Movements of deep-sea red crab (*Geryon maritae*) off South West Africa/Namibia

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Of 10 246 red crabs tagged between 1979 and 1984 on the continental slope of Namibia, a total of 1 604 were recaptured by commercial fishermen. Three tagging methods were tested. The most effective method was by inserting the tag through the epimeral suture. Though tagged crabs were released over a range of depths (from 400 to 900 m), the distances that they covered while at large were found to be unrelated to the depth at which they were released. No significant differences were found for distances moved by males compared to immature females, but differences ($P < 0{,}01$) did indicate that large males (≥ 105 mm carapace width (CW)) move farther than small males. Mature females moved significantly farther ($P < 0{,}001$) than the other crabs and over 32% moved > 100 km. The farthest distance covered by a single crab was 380 km. No seasonal trends regarding distances or direction moved were noted for either sex or size groupings examined. Mature females did show a tendency, although unrelated to season, to move northwards. Movements of crabs by depth suggested that, although crabs of all sizes and sexes move freely between depths, small males (< 100 mm CW) do tend to favour deeper water than larger males and *vice versa*. Female crabs tend to favour shallow depths and, of those tagged at 800 and 900 m, over 60% were recaptured shallower than 700 m. Based on the results of this study, it is considered that the movement pattems of *G. maritae* could best be described as nomadic. A possible reason for the fact that mature females display different movement patterns compared to other crabs in the population is discussed, as are possible implications to the fishery of crab movements between Namibia and Angola.

Uit 'n totaal van 10 246 rooikrappe, tussen 1979 en 1984 op die vastelandse helling van Namibië gemerk, is altesaam 1 604 deur handelsvissers terugbesorg. Drie merkmetodes is beproef en een, waarvolgens die merk deur die epimere naat gesteek is, is heelwat doelmatiger as die ander twee bevind. Hoewel krappe op verskillende dieptes (van 400 tot 900 m) gemerk is, het die afstand deur hulle afgelê in die see nie verband gehou met hul diepte by vrylating nie. Daar is geen beduidende verskille gevind vir afstande afgelê deur mannetjies, vergeleke met onryp wyfies nie, maar verskille ($P < 0{,}01$) het daarop gedui dat groot mannetjies (rugdopwydte ≥ 105 m) verder as klein mannetjies beweeg. Geslagsryp wyfies het aansienlik verder ($P < 0{,}001$) as alle ander krappe in die bevolking beweeg, en van al die gemerkte geslagsryp wyfies wat teruggestuur is, het meer as 32% > 100 km beweeg. Die grootste afstand deur 'n enkele krap afgelê, was 380 km. Wat die afstand of rigting beweeg betref, is geen seisoenmatige tendense opgemerk vir enige van die geslags- of groottegroeperings wat ondersoek is nie, maar geslagsryp wyfies het 'n nie-seisoenmatige neiging getoon om noordwaarts te beweeg. Bewegings van krappe volgens diepte het daarop gedui dat, alhoewel krappe van alle groottes en geslagte vryelik tussen dieptes beweeg, klein mannetjies (rugdopwydte < 100 mm) wel geneig is om dieper water te verkies as groter mannetjies, en andersom. Wyfiekrappe gee meesal voorkeur aan vlakker water en, van dié wat by 800 en 900 m gemerk is, is oor die 60% weer vlakker as 700 m gevang. Op grond van die resultate van hierdie studie, kan gesê word dat *G. maritae* die beste by 'n nomadiese tipe van gedragspatroon inpas. 'n Moontlike rede vir die feit dat geslagsryp wyfies se bewegingspatrone verskil van dié van ander krappe in die bevolking, asook moontlike implikasies vir die vissery, van krapbewegings tussen Namibië en Angola, word bespreek.

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The deep-sea red crab, *Geryon maritae*, has a wide distribution ranging from Spanish Sahara to the Valdivia Bank off the Namibian coast (Manning & Holthuis 1981). Over large areas of this distribution it occurs in commercially exploitable quantities and this fact has contributed to the considerable amount of scientific attention which the species has received over recent years.

Despite a substantial amount of literature dealing with its general ecology and the potential for its exploitation off the African west coast [*inter alia* Dias & Seita Machado 1973 (Angola); Cayré & Bouchereau 1977 (Zaire); Le Loeuff, Cayré & Intés 1978 (Ivory Coast); Beyers & Wilke 1980 and Melville-Smith 1985 (Namibia); Gaertner, Le Hir & Sylla 1985 (Senegal)], there has been no published research on the extent of its movements, or whether any migration patterns exist. There consequently is no knowledge about the exclusivity of any part of the crab's distribution to particular territorial waters. Naturally this has important consequences with regard to stock assessments and the setting of catch quotas.

In order to obtain some understanding of the movements (and other biological information) of red crab off the Namibian coast, several tagging surveys were initiated during the period September 1979 to February 1984. In the course of these surveys, a wide size range of red crab was tagged in several areas of the Namibian crab grounds. In the analysis of the results, particular attention was paid to the possibility of differences existing in the magnitude and direction of movements undertaken by the different size classes and sexes.

Materials and Methods

Tagging has long been recognized as an important means of obtaining reliable data on growth and migration. The early tagging methods, such as those described by Cronin (1949), did not permit the animal to survive moulting and consequently valuable information on growth was lost. More recent tagging studies have employed techniques whereby the tag is inserted into an area of the crab's anatomy which allows the tag to be retained when the exoskeleton splits along the suture lines at moulting (Anon. 1955; Edwards 1979; Sullivan 1979).

In the first of the series of tagging surveys reported in this paper (September 1979), three tagging methods were attempted in order to assess the method most suited to the species. In all cases spaghetti-type FT-2 dart tags supplied by Floy Manufacturing Company were employed. The tagging methods used were as follows.

