CL. The equation for the relationship between wet lobster mass and CL for *P. delagoae* ($\text{mass} = 0.00187\text{CL}^{2.762}$), calculated from historical trawl data (Berry 1973), was logarithmically transformed into a linear equation ($y = 2.762x - 6.28$) and used to estimate y for the full range of CLs from the catch data. The linear increase in y with respect to x was calculated (as y/x) for each CL, for the catch data (south, central and all) and the historic data. Students t -test's were composed to determine if there is a difference in the logarithmic increase in wet lobster mass per unit CL (y/x) between 1) regions (southern and central) and 2) catch data-sets (all – 2004 and 1973).

The proportions of mature females within each 1-mm CL size-class were calculated and plotted against CL for both regions. A line of best-fit was calculated for each region using the logistic equation for estimating the percentage of sexual maturity with respect to CL (Groeneveld 2000), and by adjusting the constants in the equation (a and b) to produce a line with the least possible difference from the actual data. The logistic equation for percentage sexual maturity (f_m) is as follows:

$$f_m = \frac{1}{1 + \exp(a - bCL)},$$

where a and b are constants, and CL is carapace length. Using the logistic equation for each region the percentage of sexual maturity was calculated for each 1-mm CL for the full range of CLs recorded for both regions. A Wilcoxon Matched Pairs Test was constructed to determine if differences in frequencies estimated for the southern and central region, for each size-class, is significant. Size at sexual maturity (where $f_m = 50\%$) was estimated for both regions using the logistic equation and the respective constants (a and b) adjusted for each region.

Linear regressions of 1) CL vs. fecundity and 2) CL vs. wet berry mass were conducted for individuals collected from the southern and central regions separately, as well as both regions collectively (all). Resulting regression equations were used to estimate the fecundity and wet berry mass of lobsters for the full range of CLs recorded in the catch

data. Equations for fecundity of *P. delagoae* and *P. gilchristii*, and for wet egg mass of *P. delagoae* and *P. homarus* from previous studies (Table 1) were used to estimate fecundity and wet egg mass for the full range of CLs recorded in the catch data. Students t-tests were constructed to test for differences in the mean number of eggs per unit CL between 1) the southern and central regions, 2) *P. delagoae* and *P. gilchristii* and 3) current and past catch data for *P. delagoae*. Similarly, Students t-tests for the difference in the mean egg mass per unit CL between 1) the southern and central regions, 2) *P. delagoae* and *P. homarus* and 3) current and past catch data for *P. delagoae*.

The relationship between CL and fecundity was examined more closely with respect to stage of egg development. A linear regression analysis of CL vs. fecundity for each region was conducted for stages 1 – 3 separately. Regression equations were used to estimate the predicted fecundity in each stage, for the full range of CLs from the catch data for both regions. A one-way ANOVA was composed for each region to determine if the mean number of eggs per unit CL between stages is significantly different, with stages as a fixed factor.

Using the catch data for the frequency of females per 5 mm size-class, relative reproductive potential (RRP) for each size-class was calculated for both regions using the following equation (Groeneveld in press):

$$P_i = C_i M_i F_i,$$

where C_i is the proportion of females (of the total female catch) in size-class i , M_i is the percentage of sexually mature females in size-class i , and F_i is the fecundity (eggs per lobster) in size-class i . P values for each size-class were represented together with the catch curve and size at sexual maturity curve for both regions.

Life-time egg production per recruit (E/R) is one means of estimating how many eggs a lobster may produce over a number of years (30 years were modeled for this study), beginning at the size at 50% sexual maturity. Starting with 1000 individuals, annual increments in CL were estimated from the equation for annual growth rate from Groeneveld (2000) ($A = ((-0.0092CL)+8.94)$), and the decrease in number of survivors for each successive year calculated at a natural mortality rate of 10% (Groeneveld 2000). For each CL size-class calculated for the successive years, the number of survivors were multiplied by the proportion of mature females, and by fecundity per mature female for each respective size class. The result is the number of eggs produced by the number of survivors in each size class. Adding the resultant number of eggs for all size-classes simulates the number of eggs 1000 lobsters will produce over thirty years (relative to natural mortality and percentage sexual maturity). This result was divided by 1000 to estimate the life-time egg production per lobster.

