

## Fecundity of the deep-water spiny lobster *Palinurus delagoae* off eastern South Africa

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**Abstract**—The fecundity of a deep-water spiny lobster (*Palinurus delagoae*) was investigated using egg-bearing females caught in traps set in two regions of the South African east coast: south of Durban (South) and near Richards Bay (Central). Fisheries observers on a commercial fishing vessel collected 161 females with egg-masses in developmental Stages 1 - 3 during 2004. Egg-masses were removed, oven-dried and the eggs counted. Relationships between fecundity and carapace length (CL) were linear and females caught in the south carried significantly more eggs than those in the central region at equivalent lobster sizes. Egg-loss during incubation was 10 - 16% (for CLs of 75 - 140 mm) between the 1st and 3rd egg stages, and egg diameter increased from 0.96 - 1.04 mm in stage 3. Estimates from the present study compare well with those of two other species in this genus, and confirm that the deep-water *Palinurus* lobsters produce fewer, but larger eggs than is usual in shallow-water lobster genera. Larger eggs, well-developed larvae and a shorter pelagic drifting phase may have evolved in *P. delagoae* to counter larval over-dispersal and loss in the Agulhas Current, and to retain populations in the vicinity of the south-east African coast.

### INTRODUCTION

Several deep-water lobster genera inhabit the shelf waters of the Western Indian Ocean, along the southern and eastern coasts of Africa, Madagascar, and at submerged ridges and plateaus among islands (Holthuis, 1991). Most are rarely caught, and are known only from scattered recordings (*Puerulus angulatus*, *Palinustus mossambicus*, *Palinustus unicornutus*, *Projasus parkeri*, *Ibacus novemdentatus*) and as minor bycatches of deep-water fisheries (*Linuparus somniosus* and the *Scyllarides elisabethae*) (Groeneveld *et al.*, 1995). Two exceptions are the spiny lobsters *Palinurus delagoae* and *Palinurus gilchristi*, which support commercial fisheries in South Africa and Mozambique (Pollock *et al.*, 2000).

*Palinurus delagoae* Barnard, 1926 is distributed from 17°S (central Mozambique) to 32°S (eastern South Africa), and inhabits rocky areas and a substratum consisting of mud with a high organic content and varying quantities of sand and coral fragments at depths of 100 - 400 m (Berry, 1971). *P. delagoae* was first exploited off eastern South Africa in the 1920s (Gilchrist, 1920), and reports exist of catches of up to 5 t/trawl (Berry, 1972). Trawl catches gradually declined and after the 1960s the lobster-directed fishery diversified to catch deep-water prawns and langoustines, with smaller by-catches of lobster, red crabs and several fish and cephalopod species (Groeneveld & Melville-Smith, 1995).

Trap-fishing for *P. delagoae* commenced in 1980 in Mozambique and fishing grounds extended

from Inhaca (27°S) to the Bazaruto archipelago (21°S) (Palha de Sousa, 2001). Trap-catches peaked at >300 t/yr, but then declined, until the trap fishery was abandoned in 2000 as a result of low catch rates. Experimental trap-fishing in South Africa in 1994 - 1997 recorded initial catches of 90 t of *P. delagoae* and ~ 30 t of slipper lobster *Scyllarides elisabethae* but catches and catch rates declined sharply (Groeneveld, 2000) and no trap-fishing took place between 1998 and 2004. Exploratory trapping for *P. delagoae* off southern Madagascar and submerged sea-mounts recorded occasional good catches, but not commercially viable quantities (Roullot, 1988).

Female *P. delagoae* produce a single brood of eggs annually during summer, and incubation takes 5 - 6 months (Berry, 1973; Brinca & Palha de Sousa, 1983). Larvae are pelagic for at least two months (65 days; Kittaka *et al.*, 2001) and they are presumably widely dispersed by the south-westerly flowing Agulhas Current (Berry, 1974). Females achieve sexual maturity at 65 - 72 mm carapace length (CL) (Brinca & Palha de Sousa, 1983; Groeneveld, 2000), and adults moult once per year, between August and October (Berry, 1973). Adult *P. delagoae* grow slowly, increments decrease with increasing CL, and females grow progressively more slowly than males after reaching sexual maturity (Groeneveld, 2000). The maximum size observed is 185 mm CL, and males dominate in length classes >125 mm CL. Population size structure varies by latitude and is often stratified across depth (Cockcroft *et al.*, 1995).