Method 1: The crab was tagged dorsally between the coxa and the basi-ischium of the fifth leg. The toggle of the tag was lodged in the musculature of the coxa region.
Method 2: The tag was inserted through the epimeral suture with the toggle lodged in the branchial cavity.
Method 3: The tag was inserted through the suture line on the merus of the cheliped with the toggle imbedded in the muscle.

The crabs used in this study were caught in baited beehive crab traps, except during August 1982 when they were caught by trawling. They were transferred from the traps into holding tanks supplied with circulating sea water and were tagged and released within hours of their capture.

The following record was kept for each tagged crab; tag number, size, shell state, whether ovigerous, whether any appendages were missing and state of maturity (based on the shape of the vulvae) (Melville-Smith, in press). During the first survey (September 1979), the state of maturity of the female crabs was not recorded.

The crabs were caught and released at depths between 400 and 900 m, using a cage specially constructed for this purpose. At the areas chosen for their release, the tagged crabs were lowered in the PVC cage to between 50 and 100 m off the bottom, whereupon a door on the undersurface of the cage was triggered to open by a messenger. The benefit of releasing the crabs in this manner, was that they had some protection from predation and furthermore their position at release could be accurately pinpointed. The release cage was not used during the September 1979 survey. During that survey all the crabs were released at the surface at an approximated position (20°50'S/12°10'E). It is likely that the estimated distances moved by crabs which were returned from this survey, would have been considerably less accurate than those which were calculated for crabs returned from the three later surveys.

During the entire six-year period of this tagging study, the red crab stock was consistently fished on a year-round basis (i.e. with no closed seasons) by five Japanese fishing vessels. The fishermen were asked to retain any tagged crabs caught in their traps and to record the date, position and depth of recapture. A token reward of R1,00 ($0,50) was paid for each crab returned to the Sea Fisheries Research Institute. The fishermen were generally very co-operative.

All relevant information on recaptured crabs i.e. the date, position, depth, size, sex, shell state and maturity at tagging and at recapture was computerized for analysis. The distances moved by the crabs between tagging and recapture were calculated by trigonometry, assuming that the crabs had moved in a straight line following the shortest possible route.

It should be noted that, even though the positions at tagging and at recapture were obtained by satellite navigation equipment, errors of up to 5 nautical miles (9 km) were possible for the reported positions at which tagged crabs were recaptured. These errors are due to possible cumulative effects of incorrect satellite navigation co-ordinates between fixes, coupled with the fact that fishermen reported the position of a tag return using co-ordinates at the beginning or end of a longline, most of which are 3 to 4 nautical miles (5 to 7 km) in extent, instead of reporting the precise point on the longline where the crab was caught. When the points of tagging and recapture were far apart, the shortest straight line between

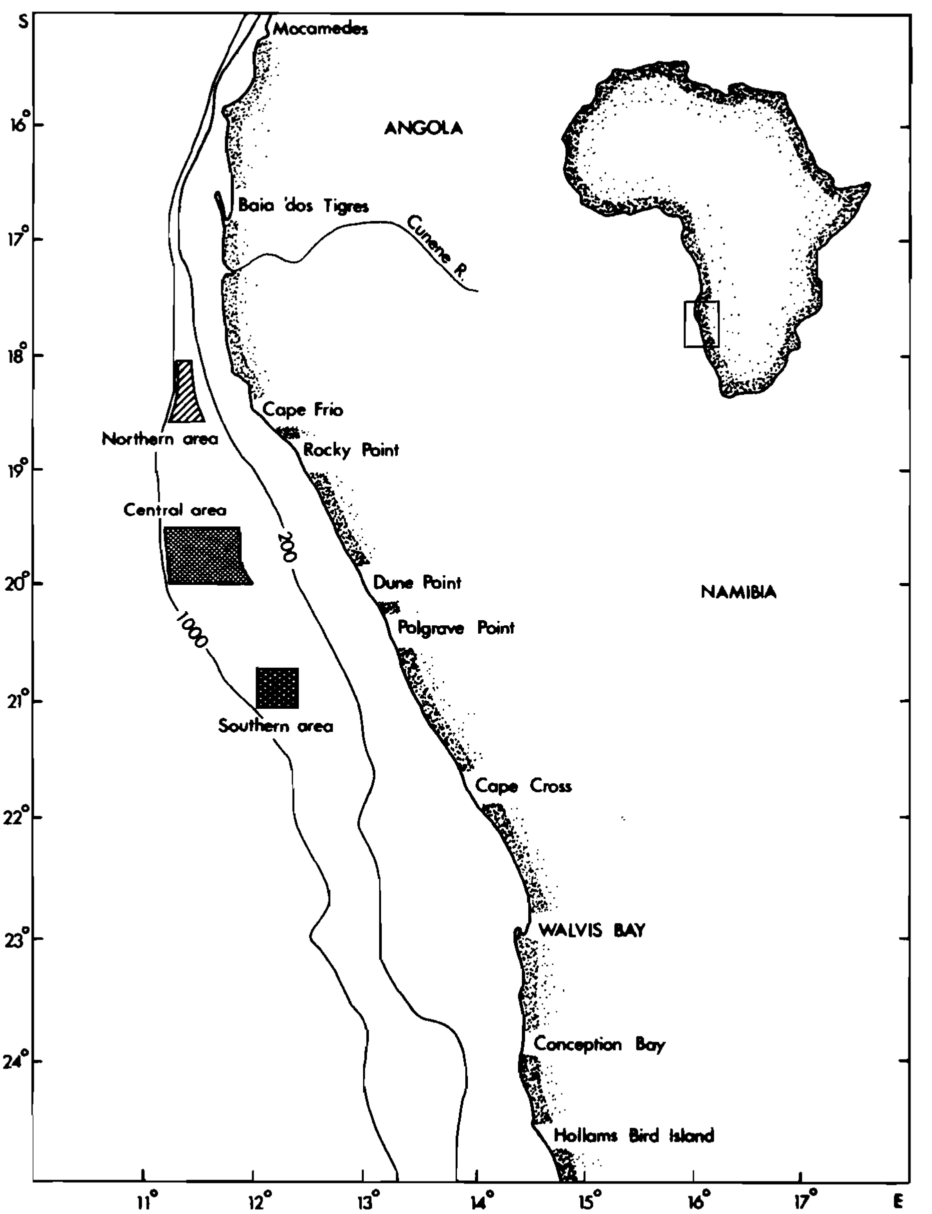

Figure 1 Areas where tagging took place. (a) Northern area: February 1984. (b) Central area: October 1982. (c) Southern area: September 1979.

the two points often crossed depths at which red crabs are not found. In these cases, the depths had obviously been detoured by the crabs, resulting in a greater distance covered than suggested by the result.