RESULTS

In total, 163 egg-bearing females were sampled for analysis of fecundity, 77 from the southern region (S-R) and 86 from the central region (C-R). Individuals ranged from 67.1

mm to 154 mm CL (mean = 102.5 mm \pm 17.0 SD). Catch data from the experimental fishery vessel provided CL and sexual status data for a further 7005 females ($n_{\text{mature}} = 4017$, $n_{\text{immature}} = 2988$) between 45 and 168 mm CL. Mean CLs for the sample data (S-R = 99 mm \pm 14.8 SD, and C-R = 104.8 mm \pm 19.0 SD) and the catch data (S-R = 68.5 mm \pm 15.7 SD and C-R = 99.9 mm \pm 18.81 SD) were higher for the central region in both

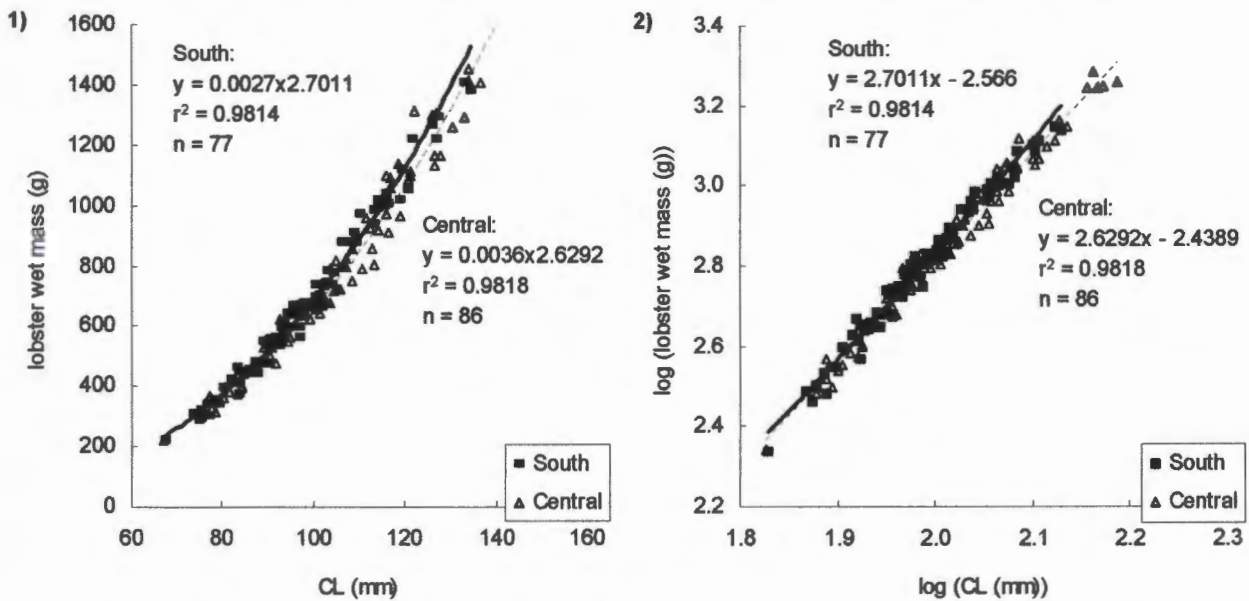


Figure 1: Regression analyses of 1) CL vs. wet lobster mass and 2) log(CL) vs. log(wet lobster mass) for the southern and central regions separately. All r^2 values are significant at $p < 0.01$.