*P. delagoae* is highly migratory, undertaking at least three migrations during the course of its lifetime. Juveniles gradually move shallower from depths >400 m as they grow larger, to recruit to adult populations at depths of 150 - 350 m (Cockcroft *et al.*, 1995). Egg-bearing females tend to concentrate in dense aggregations at shallower depths in summer, and then move deeper (>300 m) in autumn and winter after their eggs have hatched (Kondritskiy, 1976). These inshore juvenile and reproductive migrations occur over relatively short distances, because of the narrow steeply-sloping continental shelf. However, juveniles of both sexes also undertake long-distance, counter-current migrations of up to 500

km, most likely as an adaptation to redress downstream dispersal of larvae and thus retain the geographic distribution of adult populations (see Groeneveld, 2002).

Fecundity-size relationships of spiny lobsters vary spatio-temporally, and have often been determined for fished populations because they can be used together with size frequency data to assess the effects of changes of minimum legal size and exploitation rate on egg production (Annala & Bycroft, 1987; Beyers & Goosen, 1987; Goñi *et al.*, 2003; Groeneveld, 2005). The fecundity or number of eggs carried by female *P. delagoae*, was estimated by Berry (1973) from 24 females over the sexually mature size range. That study found that fewer eggs were carried, relative to the size of the animal, than had been recorded in other members of the Palinuridae. The aims of the present study were (1) to determine the fecundity-size relationships of *P. delagoae* from two areas along the east coast of South Africa and compare them with the earlier relationship of Berry (1973), (2) to estimate egg loss during incubation, and (3) to compare fecundity-size relationships for *P. delagoae* with information available for other *Palinurus* species.

## MATERIALS AND METHODS

Random samples of egg-bearing (berried) female lobsters were collected by fisheries observers from traps set during an experimental fishery along the KwaZulu-Natal (KZN) coast of South Africa in 2004 (Fig. 1). A wide size range of females was collected from the South (30 - 31°S) and Central regions (28 - 29°S), frozen intact at sea, and transported to the laboratory. Carapace Length (CL  $\pm$  0.1 mm) was measured mid-dorsally from the tip of the rostrum to the posterior edge of the carapace, and total wet mass (TM, in grams) determined. The egg masses of the berried females were then removed and egg diameters were measured from subsamples of five eggs/female from each development stage, using a binocular microscope at 40 x magnification. Stage 1 egg-masses (no eyespots; eggs uniformly bright orange) were separated from Stage 2 (small eyespots) and Stage 3 eggs (eyesspots large; eggs discoloured). Egg masses were weighed and oven-dried at 80°C

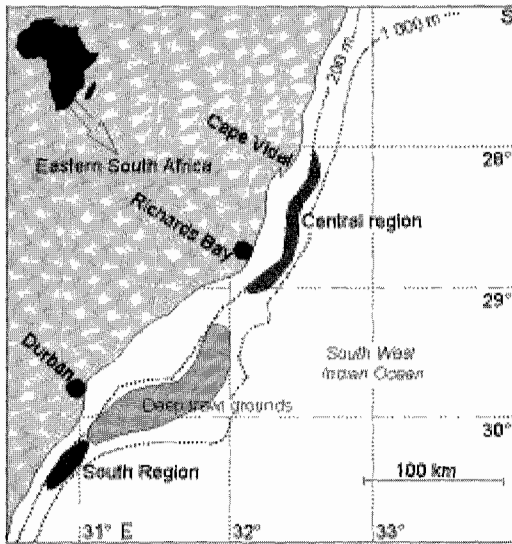


Fig. 1. The east coast of South Africa showing the South and Central regions from where egg-bearing female *P. delagoae* were collected

for 18 h. Extraneous material was removed manually and the total dried egg mass per female was weighed. Subsamples of dried eggs (approximately 100 eggs weighing 0.1 - 0.3 g) were taken from 10 randomly selected egg masses in each developmental stage, the number of eggs in the subsample was counted, and fecundity was estimated according to the equation:

$$F = (W_t / W_s) E_s$$

where  $W_t$  is the total dry weight of the egg sample,  $W_s$  the subsample weight, and  $E_s$  the egg count of the subsample. The average numbers of eggs/gram counted per egg stage were used to calculate fecundity of individuals for which eggs were not counted.