The recognized techniques for analysing data on migrations, such as those described by Jones (1976) and used in other studies of this type (*inter alia* Saila & Flowers 1968; Campbell & Stasko 1985), were not used in this report because of the unusual distribution of the red crab population off Namibia. Red crabs in this region, are only found along a narrow bathymetric corridor running between 350 and 900 m. Within the boundaries of these depths, the crabs can only move in a north-westerly or south-easterly direction (these directions henceforth termed northwards or southwards for convenience) following the shape of the depth contours (Figure 1). Because the crabs are restricted to north – south movement patterns, the vector describing the mean direction of movement is obvious from simple proportional ratios (usually expressed

Table 1 The number of crabs tagged during this study, their position at release and the proportion recaptured as at January 1986. 'R' indicates the catch position when catch and release positions differed within an area

Survey dates	Catch and release position	Release depth (m)	No. tagged			No. recaptured			Percentage return
			Male	Female	Total	Male	Female	Total	
12.9.79 – 18.9.79	20°50'S/12°10'E (R)	400 – 650	4 875	579	5 454	266	8	274	5,0
12.8.82	18°06'S/11°18'E	900	103	16	119	28	3	31	26,1
14.8.82	17°30'S/11°21'E	400	0	56	56	0	17	17	30,4
14.8.82	17°29'S/11°15'E	580	4	14	18	1	1	2	11,1
15.8.82	18°26'S/11°21'E	710	40	19	59	7	6	13	22,0
15.8.82	18°26'S/11°21'E	800	9	4	13	4	0	4	30,8
16.8.82	18°32'S/11°23'E	590	50	33	83	12	6	18	21,7
16.8.82	18°29'S/11°24'E	500	10	11	21	1	2	3	14,3
16.8.82	18°27'S/11°26'E	400	8	8	16	1	0	1	6,0
16.8.82	18°58'S/11°22'E	503	7	41	48	0	7	7	14,6
18.8.82	18°56'S/11°18'E	600	36	44	80	18	7	25	31,3
18.8.82	18°56'S/11°16'E	700	39	21	60	11	5	16	26,7
18.8.82	18°56'S/11°14'E	780	11	3	14	5	0	5	35,7
19.8.82	19°55'S/11°40'E	498	6	2	8	2	0	2	25,0
19.8.82	19°55'S/11°36'E	600	14	5	19	4	0	4	21,0
20.8.82	20°55'S/12°17'E	596	4	3	7	1	0	1	14,3
20.8.82	20°55'S/12°17'E	596	9	8	17	1	3	4	23,5
			350	288	638	96	57	153	24,0
10.10.82	20°00'S/11°45'E (R)	500	85	43	128	29	15	44	34,4
10.10.82	20°00'S/11°39'E (R)	600	87	66	153	39	32	71	46,4
11.10.82	20°00'S/11°34'E (R)	700	62	23	85	26	8	34	40,0
11.10.82	20°01'S/11°29'E (R)	800	224	4	228	91	0	91	39,9
14.10.82	19°29'S/11°13'E (R)	900	772	35	807	262	17	279	34,6
15.10.82	19°30'S/11°16'E (R)	800	115	11	126	26	4	30	23,8
15.10.82	19°32'S/11°22'E (R)	700	158	43	201	66	15	81	40,3
17.10.82	19°33'S/11°33'E (R)	500	173	328	501	43	118	161	32,1
17.10.82	19°30'S/11°25'E (R)	600	72	49	121	24	14	38	31,4
18.10.82	21°01'S/12°21'E	600	40	8	48	16	4	20	41,7
			1 788	610	2 398	622	227	849	35,4
13.2.84	18°31'S/11°24'E (R)	500	47	24	71	12	7	19	26,8
13.2.84	18°29'S/11°22'E (R)	600	43	27	70	14	2	16	22,9
14.2.84	18°30'S/11°20'E (R)	700	28	37	65	9	6	15	23,1
14.2.84	18°30'S/11°18'E (R)	800	33	30	63	14	5	19	30,2
15.2.84	18°30'S/11°17'E (R)	900	149	11	160	32	2	34	21,3
16.2.84	18°03'S/11°20'E	800	81	33	114	17	4	21	18,4
16.2.84	18°02'S/11°19'E	900	2	2	4	0	0	0	0
17.2.84	18°02'S/11°22'E	600	86	34	120	20	6	26	21,7
17.2.84	18°02'S/11°20'E	700	113	12	125	15	3	18	14,4
18.2.84	18°10'S/11°27'E	400	53	142	195	3	13	16	8,2
18.2.84	18°01'S/11°26'E	500	41	77	118	5	11	16	13,6
19.2.84	18°17'S/11°28'E	400	56	103	159	11	25	36	22,6
19.2.84	18°12'S/11°23'E (R)	500	49	74	123	5	13	18	14,6
20.2.84	18°17'S/11°23'E	600	72	38	110	24	8	32	29,1
20.2.84	18°17'S/11°23'E (R)	700	37	37	74	11	10	21	28,4
21.2.84	18°12'S/11°21'E (R)	800	70	24	94	12	3	15	16,0
21.2.84	18°22'S/11°21'E	900	57	34	91	4	2	6	6,6
			1 017	739	1 756	208	120	328	18,7

as a percentage) of crabs moving in one direction or from one depth to another.

