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LONG-DISTANCE MIGRATION OF THE ROCK LOBSTER *PALINURUS DELAGOAE* OFF SOUTH AFRICA AND MOÇAMBIQUE

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Long-distance migration patterns of deep-water rock lobster *Palinurus delagoae* were investigated using tag-recapture data obtained over a period of 6 years (1995–2000). Of 7 654 animals tagged, 363 (4.7%) were recovered from South African and seven (0.1%) from Moçambican waters. Lobsters remained at large for up to 3.2 years and migrated distances of up to 495 km. Some 48.3% of juvenile lobsters (carapace length <65 mm) but only 2.1% of larger lobsters migrated further than 20 km. Movements were mostly north-eastwards (91.7% of migrants), for both sexes, and the migration rate of the fastest 5% of migrants was 0.43 km day^{-1}. *P. delagoae* seems to have evolved long-distance, counter-current migrations as a retention mechanism to maintain its populations off both South Africa and Moçambique. The resource needs to be managed jointly between the two countries.

Key words: counter-current migration, larval dispersal, *Palinurus delagoae*, tag-recapture

The larval stage of lobsters is a dispersal phase during which pelagic phyllosoma larvae are exposed to oceanic processes for extended periods (Cobb 1997, Booth and Ovenden 2000). This is especially so for rock (spiny) lobsters, which have long larval stages of 6–24 months (Booth and Phillips 1994). Where such larvae occur in strong currents, there must be behavioural mechanisms to compensate for their downstream dispersal in order to maintain the geographic distribution of benthic populations. These include shortening of pelagic larval periods, as in clawed lobsters (Cobb 1997), strong forward-swimming capabilities of post-larvae or pueruli (Rooney and Cobb 1991, Katz *et al.* 1994), larval retention in eddies (Chiswell and Booth 1999), oceanic larval dispersal and return processes (Pollock 1989, 1995), and migrations of juvenile and adult lobsters, often against prevailing currents (Moore and MacFarlane 1984, Bell *et al*. 1987, Booth 1997, Groeneveld and Branch 2002). Although most of these studies addressed a single behavioural mechanism, it is likely that the dispersal and return of lobster larvae are regulated by a combination of them.

Palinurus delagoae inhabit rocky and organically rich, muddy substrata of the deep (100–600 m), South-East African continental shelf. The population extends from central Moçambique and southern Madagascar to the Eastern Cape, South Africa (Pollock *et al.* 2000). They form an important bycatch in the multi-species crustacean trawl fisheries of South Africa and Moçambique, and have also been targeted by a trap-fishery at various periods between 1980 and 1999 (Groeneveld and Melville-Smith 1995, Groeneveld and Cockcroft 1997, Palha de Sousa and Fielding 1998).

Population studies have indicated that *P. delagoae* is migratory (Koyama 1971, Berry 1972, 1973, Kondritskiy 1976, Cockcroft *et al.* 1995). Juveniles inhabit deep, offshore waters (400–600 m) and move shorewards to recruit to the adult population at depths of 150–350 m. Egg-bearing females tend to concentrate in shallow water (150–160 m) in summer, then move offshore to depths >300 m in autumn and winter. These migrations occur over relatively short distances, because of the narrow width of the continental shelf off most of the South-East African seaboard.

Adult *P. delagoae* generally live beneath the strong south-westerly flowing Agulhas Current. Therefore, it is likely that their pelagic larvae will be dispersed downstream, and that behavioural mechanisms act to retain larvae close to their origin or to return them to suitable habitat. A study of the congeneric species *P. gilchristi* in the Agulhas Current showed that juveniles migrated up to 800 km against prevailing currents (Groeneveld and Branch 2002). The present study investigates counter-current migration as a possible return mechanism in *P. delagoae*.

MATERIAL AND METHODS

In all, 7 654 healthy lobsters of both sexes, all of commercial sizes (55–140 mm carapace length *CL*),

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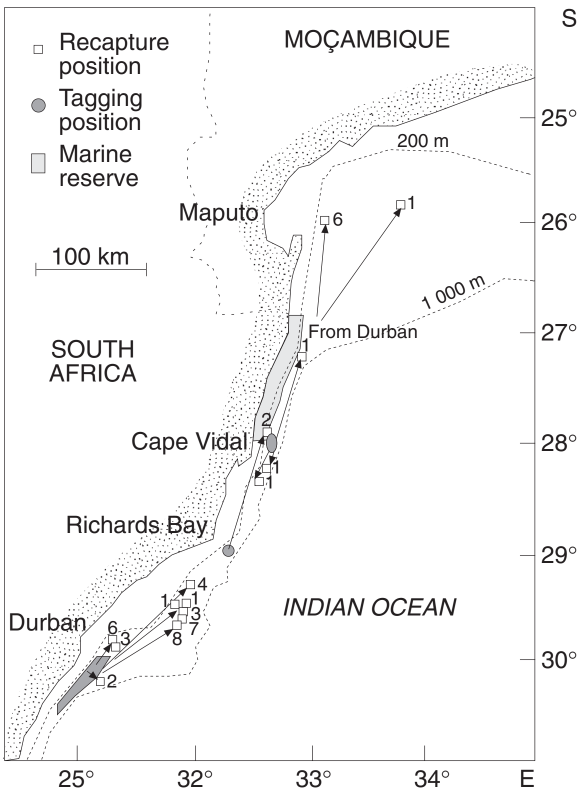