Wet lobster mass correlates strongly to CL for both the southern and central region ($r^2 = 0.98$ for both regions), at a significance level of $p < 0.01$ (Figure 1.1). The mean linear increase in y (= $\log(\text{mass})$) per unit increase in x (= $\log(\text{CL})$) is significantly higher for the southern region than the central region ($t = 5.17$, d.f. = 124, $p < 0.001$). Thus the proportional increase in wet lobster mass with increasing CL is higher for the southern region. Similarly, the mean linear increase in y with increasing x , and therefore the proportionate increase in wet lobster mass with increasing CL, is significantly higher for the catch data for 2004 than for the historic data (Berry 1973) ($t = 44.2$, d.f. = 124, $p <$

0.001). The relationship between CL and wet lobster mass for the catch data (2004) was explained by the equation: $\text{mass} = 0.0036x^{2.636}$ ($r^2 = 0.98$, significant at $p < 0.001$).

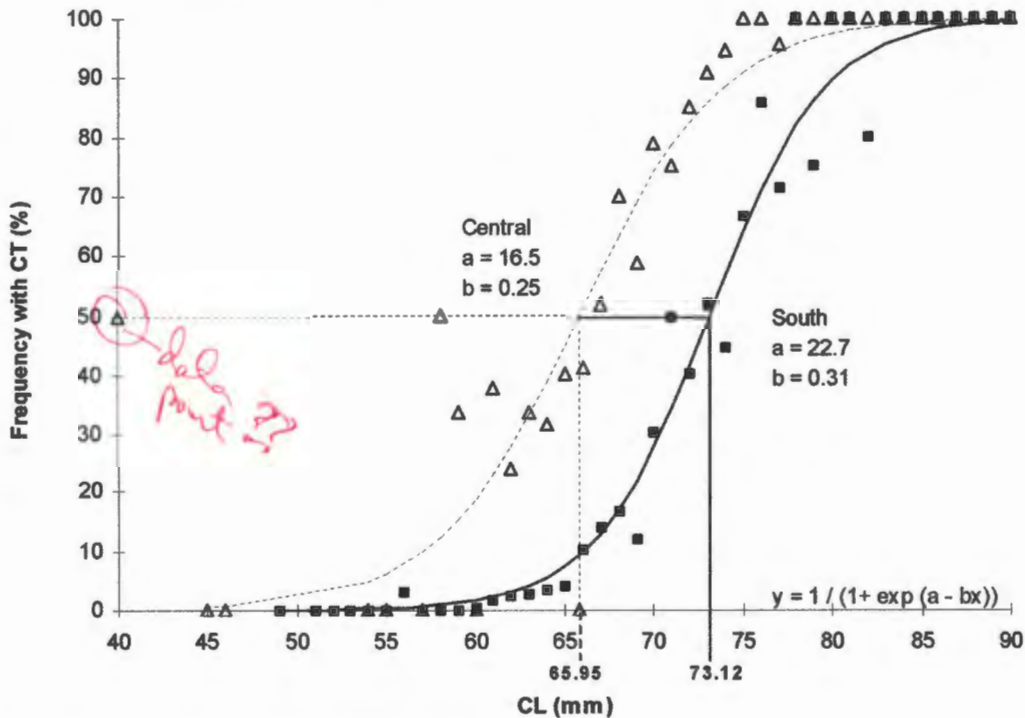


Figure 2: Size-frequency distribution of mature females in each 1 mm-CL size-class for the southern and central region. Carapace length at 50% maturity is displayed for both regions.

Matched pairs test for the percentages of sexual maturity estimated for each CL size-class differed significantly between the southern and central region ($Z = 3.06$, $p = 0.002$, $N = 63$). Size at 50% sexual maturity is lower for the central region (65.95 mm CL) than for the southern region (73.12 mm CL) (Figure 2). A previous estimate by Groeneveld (2000) using the setal method ($f_{50} = 67.3$ mm) is similar to the mean size at sexual maturity for both regions together ($f_{50} = 69.5$ mm).