This study reports on the results obtained from four tagging surveys, the positions and dates of which are documented in Table 1. For various reasons dealt with in the discussion, there were discrepancies between the four surveys regarding the percentage of tagged crabs returned by the fishermen, and consequently direct comparisons between surveys are not possible.

Where trends of crab movement have been examined for different regions of the grounds, the four surveys have been grouped into a northern, central and southern area (Figure 1). As can be seen from Table 1 these areas have been largely based on the positions where tagging took place during three of the four surveys. Results from the August 1982 data have been used to supplement the data on the three areas where applicable (Table 1).

For much of the analysis of movement, the October 1982 data has been selected to illustrate the trends. The chief reason for this is that that survey was conducted in the central area of the crab grounds and was therefore probably most representative of the Namibian red crab fishery. Other reasons are that (a) it covered the total depth range of the crab, (b) all crabs caught were tagged (so that the ratios of crabs tagged corresponded with their densities at the various depths) and (c) it was the most successful tagging survey in terms of the condition of the crabs at release and, correspondingly, the number of crabs that were returned.

Results

Time at liberty

Of the 10 246 crabs tagged between 1979 and 1984, 1 604 have been recaptured (until January, 1986) with reliable information (Table 1). In all four of the surveys undertaken during the course of this study, the vast majority of tagged crabs (particularly those that had been tagged as mature females) were recaptured within the first year of their release. This trend is clearly illustrated by the comprehensive October 1982 survey data (Figure 2). Small numbers of crabs tagged in September 1979 continue to be recaptured. The last recaptured crab had been at large 2 236 days (over six years).

Tagging methods

Results of the three methods of tagging used during September 1979 are presented in Table 2. The H_0 that the likelihood of a crab retaining its tag through a moult would be equally probable with the three tagging methods was tested with a chi-square test. The calculated value of 37,9 permits rejection of the H_0 at $P < 0{,}01$. Suture tagging is clearly a better method than the others and was used in all subsequent crab tagging surveys.

Effects of distance between points of capture and release

Herrnkind, VanderWalker & Barr (1975), quoted by Herrnkind 1980, have shown that nomadism in lobsters may be induced by displacing them from their home range or a familiar region. When capturing, tagging and releasing crabs at the depths discussed in this report, it is unlikely that the tagged animals would have been released in their home range (assuming that they have such a range). However, by using the release apparatus described earlier, it could be assumed that they were probably released into an environmentally familiar region.

During the October 1982 and February 1984 surveys, approximately half of the crabs that were tagged, were released

Table 2 Returns from each tagging method used during September 1979

Crab number	Fifth leg	Suture	Claw
Tagged	1 815	1 821	1 818
Returned (unmoulted)	94	39	36
Returned (moulted)	12	68	17
Returned (total)	106	107	53
Percentage moulted	11,3	63,6	32,1

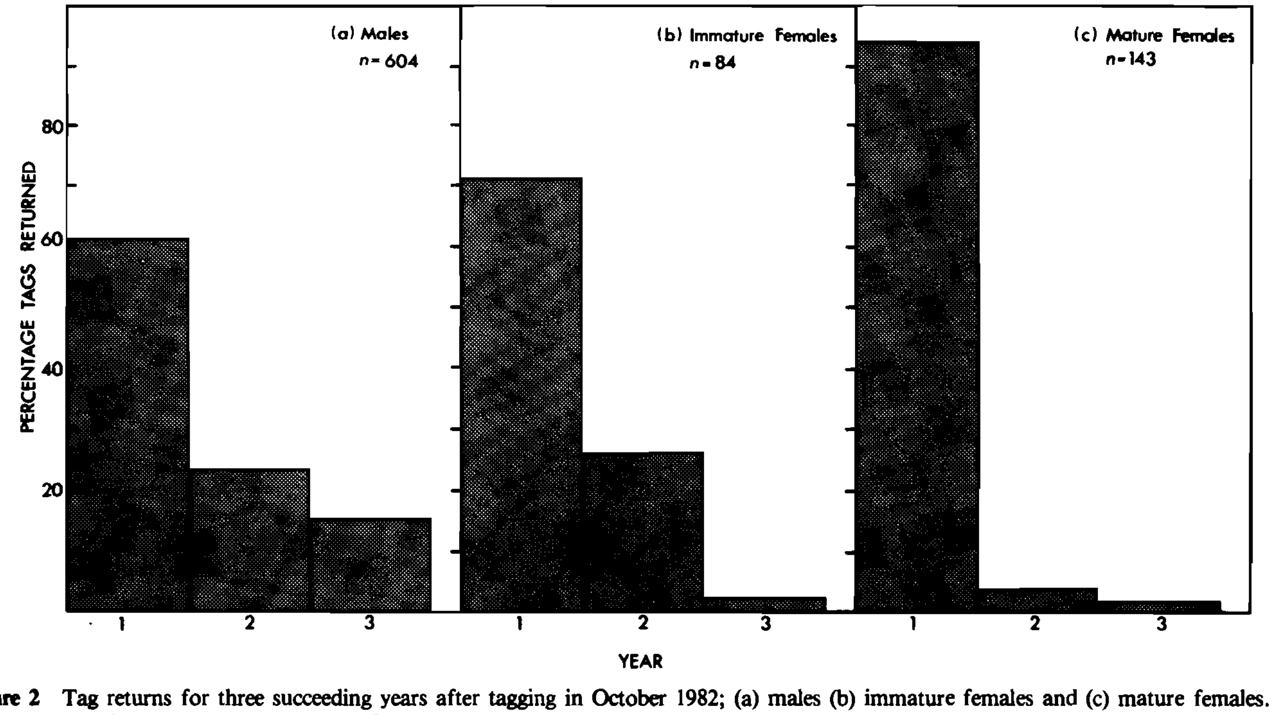

Figure 2 Tag returns for three succeeding years after tagging in October 1982; (a) males (b) immature females and (c) mature females. The sizes and maturity states are those recorded at release of the crabs.

at the position of their capture (Table 1), while the other half were released approximately 10 nautical miles away. An analysis of the distances moved by male crabs failed to show any significant difference ($P > 0,10$) between the distances moved by crabs released at their point of capture and those released farther away.

