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THE IMPACT OF EMIGRATION ON POPULATION ESTIMATES OF DEEP-SEA RED CRAB *CHACEON MARITAE* OFF NAMIBIA

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Underwater photography and tag-recapture methods have previously been found to be the most accurate means of assessing the size of the population of *Chaceon maritae* off southern Africa. However, recent population estimates made by the tag-recapture method appear to be too high. Sources of bias in the estimate that led to violations of assumptions of the Petersen method were investigated. Females migrate into Angola and tend to travel farther than males. Population estimates that used information for males only or that accounted for emigration to Angolan waters are therefore too high. Another source of bias included under-reporting of tag recaptures in 1993.

Key words: emigration, population estimate, red crab, tag-recapture

The deep-sea red crab *Chaceon maritae* fishery off Namibia started in 1973 (Beyers and Wilke 1980) and expanded rapidly, the largest annual catch of 10 000 tons being recorded during 1983. Subsequently, catches varied between 6 000 and 8 000 tons until 1989, after which there was a sharp decline. Annual catches in the 1990s remained low and varied between 2 000 and 3 000 tons. In 1993, a depth restriction of 500 m was introduced; later that year it was changed to 400 m. The restriction prevented fishing vessels from operating at the shallow end of the species' range, and was designed to protect female crabs, because of the tendency of the latter to inhabit waters shallower than 500 m (Beyers and Wilke 1980, Melville-Smith 1988a).

Because the fishery is managed according to a total allowable catch (*TAC*), reliable population size estimates are crucial. Several methods have been used for assessing the population size of *C. maritae*, including trawl surveys, effective fishing area, underwater photographic surveys and tag-recapture studies (Melville-Smith 1988b, Beyers 1994). Of these, tag recaptures and underwater photographic surveys have been considered to be the most accurate (Melville-Smith 1988b). Because photographic surveys are expensive and time-consuming, analysis of tag recaptures has become the preferred method.

There have been concerns that population estimates made by the tag-recapture method may have been too high. Two possible sources of bias were under-reporting of recaptures and emigration from the fishing grounds. Although under-reporting is difficult to quantify, emigration was considered to be the most likely source of error. It would have contributed to excessively high estimates of population size, particularly because a depth restriction of 400 m had been enforced since 1993. The recapture of tags in the previously largely ignored Angolan fishing grounds is a further likely source of bias.

This study aims to determine the impact of emigration on population estimates from tag-recapture, and to investigate a method to reduce resultant bias.

MATERIAL AND METHODS

For the purpose of this study, crabs were collected from commercial crab-fishing vessels between 1991 and 1994 and tagged with T-bar tags (Hallprint, Australia) by inserting them into the epimeral suture (Melville-Smith 1987, Beyers 1994). Data recorded were position and depth of release, date and sex. Crabs were released using a cage that was opened 20-30 m from the bottom. Crabs were released between 500 and 800 m deep in three main regions: 18–19°S, 19–20°S and 20–21°S. Release positions were spread over intervals of 10 or 20 miles in each region. Commercial fishers were asked to return recaptured tagged crabs to the Namibian Ministry of Fisheries and Marine Resources and to give information on recapture date, catch position and depth caught.

Only crabs recaptured within one year of release were used in the assessment. An estimate of stock size was calculated using Bailey's modification of the Lincoln index (Ricker 1975) and the following equation (see Melville-Smith 1988b, Beyers 1994):