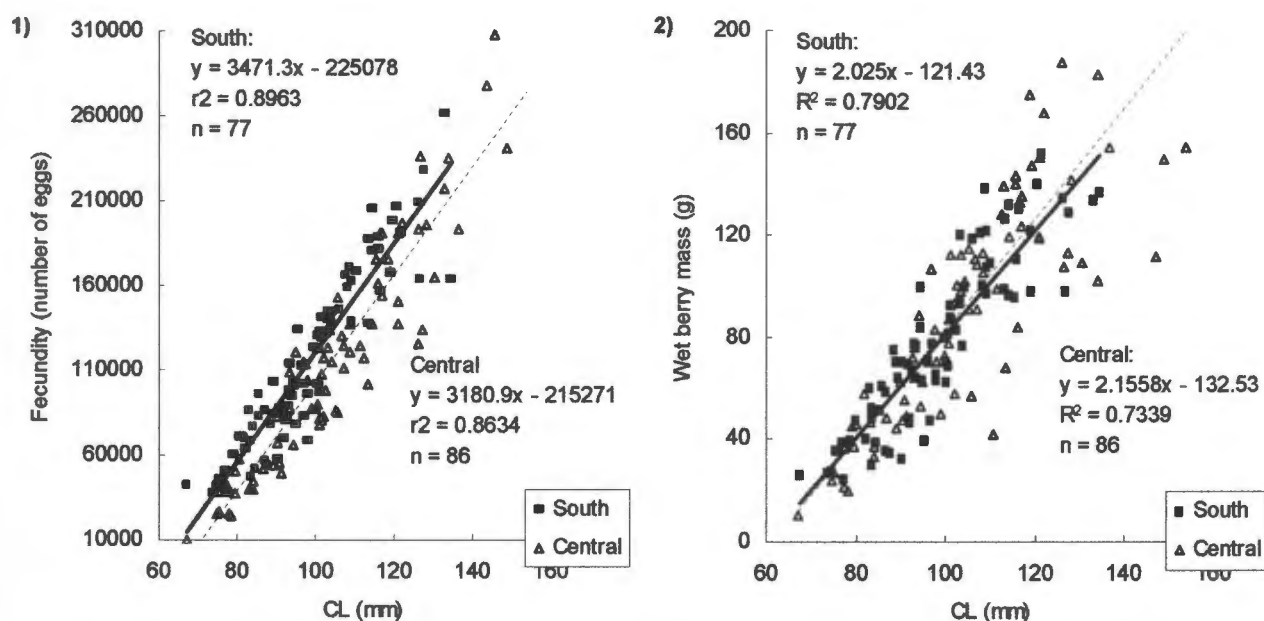


Figure 3: Regression analyses of 1) CL vs. fecundity and 2) CL vs. wet berry mass for the southern and central regions separately. All r^2 values are significant at $p < 0.001$.

A strong linear relationship between CL and reproductive output (fecundity and egg mass) existed for both regions separately (Figure 3) and collectively (Table 1) – significant at $p < 0.001$. The mean number of eggs per unit CL for the southern region (1604 eggs/mm \pm 597SD) is significantly higher than for the central region (1395 eggs/mm \pm 571SD), however no significant difference between the two regions was found for the mean egg mass per unit CL (Table 1).