A comparison of movement by sex, size and maturity

Chi-square contingency tests were performed on a portion of the data in order to investigate whether the size, sex or maturity of the crabs played any part in the extent of their movements. In order to eliminate unnecessary variables which may have interfered with the results, only crabs tagged during October 1982 between latitudes 19°30'S and 20°00'S were used in the sample analysed.

The crabs used in this study were tagged and released at different depths. To test whether this variable could be disregarded, the distances moved by male crabs tagged deeper than 750 m and those tagged shallower than this depth were compared. This test was only performed on a male crab sample, because female crabs are not sufficiently abundant at depths greater than 600 m on which to perform a meaningful test. There was no significant difference in the distances covered by the two groups of males ($P > 0,10$), and depth was consequently ignored when testing distances moved by the sexes and different size or maturity stages.

A further analysis was performed on male crabs to establish whether the distance they moved was size related. Large males (⩾ 105 mm CW) were found to move significantly farther than smaller individuals ($P < 0,01$) but, considering that the distances covered by males of all sizes were so limited (only about 10% of all the male crabs moved ⩾ 36 km), no further effort was made to analyse the data separately for different size classes.

The distances covered by all male crabs were tested against the movements of immature females to determine whether the distances that they moved were sex related. There was no significant difference ($P > 0,50$) between the two groups so they were combined and tested against the distances covered by mature females. The data showed a highly significant trend ($P < 0,001$) pointing to the fact that mature females move greater distances than the rest of the population. In all further analyses mature females were treated separately from the rest of the crabs.

Direction and distances moved

A detailed analysis of the data failed to reveal any seasonal trends associated with the distance and direction covered by the crabs between the point of tagging and recapture. Other trends, the significance of which is less apparent, have been noted in the data and are discussed below.

Data from all surveys showed that the crabs were relatively near to their point of release when recaught within the first 90 days after tagging. Thereafter they dispersed unpredictably as is evident from the fluctuating means and high standard deviation recorded in Table 3.

Both Table 3 and Figure 3 show that mature female crabs tagged in all areas were prone to extensive movement compared to other crabs in the population. Approximately 32% of the mature female crabs moved > 100 km compared with only 3% of the males and immature females. Only 33 crabs (2,3% of all returns) moved more than 200 km and all but four were mature females. The farthest distances covered were 380 km in a northerly direction and 344 km southwards. A few of the more spectacular rovings (in terms of distance covered) by crabs tagged in different areas are shown in Figure 4.

The proportions of tag returns north or south of their release positions respectively, were analysed separately for mature females, and for males together with immature females (Table 4). The results show a particularly strong tendency for the mature female crabs to have moved north rather than

Table 3 Means and standard deviations (in km) for distances moved northwards and southwards from each area for periods of up to six years

			Distance covered in km (mean and standard deviation)								
Area	Category	Direction	1st quarter	2nd quarter	3rd quarter	4th quarter	2nd year	3rd year	4th year	5th year	6th year
North	Males and immature females	North	11,9 ± 7,2 n = 53	19,6 ± 16,4 n = 21	30,4 ± 33,3 n = 15	27,0 ± 17,5 n = 11	15,3 ± 18,5 n = 34				
		South	12,1 ± 8,1 n = 55	28,1 ± 31,7 n = 29	16,6 ± 13,1 n = 14	37,3 ± 37,1 n = 9	20,9 ± 13,0 n = 57				
Central	Males and immature females	North	14,0 ± 14,9 n = 51	20,9 ± 28,3 n = 74	18,0 ± 19,1 n = 67	16,6 ± 19,3 n = 20	28,3 ± 38,7 n = 78	23,2 ± 13,3 n = 42			
		South	11,9 ± 11,5 n = 22	16,4 ± 14,2 n = 59	16,4 ± 15,8 n = 71	15,1 ± 13,0 n = 24	17,8 ± 13,0 n = 72	25,0 ± 14,9 n = 36			
South	Males	North	34,0 ± 5,6 n = 15	39,2 ± 31,1 n = 57	43,0 ± 45,5 n = 30	52,7 ± 43,4 n = 27	72,0 ± 69,3 n = 24	41,9 ± 37,3 n = 13	68,4 ± 42,7 n = 21	52,0 ± 44,5 n = 7	49,9 ± 27,9 n = 10
		South	n = 0	5,5 n = 1	n = 0	n = 0	25,7 ± 19,3 n = 6	31,0 ± 17,8 n = 20	39,4 ± 7,9 n = 7	63,2 ± 35,6 n = 15	81,5 ± 52,9 n = 7
North	Mature females	North	48,2 ± 70,2 n = 9	119,0 ± 39,6 n = 15	51,7 ± 33,3 n = 9	88,7 ± 28,8 n = 3	51,5 ± 26,3 n = 8				
		South	24,5 ± 22,3 n = 8	120,2 ± 76,7 n = 4	13,7 ± 6,8 n = 5	88,6 ± 129,6 n = 6	90,0 ± 66,6 n = 8				
Central	Mature females	North	39,4 ± 46,8 n = 20	67,5 ± 62,3 n = 35	155,2 ± 86,6 n = 29	131,6 ± 81,2 n = 15	99,7 ± 82,3 n = 16	344,2 ± 44,1 n = 4			
		South	12,1 ± 10,6 n = 23	17,8 ± 23,8 n = 17	9,5 ± 3,8 n = 4	41,4 n = 1	32,4 ± 16,4 n = 7	n = 0			
South	Females	North	86,4 n = 1	49,1 ± 20,2 n = 3	160,7 ± 58,1 n = 3	142,2 ± 101,9 n = 3	n = 0	n = 0	316,8 n = 1	n = 0	n = 0
		South	n = 0	n = 0	n = 0	10,8 n = 1	102,6 n = 1	n = 0	n = 0	n = 0	n = 0