Fig. 1: The east coast of South Africa and southern Moçambique, showing the tagging and recapture locations of 47 *P. delagoae* that migrated ≥20 km, 1995–2000

were tagged over a 3-year period (1995–1997) off the east coast of South Africa between Cape Vidal and Durban (Fig. 1, Table I). Tags were inserted into the abdominal musculature of the lobster, dorso-laterally between the posterior edge of the carapace and the first abdominal segment, or between the first and second abdominal segments. The sex, *CL* (± 0.1 mm, measured mid-dorsally from the rostrum to the posterior edge of the carapace), location, depth and date of release of each lobster were recorded. All lobsters were released at the sea surface. Recaptured lobsters provide information on the time between release and recapture (time at large), distance and direction moved and the rate of movement.

Distances moved were calculated as the shortest distance between release and recapture. However, this is likely to be an underestimate of distances travelled, because movement would seldom have been in a straight line. Error estimates were based on the characteristics of the trap-fishery. Longlines with traps are generally 2–4 km long, and the reported capture location of a tagged lobster therefore has an error margin of ±4 km. Release location also has a bias associated with horizontal displacement of surface-released lobsters by currents. A maximum displacement of ±4 km was assumed and, based on the maximum combined error of ±8 km, lobsters were classified as resident (recaptured <20 km from where they were tagged) or migrant (recaptured ≥20 km away).

Both male and female *P. delagoae* attain sexual maturity at about 67 mm *CL* (Groeneveld 2000). To determine whether migration was size-dependent, distances moved by lobsters in three size categories, small juveniles (*CL* <65 mm), juveniles and small adults (65 mm ≤ *CL* <71 mm) and adults only (*CL* ≥71 mm) were compared by means of ANOVA. Differences within categories were then compared using a multiple comparison Tukey-test (Zar 1984).

Migration rates (km day^{-1}) were estimated for individuals that moved ≥20 km. However, the mean migration rates would underestimate the actual rates (if the distance measured was a straight line), and because time at large is likely to be longer than time actually spent migrating. Therefore, migration rates for the fastest 5% of lobsters were also calculated.

Table I: Numbers of *P. delagoae* tagged per year and recaptures made in subsequent years, up to December 2000. No trap-fishing occurred after 1997, and recaptures thereafter were made by trawlers

Lobsters tagged		Number of lobsters recaptured				
Year	*n*	1996	1997	1998	1999	2000
1995	4 130	217	24			
1996	1 524	79	4			
1997	2 000			9	30	7
Total	7 654	296	28	9	30	7

RESULTS

Of the 7 654 tagged lobsters, 370 (4.8%) were recovered from commercial traps and trawl catches off South Africa and Moçambique between 1995 and 2000. Individuals remained at large for up to 3.2 years and the farthest straight-line migration was 495 km. Distances moved increased with time spent at large (Fig. 2). Of the 308 recoveries made within the first year of release, only 10 (3.2%) moved ≥20 km. However, of 55 lobsters recovered in the second year, 31 (56.4 %) moved ≥20 km. Of these, six moved between 400 and 450 km,