Linear regressions of fecundity as a function of CL were calculated using a least-squares fit, and regression slopes and elevations compared using Student's *t*-tests and analysis of covariance (ANCOVA), followed by a Tukey post-hoc test (Zar, 1984). Egg loss during incubation was estimated by comparing the CL/fecundity regressions of females with eggs in different stages. Egg diameters were compared among stages using a single factor ANOVA.

## RESULTS

Data were available for 161 female lobsters, ranging in size from 67.1 to 153.8 mm CL (220 - 1810 g TM), and a non-linear length-mass relationship closely fitted the raw data from defrosted females ( $r^2 = 0.98$ ; Fig. 2a, Table 1). Dried egg masses weighed an average of 24% of wet mass and water-loss spanned 65 - 87% across the size range examined (Fig. 2b). The average numbers of eggs per gram dry mass ( $\pm$  SD) were  $5700 \pm 312$  for Stage 1,  $5582 \pm 429$  for Stage 2 and  $5205 \pm 433$  for Stage 3.

Regressions showed that fecundity increased linearly with increasing CL (Table 1). Fecundity-size relationships differed significantly between the South and Central regions (*t*-test, d.f. = 157,  $t = 4.74$ ,  $p < 0.05$ ; Fig. 3a), and also among egg stages (ANCOVA,  $F_{2,155} = 4.24$ ,  $p < 0.05$ ; Fig. 3b). The fecundity of females with Stage 1 eggs differed significantly from that of females with Stage 3 eggs (Tukey test, d.f. = 97;  $q = 3.403$ ;  $p < 0.05$ ), but there were no significant differences between stages 1 and 2 or stages 2 and 3.

The average egg diameter increased from  $0.96 \pm 0.07$  mm (SD) in Stage 1 eggs ( $n = 45$  eggs), to  $1.01 \pm 0.06$  mm in Stage 2 ( $n = 75$ ) and to  $1.04 \pm 0.07$  mm in Stage 3 ( $n = 45$ ), and these increases were statistically significant (ANOVA,  $F_{2,162} = 18.55$ ,  $p < 0.001$ ).

Both fecundity/CL and fecundity/TM relationships were determined, but because CL is the standard measurement used in the majority of comparative studies and because the CL/TM regression had a high coefficient of determination ( $r^2 = 98\%$ ), only the results of the length analysis are graphically present. Nevertheless, the equations of the WBM/CL, DBM/CL and the fecundity/TM relationships are included in Table 1 for reference purposes. Female *P. delagoae* in the South region carried significantly more eggs than in the Central region, and fecundities in both these regions were lower than the estimate of Berry (1973), by over 60 % for smaller individuals of 70 mm CL, but similar for larger specimens of 120-130 mm CL (see Fig. 4). The difference in fecundity of lobsters from the South and Central regions is size-specific - a female of 70 mm CL produces 55% less eggs