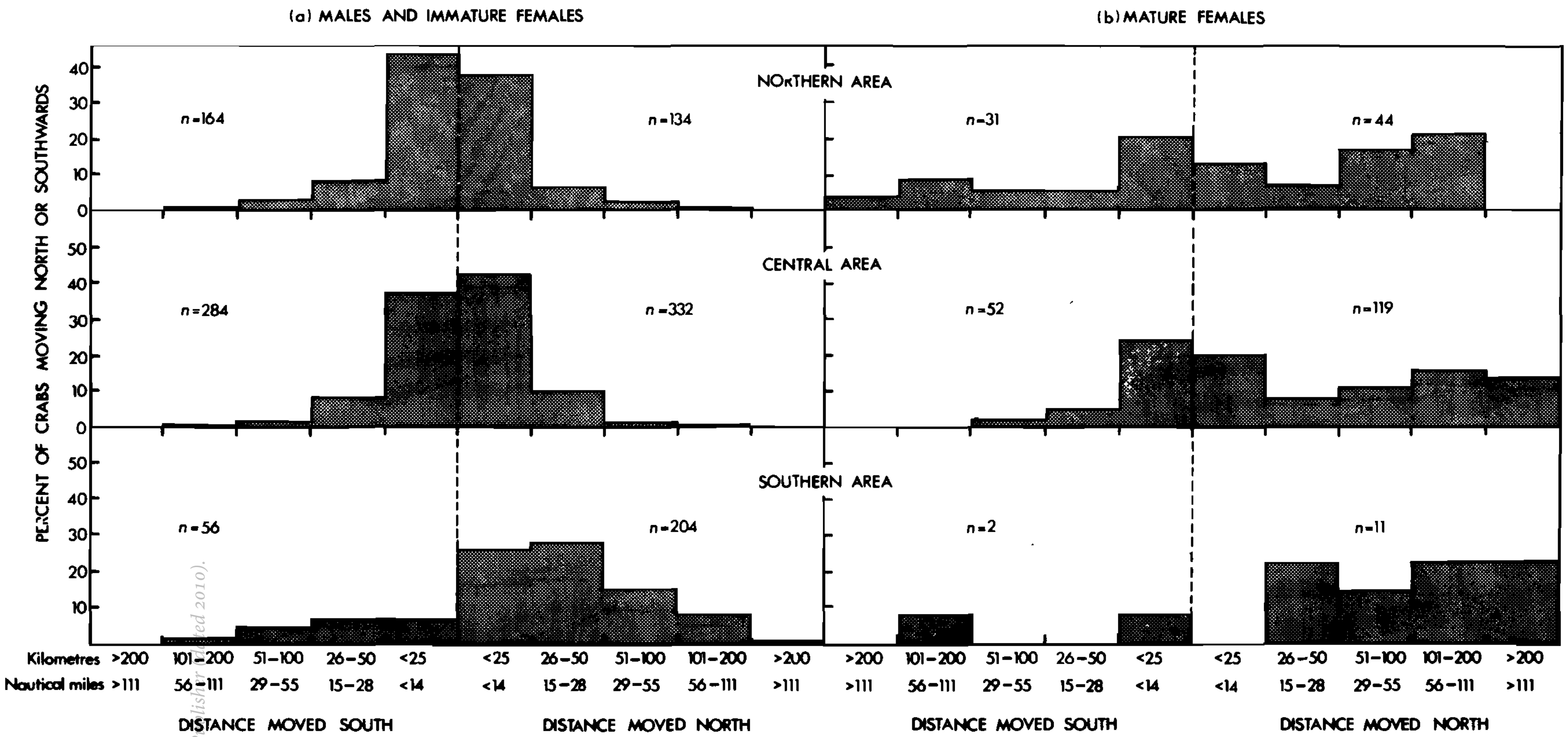

Figure 3 Distances moved northwards and southwards by red crabs tagged in three areas; (a) males and immature females, (b) mature females.