Table 1: Regression equations and statistical analyses used for comparisons of CL vs. F and CL vs. egg mass between regions, species and current and past catch data. 2004 r^2 values are significant at $p < 0.01^*$ and $p < 0.001^{}$. Significant results from statistical analyses are indicated in bold print.**

Relationship	Comparison	Regression equations	Statistical analysis	Source
CL vs. F	South vs. Central	$F = 3471.3CL - 225078$ $r^2 = 0.90^{**}$ $F = 3180.9CL - 215271$ $r^2 = 0.86^{**}$	T-test: $t = 2.04$, d.f. = 128, $p < 0.005$	Catch data – 2004
	<i>P. delagoae</i> - 2004 vs. 1973	$F = 3119CL - 200530$ $r^2 = 0.84^{**}$ $F = 2280CL - 147200$	T-test: $t = -1.8$, d.f. = 128, $p = 0.08$	Catch data – 2004, Berry 1973
	<i>P. delagoae</i> vs. <i>P. gilchristii</i>	$F = 3119CL - 200530$ $r^2 = 0.84^{**}$ $F = 1778CL - 73717$	T-test: $t = 4.1$, d.f. = 128, $p < 0.001$	Catch data – 2004, Groeneveld in press
	South: stage 1 vs. stage 2 vs. stage 3	$F = 3381.2CL - 218459$ $r^2 = **$ $F = 2996.7CL - 176669$ $r^2 = **$ $F = 3341.2CL - 217726$ $r^2 = **$	ANOVA: $F_{1,177} = 0.056$, $p = 0.95$	Catch data – 2004
	Central: stage 1 vs. stage 2 vs. stage 3	$F = 2884.1CL - 184724$ $r^2 = *$ $F = 3302.5CL - 224016$ $r^2 = *$ $F = 3125.1CL - 213065$ $r^2 = *$	ANOVA: $F_{1,171} = 0.52$, $p = 0.5$	Catch data – 2004
CL vs. egg mass	South vs. Central	Egg mass = $2.025CL - 121.43$ $r^2 = 0.79^{**}$ Egg mass = $2.156CL - 132.53$ $r^2 = 0.73^{**}$	T-test: $t = -0.5$, d.f. = 134, $p = 0.6$	Catch data – 2004
	<i>P. delagoae</i> - 2004 vs. 1973	Egg mass = $2.1CL - 129.96$ $r^2 = 0.76^{**}$ Egg mass = $1.5CL - 73.7$	T-test: $t = 2.52$, d.f. = 134, $p < 0.05$	Catch data – 2004, Berry 1973
	<i>P. delagoae</i> vs. <i>P. homarus</i>	Egg mass = $2.1CL - 129.96$ $r^2 = 0.76^{**}$ Egg mass = $13CL + 59.7$	T-test: $t = 4.15$, d.f. = 134, $p < 0.001$	Berry 1973

Equations for fecundity between 2004 and 1973 data produce similar estimates for F (relative to CL) while estimates of egg mass (relative to CL) differs between the two catches (means for 2004 and 1973 data are $1 \text{ g/mm} \pm 0.39\text{SD}$ and $0.87 \text{ g/mm} \pm 0.40\text{SD}$ respectively). Comparisons between species reveal that *P. gilchristii* produces on average significantly more eggs per unit CL than *P. delagoae* ($1445 \text{ eggs/mm} \pm 532\text{SD}$ and $1167 \text{ egg/mm} \pm 196\text{SD}$ respectively). *P. delagoae* produces on average a higher egg mass per

mmCL ($1 \text{ g/mm} \pm 0.39\text{SD}$) than *P. homarus* ($0.79 \text{ g/mm} \pm 0.18\text{SD}$). For both the southern and central region no significant difference was found in the mean number of eggs per unit CL between the three stages. Thus, no significant egg-loss occurs through egg stages 1 – 3 for *P. delagoae*.