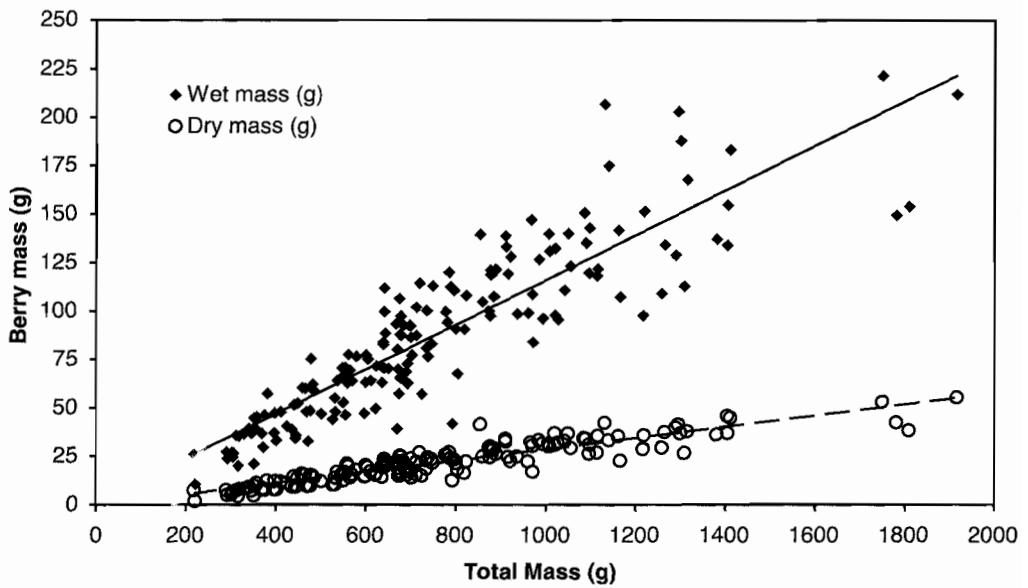
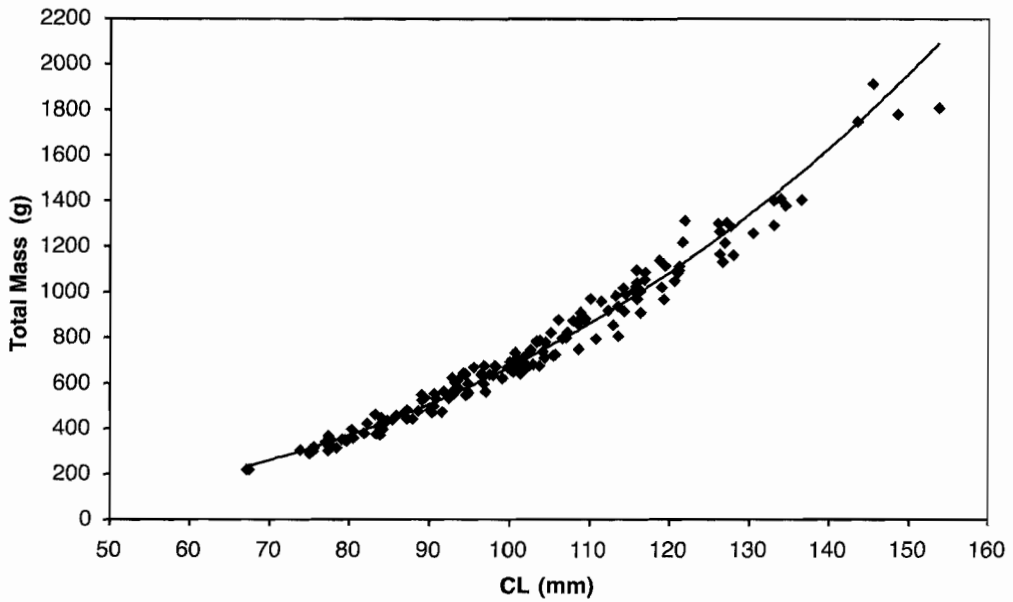


Fig. 2. (a) Relationship between carapace length (CL) and total wet mass (TM) of egg-bearing female *P. delagoae*, and (b) relationships between wet (WBM) and dry berry mass (DBM) with total lobster mass

**Table 1.** *Palinurus delagoae*. Regression statistics for relationships among CL (mm) and Total Mass (TM, in grams), wet and dried berry mass (WBM and DBM, in grams) and fecundity (F, as eggs carried per female) in two areas (South [S] and Central [C]) and three developmental stages (Stages 1, 2 & 3). Regression statistics for relationships between total lobster mass and fecundity are also included

Regressions	Area	Egg stage	Equations	n	r <sup>2</sup>
CL vs. TM	S & C	1 - 3	TM = 0.0035 CL <sup>2</sup> - 6412	161	0.98
TM vs. WBM	S & C	1 - 3	WBM = 0.1152 TM + 0.6965	161	0.80
TM vs. DBM	S & C	1 - 3	DBM = 0.0292 TM - 0.5787	161	0.85
CL vs. WBM	S & C	1 - 3	WBM = 2.2254 CL - 139.72	161	0.79
CL vs. WBM	S	1 - 3	WBM = 2.025 CL - 121.43	77	0.79
CL vs. WBM	C	1 - 3	WBM = 2.3166 CL - 147.88	84	0.78
CL vs. DBM	S & C	1 - 3	DBM = 0.5608 CL - 35.87	161	0.83
CL vs. DBM	S	1 - 3	DBM = 0.5969 CL - 37.926	77	0.78
CL vs. DBM	C	1 - 3	DBM = 0.5636 CL - 37.563	84	0.82
CL vs. Fecundity	S	1 - 3	F = 3216.2 CL - 201559	77	0.86
CL vs. Fecundity	C	1 - 3	F = 3040.6 CL - 202037	84	0.81
CL vs. Fecundity	S & C	1	F = 3205.3 CL - 204501	39	0.81
CL vs. Fecundity	S & C	2	F = 2981.1 CL - 183748	64	0.76
CL vs. Fecundity	S & C	3	F = 2921.5 CL - 189001	58	0.86
TM vs. Fecundity	S	1 - 3	F = 174.43 TM - 5471.1	77	0.89
TM vs. Fecundity	C	1 - 3	F = 152.39 TM - 4974.3	84	0.81
TM vs. Fecundity	S & C	1	F = 167.67 TM - 1912.6	39	0.82
TM vs. Fecundity	S & C	2	F = 157.71 TM + 3385.5	64	0.80
TM vs. Fecundity	S & C	3	F = 150.53TM - 6748.9	58	0.88