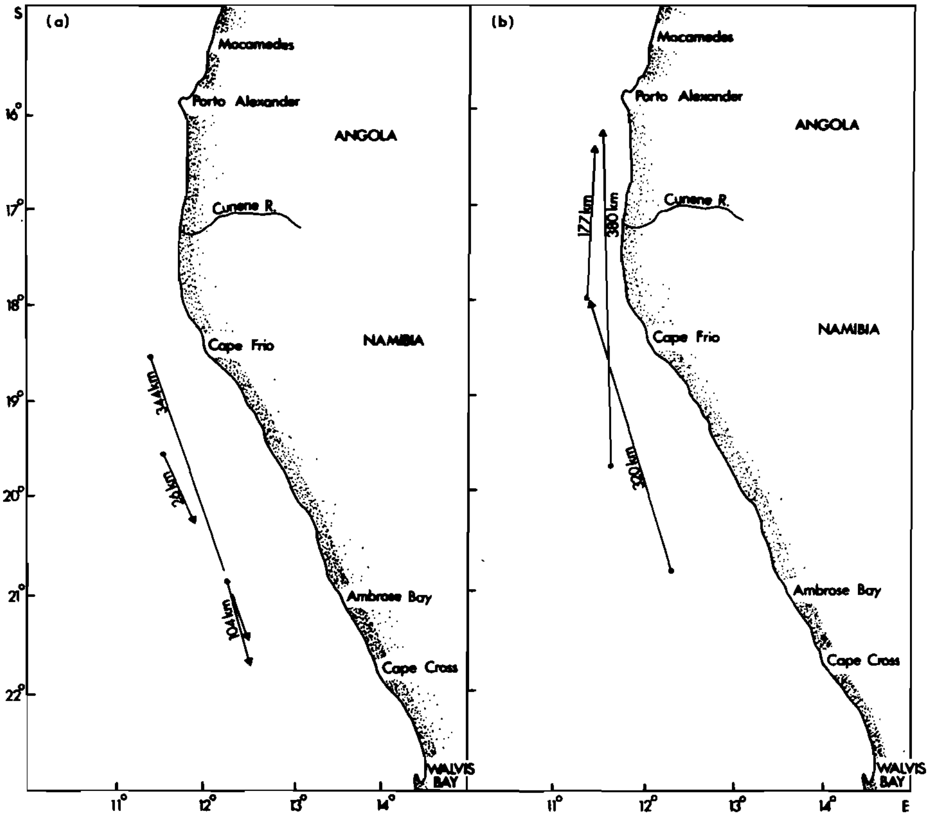

Figure 4 Farthest movement (a) southwards and (b) northwards by crabs released in each of the three tagging areas. In all cases the crabs were mature females.

Table 4 Ratio of tagged crabs recovered north to those recovered south of their release positions. Returns for the northern central and southern areas were recaptured over two-, three- and six-year periods respectively

	Males and immature females			Mature females		
	Southwards	Northwards		Southwards	Northwards	
Area	(Number)	Number	%	(Number)	Number	%
Northern	164	134	45,0	31	44	58,7
Central	284	332	53,9	52	119	69,6
Southern	56	204	78,5	2	11	84,6

south. Furthermore, where mature female red crabs did move south, the distances that they covered were generally smaller than those of crabs that had gone north (Table 3 and Figure 3). Of the 83 mature female crabs that moved more than 100 km (Figure 3), 89% of them went northwards.

Speed of movement

The mean velocity of dispersion of crabs as deduced from tag returns is presented in Table 5. Mature females moved faster than males and immature females, reflecting the greater distances travelled by them while at large. Some crabs covered vast distances in a relatively short period and individual velocities for mature female crabs were as high as 2 km per day.

Depth

Despite careful analysis of the depth movements of crabs of different sizes, states of maturity and sex, no seasonal trends could be found in data from any of the tagging surveys. Data on male crabs from the October 1982 tagging survey were analysed (Tables 6 to 8) in order to examine whether any trends existed in the redistribution by depth of crabs subsequent to their tagging. As discussed earlier, only male crabs were used, because of the scarcity of females at deeper depths. Furthermore, the analysis was limited to returns from October 1982 because that survey provided the best depth coverage.

Examination by depth (Table 6), shows that crabs that were tagged deep (800 and 900 m) were generally recaptured shallower, while those tagged shallow (500 m) generally moved deeper. Crabs tagged between 600 and 700 m showed depth displacement values closest to a 50:50 ratio. Although the above observations are rather predictable, given that red crab are only found between certain well defined depth limits off the Namibian coast, they are nevertheless presented because of their bearing on Tables 7 and 8.

The mean depth at recapture for crabs released at five depths is shown in Table 7. The results show an obvious correlation between the depth at tagging and the depth at recapture, particularly for crabs that were returned prior to

Table 5 Mean velocities in northward and southward directions, calculated from tag recoveries over a three-year period for two crab categories tagged in the central area

Males and immature females		Mature females	
Southwards (km day^{-1})	Northwards (km day^{-1})	Southwards (km day^{-1})	Northwards (km day^{-1})
0,05 (n = 284)	0,05 (n = 332)	0,11 (n = 52)	0,46 (n = 119)

Table 6 Numbers of males tagged in the central area which were recovered either deeper, shallower or at the same depth as at tagging

Tagging depth (m)	Depth movement (numbers of crabs)		
	Deeper	Shallower	Same
500	44	21	3
600	28	32	1
700	42	48	0
800	18	88	6
900	0	248	0

Table 7 Depth at tagging and corresponding depth at recapture for moulted and unmoulted males from the October 1982 survey

Tagging depth (m)	Mean depth at recapture (m)								
	Unmoulted	*n*	*sd*	Moulted	*n*	*sd*	Total	*n*	*sd*
500	554	55	106	610	13	99	565	68	106
600	588	48	101	647	13	107	601	61	104
700	661	52	119	692	38	113	674	90	117
800	690	65	111	702	47	103	694	112	107
900	721	201	119	702	47	125	717	248	120

Table 8 Recaptures deeper and shallower than 700 m, of two size categories of unmoulted males returned at 500 and 900 m respectively in October 1982

	< 100 mm CW	⩾ 100 mm CW
Releases at 500 m	$n = 25$	$n = 30$
Mean depth at recapture	575	537
% recaptured > 700 m	28	3
Releases at 900 m	$n = 129$	$n = 72$
Mean depth at recapture	757	656
% recaptured < 700 m	27	58

moulting. The fact that crabs recaptured subsequent to moulting showed less correlation could be ascribed to two causes; first, those crabs that had moulted before recapture had generally been at large longer than those that had not moulted and therefore would have had more time to redistribute themselves. The second and, in my view, more likely possibility, is that the depth of recapture is related to the size of the crab. To test this possibility, the male crabs tagged at 500 and 900 m during October 1982 were analysed in two size categories (Table 8). The table shows that the smaller crabs tagged and released at 500 m tended to move deeper than the larger crabs, though not by a significant amount ($P > 0{,}10$). Expressed as a percentage, however, the results show that 28% of the smaller crabs moved to depths > 700 m while only a single individual (3%) in the larger size class moved deeper than that. In contrast, for crabs tagged and released at 900 m, the larger size classes moved into shallower water than did the small crabs (240 m shallower for larger and only 140 m for the smaller crabs). This difference was significant ($P < 0{,}001$). In addition, the proportion of large-sized crabs moving into shallower water (i.e. < 700 m) was more than double that of small-sized animals (58 compared with only 27%).