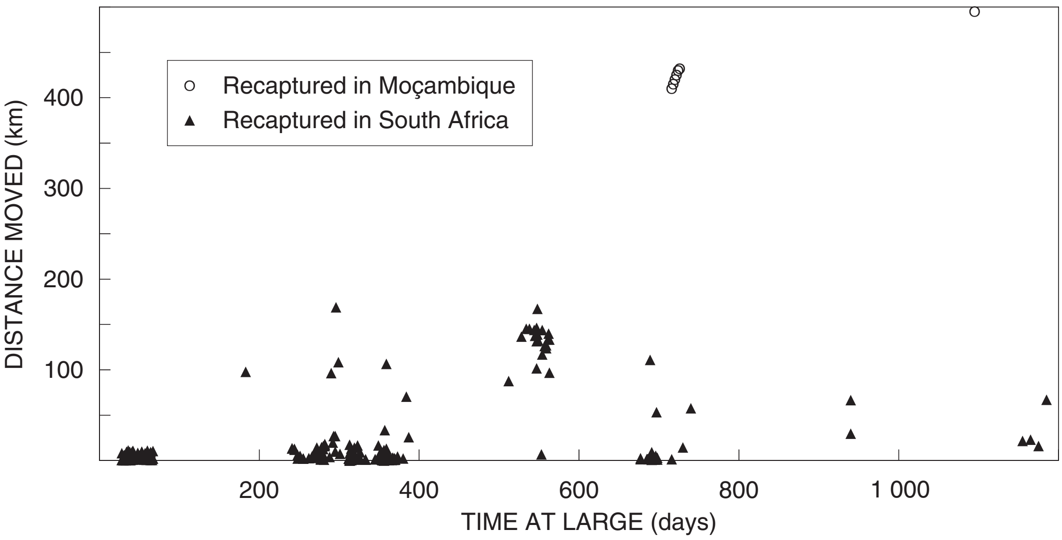

Fig. 2: Relationship between distance moved and time at large for *P. delagoae* recaptured in South African and Moçambican waters, 1995–2000

from South African to Moçambican waters. Of seven third-year recoveries, six (85.7%) moved ≥20 km. One of these was recaptured off Moçambique, 495 km from where it was tagged. A marine reserve precluded fishing between 27 and 28°S (Fig. 1), resulting in the absence of recaptures with movements of between 200 and 400 km (Fig. 1).

The majority (93.6%) of lobsters that moved ≥20 km was <70 mm (Fig.3). About half (48.3%) of the juvenile lobsters (<65 mm) migrated ≥20 km (average distance 79.4 ± 119.3 km, n = 87), compared to only 6.0% of lobsters 65–71 mm (9.2 ± 21.9 km, n = 50), and only 1.3% of adult lobsters >71 mm (4.3 ± 8.2 km, n = 233; Table II). Distances moved in the three size categories were significantly different ($F_{2,367}$ = 53.5, p < 0.001). The Tukey test revealed that small juveniles moved greater distances than large lobsters.

Of the 47 lobsters that moved ≥20 km, 43 (91.5%) migrated north-eastwards (Fig.1). The remaining four lobsters moved relatively short distances to the south (two animals; 33 and 53 km) and south-east (two animals; both 27 km).

Male and female juveniles both migrated long distances (Fig. 3, Table II). More females than males were released (4 312 females v. 3 342 males) and recaptured (245 females v. 125 males). The proportion of females increased from 56.3 to 66.2% between release and recapture.

The mean migration rate, based on movements of ≥20 km but irrespective of time at large, was 0.26 ± 0.17 km day^{-1} (n = 47). A more realistic estimate, based on the fastest 5% of lobsters, was 0.43 ± 0.14 km day^{-1} (n = 18).

DISCUSSION

Many lobsters tagged in this study retained their tags for several years and registered positive growth, implying that they had moulted. Tagged females were also able to bear eggs (pers. obs.) and many tagged lobsters moved substantial distances. Therefore, it is assumed here that the tags did not adversely affect normal behaviour of the lobsters under study.

The "realistic" rate of migration by *P. delagoae* of 0.43 km day^{-1} is similar to that of the fastest 5% of *P. gilchristi* (0.61 km day^{-1}) along the Southern Cape coast (Groeneveld and Branch 2002). These rates

Table II: Mean distances moved by three size-classes of male and female *P. delagoae*

Size-class	Males		Females	
	n	Distance (km) ±SD	n	Distance (km) ±SD
CL < 65 mm	36	79.7±138.0	51	79.2±105.5
65 mm<CL<71 mm	23	4.4±4.4	27	13.4±29.1
CL > 71 mm	66	5.1±13.8	167	3.8±4.3