in the Central region, but once lobsters reach 130 mm CL egg-production in the two regions differ by only 10%. Small individuals in both regions furthermore produce few eggs (10 000 - 25 000 eggs/female of 70 mm CL) relative to large females (>200 000 eggs/female of 130 mm CL), and this would have implications for any minimum size limit based on size at maturity.

## DISCUSSION

Spatial and inter-annual variations in fecundity are common among lobsters and often extend to variations in growth rate, size at maturity and average lobster size (Beyers & Goosen, 1987; Melville-Smith *et al.*, 1995; Goñi *et al.*, 2003; Groeneveld, 2005). The physical and environmental causes are, however, difficult to establish, especially in deep-water species such as *P. delagoae* where benthic observations are scarce and sampling is generally restricted to on-board monitoring. Nevertheless, a lower numerical abundance and smaller average lobster size in the southern range of the KwaZulu-Natal coast, around 30-31°S (Groeneveld & Cockcroft, 1997), may be a result of lobster catches made by nearby deep-

water trawling (see Fig. 1 and Groeneveld & Melville-Smith, 1995; Fennessy & Groeneveld, 1997). If so, relatively higher fecundity in the southern range may reflect a density-dependent compensatory response, as was also found by Demartini *et al.* (1993) in exploited populations of *Panulirus marginatus*.

*Palinurus delagoae* appears to be slightly less fecund than *Palinurus gilchristi* but more fecund than *Palinurus elephas*, which occurs in the North Atlantic Ocean and Mediterranean Sea (Fig. 4). Fecundity of deep-water *Palinurus* lobsters is lower than in shallow-water *Jasus* and *Panulirus* lobsters (Pollock & Melville-Smith, 1993). One explanation may be that higher levels of egg-production in shallow-water lobsters have evolved as a response to high levels of predation on larvae that spend much time nearshore, where planktonic and nektonic predators are abundant. In contrast, *P. gilchristi* and *P. delagoae* release their larvae further offshore, where predation is presumably less intense. Thus, larval mortality rates are possibly reduced, and selective pressure towards higher fecundity may be smaller in the deep-water species (Pollock & Melville-Smith, 1993).