The above observation suggests that, although red crabs move across a wide depth range, they do have preferential depths that may be related to size. These preferences have given rise to the characteristic trends documented by Beyers & Wilke (1980), namely that the mean size of male crabs decreases with depth. Likewise, of the 21 recaptured female crabs that were tagged at 800 and 900 m during the October 1982 survey (Table 1), 66% were taken < 700 m. This conforms to the observed pattern reported in the literature (*inter alia* Dias & Seito Machado 1973; Cayré & Bouchereau 1977; Beyers & Wilke 1980) of the sex ratio in shallower water being biased in favour of females.

Discussion

The great differences between the percentage of crabs recaptured during the various surveys can be ascribed to a number of reasons. Because of insufficient publicity, the 1979 survey elicited a poor response from the fishermen to return tagged crabs. The August 1982 survey utilized trawled crabs, which were obviously more stressed when tagged than trap-caught crabs, presumably decreasing their survival. During the October 1982 survey only 'lively' trapped animals were used and the apparent high recovery (Table 1) was not unexpected. The February 1984 survey was unfortunately conducted during an anomalous intrusion of particularly warm Angolan equatorial water into Namibia. The crabs suffered the effects of being brought up from deep water (< 8°C) and being kept in warm surface water (> 22°C) circulating in holding tanks prior to tagging and release. The temperature shock resulted in a high mortality of crabs in the holding tanks and probably adversely affected the survival of the tagged animals during the first few hours after their release.

The biases which may be introduced into analysis of movements recorded from tag recovery data supplied by commercial fishing vessels have been well documented by *inter alia* Bennett & Brown (1983), Campbell & Stasko (1985) and Diamond & Hankin (1985). These biases generally take two forms. First, a lack of co-operation on the part of the fishermen and, secondly, an unequal distribution of fishing effort during the course of the year or over the extent of the fishing grounds.

The most apparent bias which was experienced during this study, has been the general confinement to recognized Namibian commercial red crab fishing areas. Red crab have been recorded from 270 to 900 m off Namibia (Melville-Smith, in press), but because catch per unit effort is uneconomical on the fringes of these depths, fishing has been restricted to between ~380 and 850 m. For the same reason, commercial fishing seldom extends south of latitude 22°00'S, even though *G. maritae* has been recorded as far south as 27°03'S (MacPherson 1983).

The northern extent of the Namibian red crab ground is restricted by territorial limits rather than catch considerations. To date 17 tagged crabs have been returned from inside Angolan territorial waters (the farthest north being 16°12'S/11°31'E), but the amount of effort directed at red crab fishing in those waters has been minimal compared to that off the Namibian coast.

The result of these sampling biases is that the mean distances (Table 3) and numbers of crabs in the northern area recorded as moving northwards (Tables 3, 4 and Figure 3) were probably underestimates. Likewise, the same biases apply in Tables 3, 4 and Figure 3 for crabs moving southwards in the southern area. Owing to the fact that mature female red crabs have been shown to move greater distances than other red crabs in the population, it is probable that these results were more biased than those for males and immature females.

With regard to depth movements, the lack of commercial fishing effort deeper than 850 m would have led to underestimations in the numbers of crabs recorded as moving deeper than 900 m (Tables 6 to 8) as well as in their mean depth at recapture (Tables 7 and 8). Inshore roaming by crabs is less likely to have been underestimated because commercial fishing takes place in water shallower than the depths at which the animals were tagged.

The overall impression from the results of this study is that the movements of both male and female red crab tend to fit the nomadic pattern of behaviour described by Herrnkind (1980). This behaviour is not unexpected, because the habitat of the red crab has few of the controlling factors identified as giving rise to either the homing or migration patterns recognized by Herrnkind (1980).

A common element present in Herrnkind's description of both these behavioural patterns was the strong controlling influence of environmental conditions such as bottom surge, photoperiod and temperature changes. An assumed absence of these environmental influences in the deep has been suggested as the reason for *G. maritae* displaying a year-round reproductive cycle (Melville-Smith, in press). For the same reason, nomadism would be a logical behavioural option for a large deep-water scavenging crustacean.

The fact that large males (⩾ 105 mm CW) have been shown to move significantly farther than small ones, may possibly be attributed to their greater size enabling them to cover distance with less effort. However, it cannot explain the extensive movements observed for mature female crabs, since the mature females which undertook the extensive movements recorded during this study, were virtually all smaller than large males.

Bennett & Brown (1983) noted for *Cancer pagurus* and Fee (1984) for blue crab (*Callinectes sapidus*) that mature females moved farther than other crabs of those species. In both cases the movements were migratory and appeared to be linked to their reproductive cycle. In the case of *G. maritae* the movements of mature female crabs have been shown by this study to be non-seasonal, often extensive and generally northward in direction. The movements do not appear to be associated with reproductive behaviour, because mating and ovigerous red crabs have been captured in both the northern and southern regions of the grounds.

One explanation which fits the above behaviour, is that mature females are particularly active foragers and therefore cover greater distances than the rest of the population. This hypothesis may be substantiated by the fact that a far greater percentage of mature females was recaptured in their first year of release than males and immature females (Figure 2). Since all recaptured animals were caught in baited traps, this implies a higher rate of foraging in mature females.

The trend displayed by mature female crabs to move in a generally northerly direction may be similarly explained. Commercial catch statistics for the red crab fishery show that catch per unit effort (in terms of numbers of crabs caught per trap) increases from south to north on the Namibian grounds (Melville-Smith unpub. data). This suggests that the environmental conditions (food availability, sediment type etc.) are probably more favourable for crabs in the north than in the south. Mature female crabs might be as likely to move in either of those directions when released, but those that moved north would be less likely to move away from the presumed more favourable environment, while those in the south would continue wandering in search of more suited conditions and would, in theory, ultimately move northwards.

The fact that red crabs are capable of wandering over considerable distances leaves no doubt that the Namibian and southern Angolan red crabs belong to a single stock. The results suggest that, although there is intermixing across territorial boundaries, it is of an exchange nature and does not appear to substantially benefit the crab fishery of either territory.

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