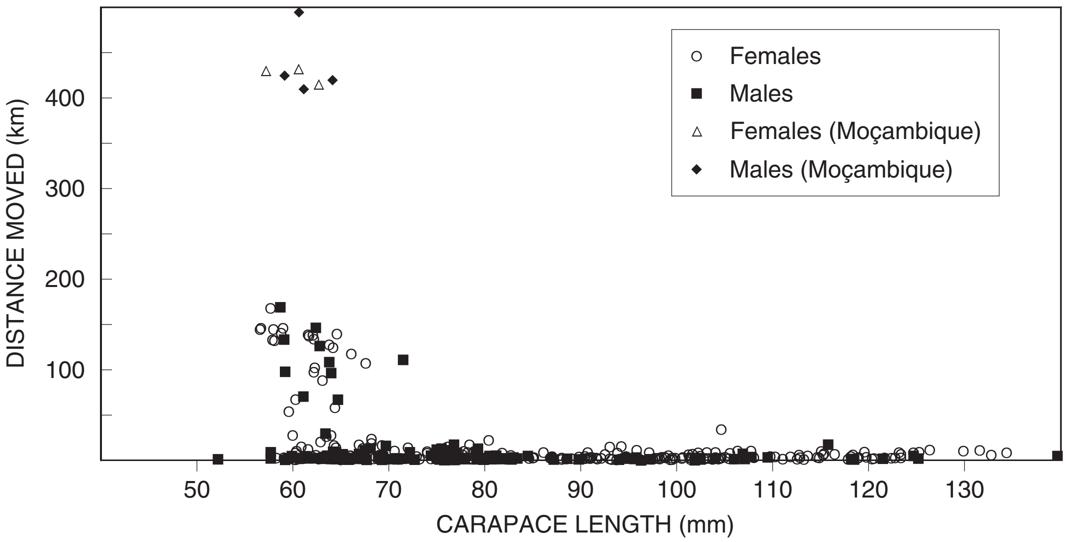

Fig. 3: Relationship between distance moved and carapace length for male and female *P. delagoae* recaptured off South Africa and Moçambique, 1995–2000

are also similar to the maximum rates reported for rock lobsters elsewhere, e.g. *Jasus verreauxi* off New Zealand (0.61 km day^{-1}; Booth 1984), *Panulirus ornatus* off New Guinea (0.61 km day^{-1}; Moore and MacFarlane 1984) and *Panulirus. cygnus* off Western Australia (0.62 km day^{-1}; Phillips 1983).

Long-distance migrations in *P. delagoae* are restricted to smaller individuals of <70 mm *CL*; larger animals did not migrate more than 20 km. In reality, the proportion of the juvenile population that migrated ≥20 km may be more than the 48.3% estimated in this study. There are several reasons for this contention. First, Moçambican fishers rarely report tag recoveries, and all tag recoveries off Moçambique would have constituted long-distance migrations. Second, the marine reserve north of the tagging sites, which was not fished, has some 100 km of good lobster habitat. Trapping there would probably have increased the number of recaptures and consequently likely increased the proportion of long-distance migrants.

Assuming that the number of males and females in a lobster population are equal, the larger proportions of females recorded at release and recovery suggest that females may have a higher catchability coefficient than males, at least during winter when most of this study was conducted. The sex composition of *P. delagoae* in catches fluctuates markedly, both monthly and with depth, perhaps reflecting segregation of sexes associated with their reproductive behaviour (Berry 1972, 1973, Kondritskiy 1976, Cockcroft *et al.* 1995).

The long-distance migration of *P. delagoae* was clearly north-eastwards, longshore and counter to the south-west-flowing Agulhas Current between Durban and southern Moçambique. Such migrations could be utilized by *P. delagoae* to counter the displacement effect of the Agulhas Current on their larvae. Such long-distance, counter-current migrations have been shown for juvenile *P. gilchristi* off the south coast of South Africa (Groeneveld and Branch 2002). Therefore both southern African *Palinurus* spp. appear to have evolved similar behavioural strategies to maintain the geographic distributions of their populations in the Agulhas Current.

Strategies other than migration may also be used by *P. delagoae* to retain phyllosoma larvae in the vicinity of the parent populations, or to return widely distributed larvae to their origin. Oceanic processes that could influence larval delivery include oceanic gyres, coastal currents, eddies, upwelling, wind-driven surface currents and fronts (Cobb 1997). Advective processes alone may not ensure larval delivery, and mid and late stage phyllosoma larvae would have to position themselves optimally in the water column (Phillips 1981, Chiswell and Booth 1999). Lobster pueruli are strong swimmers, capable of sustaining swimming speeds of 6–46 cm s^{-1} (Phillips and Olsen 1975, Lyons 1980, Macmillan *et al.* 1992). Such behavioural mechanisms need to be investigated for *P. delagoae* or *P. gilchristi*, in order to understand better their recruitment processes.

The longshore movement of juvenile *P. delagoae* has important implications for fisheries management. It confirms the belief that populations off South Africa and Moçambique belong to the same genetic stock (Berry and Plante 1973) and implies that overfishing in either region would affect the population as a whole. Therefore, targeting juvenile lobsters on the South African fishing grounds (Groeneveld 2000) may not only affect local recruitment via inshore migrations, but may also affect recruitment farther north in Moçambique. It is therefore suggested that serious consideration be given to managing the resource jointly between South Africa and Moçambique.

In conclusion, the present study supports the belief that *P. delagoae* is a highly migratory species (Berry 1973, Cockcroft *et al*. 1995, Groeneveld 2000). There are at least three migratory life-history strategies: a north-eastward long-distance, longshore migration of juveniles; an inshore ontogenetic migration, from deep water (>400 m) as juveniles to shelf water (150–350 m) as adults; and a seasonal inshore-offshore migration as reproducing adults over the shelf.

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