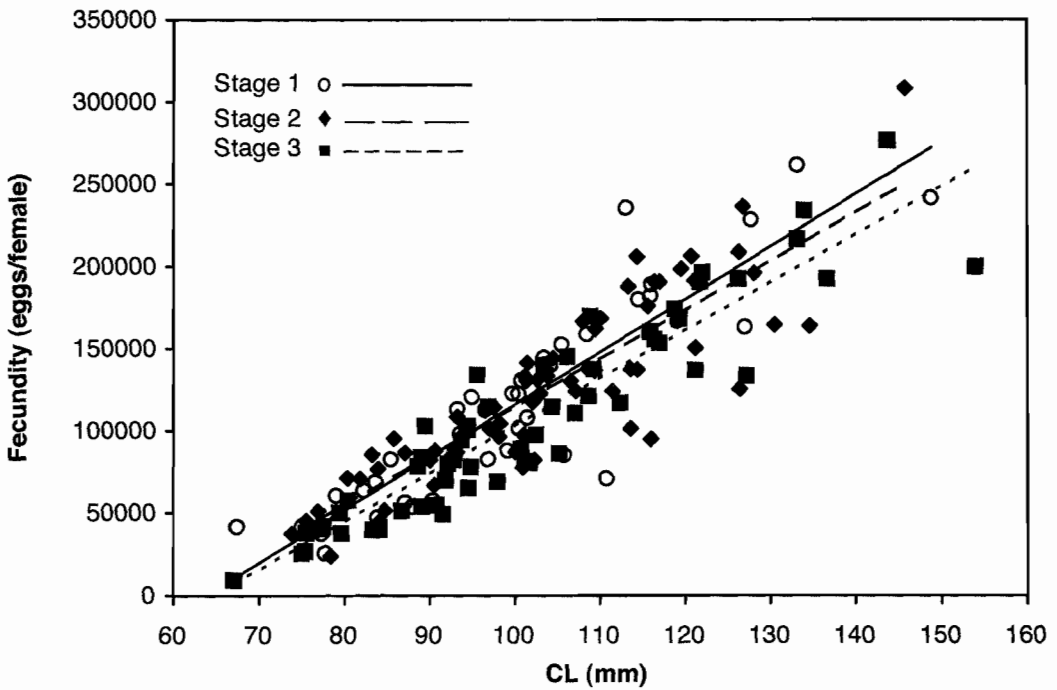
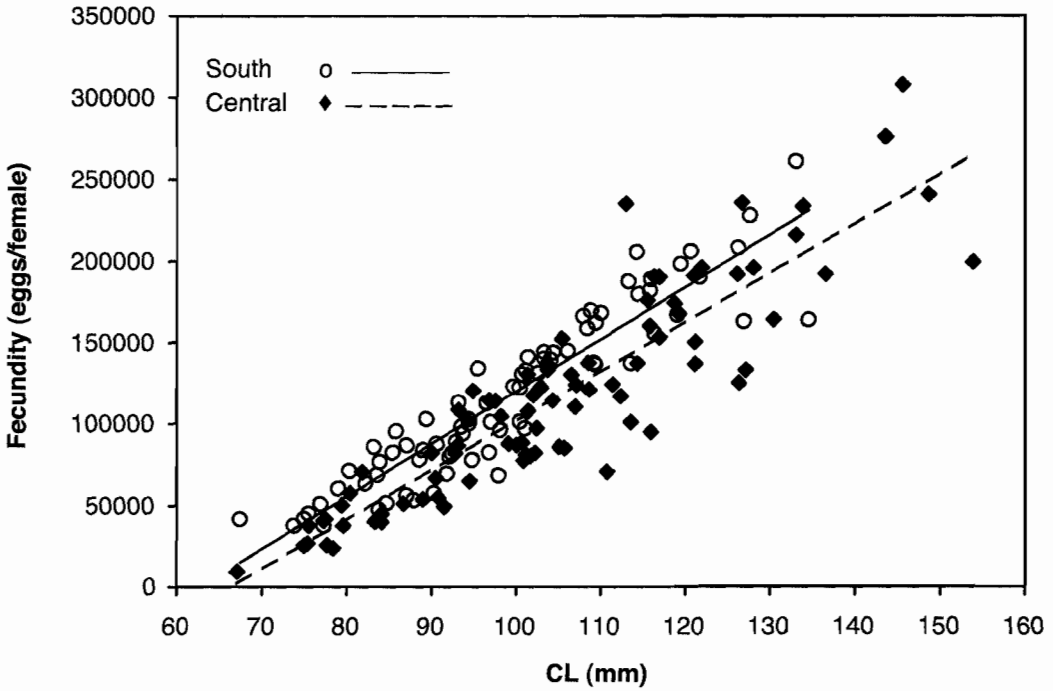


Fig. 3. (a) Fecundity/CL regressions of *P. delagoae* caught in the South and Central regions of eastern South Africa, and (b) a comparison of fecundity/CL regressions based on eggs in three developmental stages