$$\hat{N} = T(C + 1)/(R + 1) \quad , \tag{1}$$

where $\hat{N}$ is the population size in numbers, T the number

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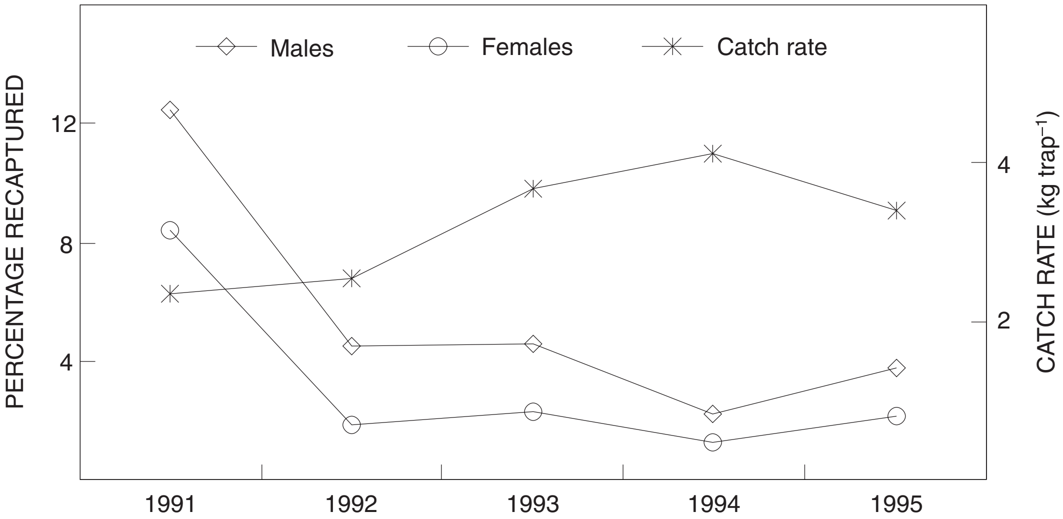

Fig. 1: Percentage tag recaptures for male and female *C. maritae* relative to catch rate for the period 1991–1995. Recapture rates for 1991 are from Beyers (1994)

of animals tagged, C the catch in numbers and R the number of tags returned.

Upper and lower 95% confidence limits of $\hat{N}$ were estimated from Pearson's formula (Ricker 1975):

$$R + 1.92 \pm 1.96 * \sqrt{R+1} \quad . \tag{2}$$

Densities were calculated using Beyers's (1994) estimates of area of occupancy in each region.

The influence of migration on population estimates from tag-recapture was assessed by calculating the distance moved according to the method of Stefánsson (1991):

$$D_{AB} = \sqrt{(\phi_A - \phi_B)^2 + (\lambda_A - \lambda_B)^2 * \cos^2[(\phi_A + \phi_B)/2]} \, , \tag{3}$$

where D_{AB} is the distance in miles between tag (A) and recapture (B) positions, and (ϕ_A, λ_A) and (ϕ_B, λ_B) are the latitude and longitude of locations A and B.

Table I: Numbers of deep-sea red crab *C. maritae* tagged and recaptured off the Namibian coast, 1991–1995. Data for 1991 are from Beyers (1994)

Area	Year tagged	Number tagged		Number recaptured		% recaptured	
		Males	Females	Males	Females	Males	Females
18–19ºS	1991	1 179	995	204	111	17.30	11.16
	1992	1 167	619	90	7	7.71	1.13
	1993	901	1 405	38	24	4.22	1.71
	1994	224	1 523	7	20	3.13	1.31
	1995	1 764	532	32	4	1.81	0.75
19–20ºS	1991	1 369	886	180	58	13.15	6.55
	1992	0	0	0	0	–	–
	1993	1 682	419	81	18	4.82	4.30
	1994	1 367	288	32	3	2.34	1.04
	1995	1 293	541	86	20	6.65	3.70
20–21ºS	1991	892	308	43	16	4.82	5.19
	1992	2 105	139	59	7	2.80	5.04
	1993	0	0	0	0	–	–
	1994	439	59	6	0	1.37	0
	1995	202	89	6	1	2.97	1.12

Emigration to Angolan fishing grounds was calculated from the equation of Gatz and Loar (1988):

$$\hat{E}_m = R_A \,/\, R_T \quad , \tag{4}$$

where $\hat{E}_m$ is the proportion that emigrated, R_A the number of tag recaptures in Angola and R_T is the total number of tag recaptures in Namibia (R_N) and Angola (R_A). Population numbers, now accounting for emigration to Angolan waters, were recalculated as

$$\hat{N} = T_N\,(C_N + 1) \,/\, (R_N + 1) \quad , \tag{5}$$

where $\hat{N}$ is the population in number in Namibian waters, C_N the catch in number in Namibian waters, and $T_N = T - T\,\hat{E}_m$ is the number of tagged animals remaining in Namibian waters. Confidence limits were calculated with Pearson's formula.