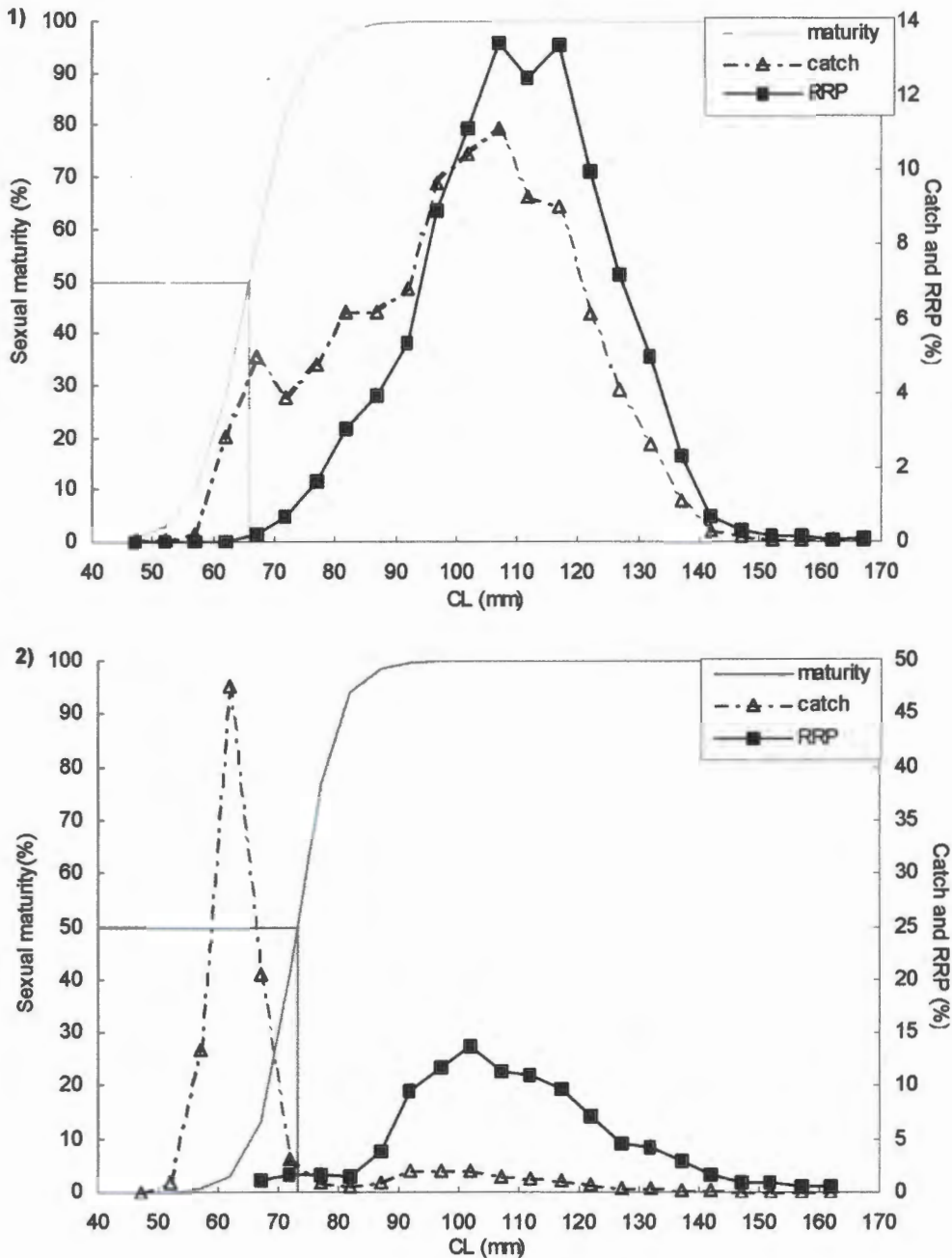


Figure 5: Relative reproductive potential per size-class represented with the female catch curve and percentage of sexual maturity curve for 1) the central region and 2) the southern region.

The distribution for RRP for the central region follows the catch distribution for females closely (Figure 5). Not for S region! Both curves have relatively normal curves and peak around similar size-classes (105 – 125 mm). The increase in the catch distribution for CLs > 60 mm for the central region indicates that the fishery mostly targets sexually mature individuals.