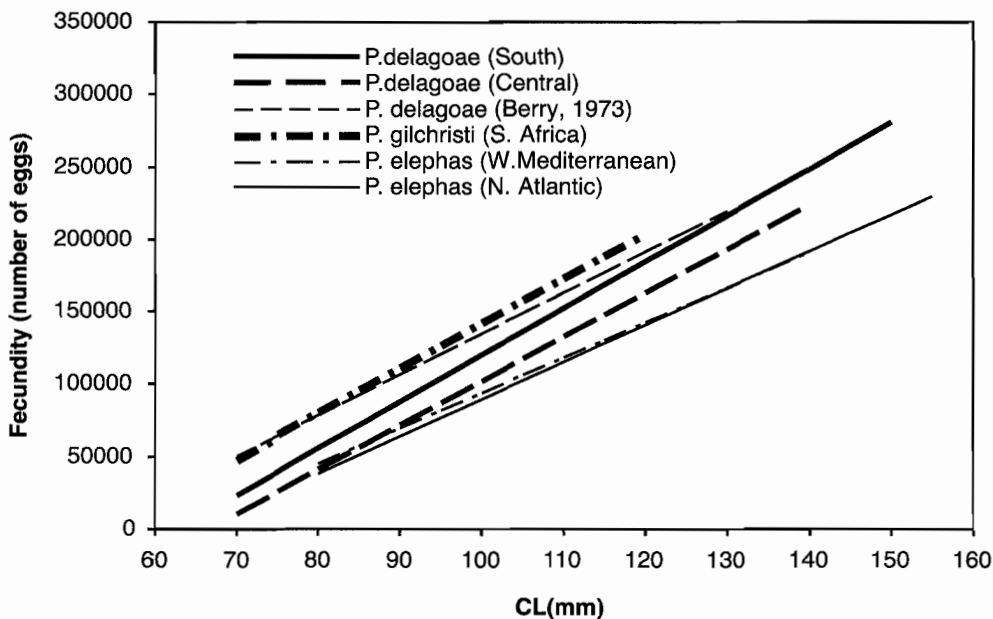


Fig. 4. Fecundity relationships of *P. delagoae* obtained in this study and from Berry (1973) compared to *P. gilchristi* from the South African south coast (Groeneveld, 2005), and *P. elephas* in the Western Mediterranean (Goñi *et al.*, 2003) and the north-east Atlantic Ocean (Mercer, 1973)

*P. delagoae* eggs are slightly larger than those of *P. gilchristi*, and the eggs of these two species are much larger than those of *Jasus* and *Panulirus* lobsters (Pollock & Melville-Smith, 1993). Larger eggs give rise to phyllosomata (technically nauplii) that hatch in an advanced stage of development, and consequently have a shorter larval drifting phase before settlement on the seafloor. This was shown during larval culture of *P. elephas* (Kittaka & Ikegami, 1988; Kittaka, 1997; Kittaka *et al.*, 2001), in which larvae metamorphosed into the first benthic stage in as little as 65 days (compared to >200 days in *Jasus* and *Panulirus*). *P. delagoae* and *P. gilchristi* in the strong Agulhas Current may have selected for stronger larvae and a shorter drifting phase to counter downstream overdispersal and retain larval populations in the vicinity of the south-east African coast. Furthermore, fewer but larger phyllosomata might have greater survivorship in the plankton compared to greater numbers of smaller, but weaker phyllosomata.

Egg-loss of *P. delagoae* between the 1<sup>st</sup> and 3<sup>rd</sup> egg stages (10 - 16% for CLs of 75 - 140 mm)

compares well with *P. gilchristi* (14 - 17%; Groeneveld, 2005) and also with *P. elephas* in the North West Atlantic Ocean (10%; Mercer, 1973), western Mediterranean (26%; Goñi *et al.*, 2003) and Corsica (28%; Marin, 1985). The range of egg-losses within the *Palinurus* genus therefore appears to be from 10 - 28%, over an incubation period of 4 - 8 months. Egg-loss may depend on method of capture i.e. traps in this study vs. hand-collection (Mercer, 1973) and trammel-nets (Marin, 1985; Goñi *et al.*, 2003). Nevertheless the rate of egg-loss appears to be proportional to the length of the incubation period (Annala & Bycroft, 1987). Egg loss in the American lobster *Homarus americanus* is 36% over a 9-month period (Perkins, 1971) or 40% over 9 - 11 months (Kuris, 1991); in the red rock lobster *Jasus edwardsii* it is 20% over five months (Annala & Bycroft 1987), and in the Australian spiny lobster *Panulirus cygnus*, losses are insignificant over its short incubation period of 3.5 - 8 weeks (Morgan, 1972).

In conclusion, this study provides a range of fecundity/size estimates for *P. delagoae* and demonstrates differences between two areas that

are approximately 200 km apart, off the KwaZulu-Natal coast. Such findings will be useful for assessments of the productivity of the resource. It furthermore shows that fecundity of *P. delagoae* is similar to that of two of its congenics, and suggests that this deep-water taxon produces fewer, but larger eggs than is common in shallow-water lobsters.

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