RESULTS

Between 1991 and 1994, 24 422 *C. maritae* were tagged in Namibian waters; 1 153 were recaptured. In 1993, the author was informed of under-reporting of tag recaptures. However, the report could not be quantified and it is not known whether there was under-reporting in other years. The percentage recaptured was highest following the 1991 tagging experiment (Beyers 1994), after which it declined towards 1994 and in the region between 19 and 21°S, and increased again in 1995 (Table I). In general, sample sizes for females were small, the percentage of tagged females recaptured being consistently lower than for males (except in the area 20–21°S), and sex ratios of tag recaptures were often similar to those of crabs tagged (Table I). Trends in the percentage of tag recaptures were inversely related to catch per unit effort (*cpue* – Fig.1).

From 1992 to 1995, the number of crabs caught by commercial vessels in the various areas ranged from 3.9 to 7.5 million, resulting in a low ratio of recaptures to number caught. Population number and density of fully recruited crabs (>75 mm carapace width) increased until 1994, after which it declined (Fig. 2). Comparing with 1991 data, the increase in density was particularly pronounced in the area 18–19°S, estimated population size increasing by more than 70% between 1991 and 1992 alone (Fig. 2). For the area 19-20ºS, the estimated population size increased by 48% up to 1993, but between 20 and 21ºS, the population increase between 1991 and 1992 was just 10% (Fig. 2). Overall, population size estimates were similar in 1991 and 1995, except between 18 and 19°S (Fig. 2).

After 1992, 532 tag recaptures had information on recapture location; they revealed that *C. maritae* move considerable distances. Pooled data for the years 1992–1995 showed that 94% of males and 60% of females moved between 0 and 5 miles from where they were tagged within a year of release (Fig. 3). The remainder moved more than 50 miles during a similar period. A similar pattern was observed for crabs tagged in 1991, although only 13% of females moved more than 50 miles (Fig. 4). Females travelled significantly farther than males (G-tests, $p > 0.001$, Zar 1996). The maximum distances travelled in a year were 120 miles for a male and 180 miles for females. Three females moved at least 180 miles from their tagging locations; they were recaptured in Angola in January 1996, some 196, 197 and 200 days after release.

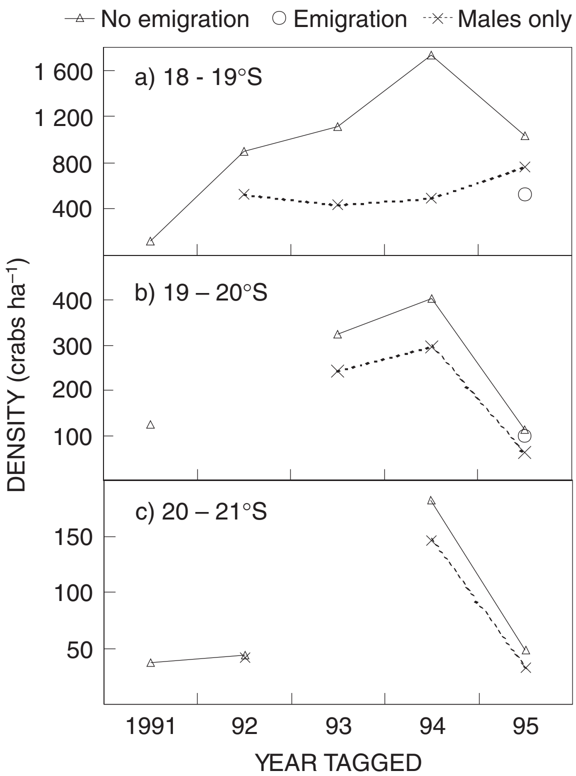

Fig. 2: Densities of fully recruited (>75 mm carapace width) deep-sea red crab *C. maritae* for (a) 18–19°S, (b) 19–20°S, (c) 20–21°S, using three scenarios: no emigration, emigration to Angola and males only. Estimates for 1991 are from Beyers (1994)

A fishing vessel reported 78 tag recaptures from Angola for the period October-December 1995, and 29 recaptures between July and September 1996. All of these were females. Of the Angolan recaptures