The catch the southern region is composed mostly of individuals between 50 mm and 70 mm CL. The distribution for RRP follows the catch distribution, both peaking around similar size classes (95 – 105 mm CL). Lobsters in the southern region reach 50 % sexual maturity around 73 mm CL. Thus the fishery in the south targets mostly sexually immature lobsters. Distributions for RRP between the regions are similar – both have relatively normally shaped curves and peak around the same value for RRP (~ 14 – 15 %), however maximum RRP is reached at a lower range for CL for the southern region. The lifetime production of eggs for lobsters in the central region was estimated at 17.6 million eggs per lobster and 22.71 million eggs per lobster in the southern region.

DISCUSSION

A few general trends in the reproductive biology of *Palinurus delagoae* were found between the southern and the central region. Lobsters in the south generally have a greater mass respect to carapace length (Figure 1). For example, lobsters from each region with equal CLs will weigh more in the southern region. The size at which lobsters reach 50% sexual maturity was shown to be significantly higher for the southern region (Figure 2). A possible explanation for both these trends is that food resources may be

more abundant, or of a better quality than for the central region, which enables lobsters to gain more weight and gain more resources needed for egg production. The southern region also produces higher numbers of eggs per unit CL than the central region (Figure 3). Interestingly, the egg mass per unit CL does not differ between the regions – for a given CL, egg mass will be equal between the regions but egg number will be lower for the central region. The lower number of eggs estimated for the central region is not due to egg-loss during incubation since no difference in the number of eggs was found between the stages. It can be inferred that lobsters in the central region produce fewer and larger eggs than those in the southern region, however the significance of this difference will have to be examined in future analyses.

Comparisons between regressions for *P. delagoae* from current (2004) and historical catch data for the east coast (Berry 1973) showed higher estimates in the mass per unit CL for the current catch data. A direct interpretation would be that there has been an increase in the amount of weight a lobster gains as it grows with respect to CL. More likely the differences have resulted from differences in the areas sampled in each study, or the methods used for weighing and measuring the variables in the past and current data. The same trend was shown for the current data with respect to egg mass per unit CL, where estimates are higher for the more recent fisheries data, however there was no such trend for fecundity (number of eggs). Differences could be interpreted as an increase in average egg size over time, but it's more likely the past data was recorded earlier in the breeding season when eggs are in earlier developmental stages and tend to be smaller.

Inter-species comparisons showed that fecundity is lower with respect to CL for *P. delagoae* than for *P. gilchristii*. However higher egg masses (relative to CL) were estimated for *P. delagoae* than for *P. homarus*. The lower fecundity in *P. delagoae* may be due to smaller sized eggs in *P. gilchristii*. Similarly, the higher mass per unit CL for *P. delagoae* may be due to *P. delagoae* producing fewer, but larger, eggs per gram of egg mass. Unfortunately regressions equations for CL vs. F and CL vs. egg mass were not both available for the two species used for comparison however *P. delagoae* has been said to produce fewer larger eggs than other palinurid species (Berry 1973).

Despite the regional differences in fecundity between the regions, regressions for CL vs. F can be used to estimate various fecundity related factors fairly accurately, which can then be used to assess aspect related to fisheries management. For example RRP can be used to determine for which CL size-classes egg-stock is highest and what the effect of the fishery is on these size classes and therefore over-all egg production. RRP reaches peaks at a smaller CL size class in the southern region than the central region. Catches in the southern region mostly targets immature females (< 70 mm CL) which will not show to effect RRP directly, since the frequencies of mature individuals per size class in the population are used to calculate RRP. The effect of harvesting immature females will only be seen in the future because it will cause an eventual decrease in number of individual that escape harvesting and live to reproduce. Catch data for the central regions shows a direct effect on RRP because a wide range of CL size classes, all of reproductive size are harvested – RRP follows the catch data quite closely. RRP is important for assessing the

effect of fishing on the potential egg-stock. RRP is an estimate of egg production for each size class in the catch.

The egg production of a single lobster as it grows through the different size-classes was estimated for both regions as life-time egg production per recruit (E/R). E/R was higher for the southern region. The difference in E/R between the regions is due to some of the trends in the reproductive biology of *P. delagoae* reported above. With a higher size at sexual maturity, individuals from the southern region will, even on their first moult, produce more eggs than those in the central region – due to the larger CL at reproduction. The effect is that a lobster from the southern region ⁵keep producing proportionately more eggs each year as it grows ~~than a lobster in the central region~~. Life-time egg production per recruit for lobsters in the southern region is 22.71 million and 17.6 million for the central region. Thus, results indicate a definite trend of increased reproductive potential towards the southern region with respect to fecundity, RRP and egg size.

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APPENDICES

APPENDICES

Appendix 1: Table for the calculation of E/R for the southern and central regions

No. years	South CL (cm)	No. survivors	Proprtion of mature femalesize	brood	South No. eggs prod * 10 ⁶ years	Central CL (cm)	No. survivors	Proprtion of mature femalesize	brood	Central No. eggs prod * 10 ⁶	
1	73.2	1000	0.5	2316261	1171.5	1	1000	0.5	1676796	838.6	
2	75.4	900	0.7	2392792	1442.1	2	900	0.7	1757697	1063.5	
3	77.4	810	0.8	2462282	1576.3	3	810	0.8	1831155	1182.9	
4	79.2	729	0.9	2525379	1599.5	4	729	0.9	1897855	1213.1	
5	80.9	656	0.9	2582671	1553.8	5	656	0.9	1958419	1187.5	
6	82.4	590	0.9	2634693	1472.0	6	590	1.0	2013410	1131.9	
7	83.7	531	1.0	2681928	1374.0	7	531	1.0	2063343	1062.2	
8	85.0	478	1.0	2724818	1270.9	8	478	1.0	2108682	987.2	
9	86.1	430	1.0	2763761	1168.7	9	430	1.0	2149849	911.8	
10	87.1	387	1.0	2799122	1070.4	10	387	1.0	2187229	838.4	
11	88.0	349	1.0	2831230	977.6	11	349	1.0	2221170	768.4	
12	88.9	314	1.0	2860384	890.9	12	314	1.0	2251989	702.4	
13	89.6	282	1.0	2886856	810.5	13	282	1.0	2279972	640.9	
14	90.3	254	1.0	2910892	736.4	14	254	1.0	2305381	583.8	
15	91.0	229	1.0	2932717	668.3	15	229	1.0	2328452	531.0	
16	91.5	206	1.0	2952534	605.9	16	206	1.0	2349401	482.5	
17	92.1	185	1.0	2970528	548.9	17	185	1.0	2368422	437.9	
18	92.5	167	1.0	2986866	496.9	18	167	1.0	2385694	397.1	
19	93.0	150	1.0	3001702	449.6	19	150	1.0	2401376	359.9	
20	93.3	135	1.0	3015172	406.5	20	135	1.0	2415616	325.9	
21	93.7	122	1.0	3027403	367.4	21	122	1.0	2428545	294.9	
22	94.0	109	1.0	3038509	332.0	22	109	1.0	2440285	266.7	
23	94.3	98	1.0	3048594	299.8	23	98	1.0	2450945	241.1	
24	94.6	89	1.0	3057750	270.7	24	89	1.0	2460625	217.9	
25	94.8	80	1.0	3066064	244.3	25	80	1.0	2469413	196.8	
26	95.0	72	1.0	3073613	220.4	26	72	1.0	2477394	177.7	
27	95.2	65	1.0	3080468	198.8	27	65	1.0	2484640	160.4	
28	95.4	58	1.0	3086692	179.3	28	58	1.0	2491219	144.8	
29	95.6	52	1.0	3092343	161.7	29	52	1.0	2497193	130.6	
30	95.7	47	1.0	3097475	145.8	30	47	1.0	2502618	117.8	
					22710.83						17595.57
					E/R = 22.71						E/R = 17.60