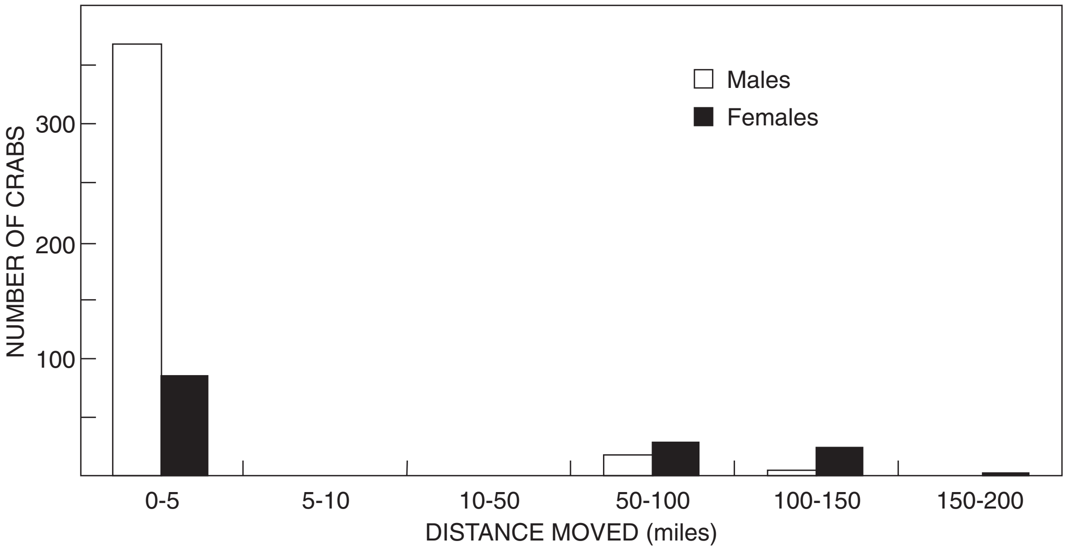

Fig. 3: Distances moved within one year of release by male and female *C. maritae* tagged in 1992, 1993, 1994 and 1995

(one year after tagging), 35 were tagged in the area 18–19°S and 15 in the area 19–20°S. These recaptures represented only those from one fishing trip in Angola. By taking the Angolan recaptures into account, the 1995 population size estimates for the area 18–19°S would have been reduced by about 49% and those for the area 19–20°S by 12% (Fig. 2).

Movements of *C. maritae* (Figs 3, 4) and previous studies indicated that population estimates were biased mostly by female migration, either to shallower water (Melville-Smith 1987) or into Angolan waters. Catches were also dominated by males: between 18 and 19°S, 60–70% of the catch in the years 1992–1994 and 85% of that in 1995 were males. Population estimates were recalculated for males only, because these were less likely to be biased (Fig. 2). Trends in population density were similar to that for the whole population, except between 18 and 19°S, where the population slowly increased towards 1995.

DISCUSSION

The simplicity and potential precision of tag-recapture methods such as the Petersen method make them popular. The Petersen method assumes a closed population, equal catchability and no tag loss. Population estimates can be obtained if births and immigration occur, but not when there are deaths and emigration (Gatz and Loar 1988). Standard methods of estimating variance or confidence limits only indicate the magnitude of error caused by random sampling, but neither the magnitude nor the direction of errors possible when assumptions are violated (Gatz and Loar 1988). Those authors showed that a small ratio of recaptured animals (R) to total animals caught (C) would result in a significant error in the resulting population size estimate, and that underestimating the $R : C$ ratio would result in a larger error than overestimating it.

Previous tag-recapture studies (Melville-Smith 1988b, Beyers 1994) were conducted prior to the introduction of the depth restriction aimed at reducing catches of females. Those studies also ignored emigration to the less intensively fished Angolan grounds. Densities in 1991 (Beyers 1994) were generally substantially lower than those calculated subsequently, especially for the area 18–19°S. Densities in the area 20–21°S were comparable to the earlier estimates made by Melville-Smith (1988b) and Beyers (1994), except in 1994. Incorporating emigration to Angola or using males only in population size estimates still resulted in density being much higher between 18 and 19°S after 1991 than in 1991 itself (Fig. 2).

The present study shows that male *C. maritae* remain in regularly fished areas, and that females tend to migrate long distances, both into shallower waters and northwards into Angola. Melville-Smith's (1987)

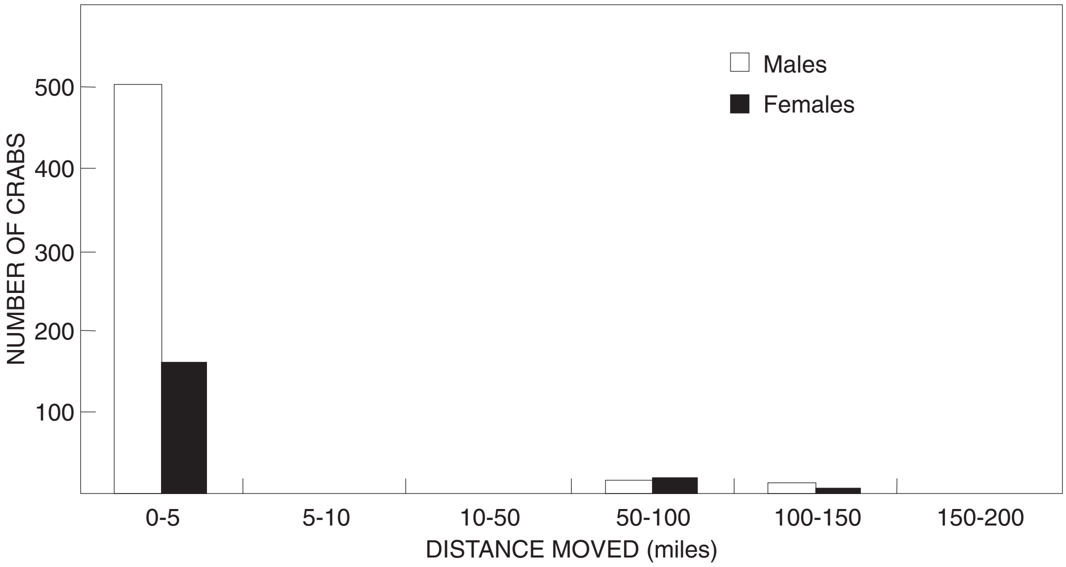

Fig. 4: Distances moved within one year of release by male and female *C. maritae* tagged in 1991. Data are from the tagging experiment of Beyers (1994)

study confirmed that females moved farther than males and tended to move northwards. Mellville-Smith (1987), citing Herrnkind (1980), also suggested that the movement could be attributed to nomadic behaviour. Apart from emigration, other factors that could contribute to low female recaptures are a higher moulting frequency of females, contributing to possible tag loss (Le Roux 1994), and a lower catchability of female crustaceans in pot fisheries (Miller 1990). Ignoring these factors would cause an overestimate of true population size. Estimates using males only or incorporating emigration to Angola are considered here to be more accurate.

Even allowing for emigration to Angola or assessing on the basis of males only, a low *R* : *C* ratio would reduce the accuracy of the estimate. A higher *cpue* would be expected should the estimates of density for the mid 1990s prove accurate. In the past, the extent of emigration to Angola was considered low, because data were only available for one fishing trip.

In summary, the higher population size estimates after 1991 can be attributed to migration of crabs to shallower water and to the depth restriction on fishing activity, which effectively prevents recaptures shallower than 400 m. More females migrate than males, and they tend to migrate farther, resulting in a total dominance of female recaptures off Angola. Males make up the bulk of the catch; therefore, population estimates based on males would be more accurate. However, estimates for the northern region (18–19°S) showed large changes after 1991. Nevertheless, post-1991 increases in *cpue* in the fishery and a simultaneous decrease in tag recaptures indicate an increase in crab abundance. Tag-recapture methods accounting for emigration can provide good estimates of population size if all recaptures from Angola are reported. Using males only in tag-recapture estimates for *C. maritae* would reduce violations of the Petersen method. Experimentation could also target tagging locations for subsequent sampling, rather than relying entirely on the commercial fishery for recaptures, so minimizing under-reporting of tag-recaptures.

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LITERATURE CITED

BEYERS, C. J. DE B. 1994 — Population size and density of the deep-sea red crab *Chaceon maritae* (Manning and Holthuis) off Namibia determined from tag-recapture. *S. Afr. J. mar. Sci*. **14**: 1–9.

BEYERS, C. J. DE B. and C. G. WILKE 1980 — Quantitative stock survey and some biological and morphometric characteristics of the deep-sea red crab *Geryon quinquedens* off South West Africa. *Fish. Bull. S. Afr.* **13**: 9–19.

GATZ, J. A. and J. M. LOAR 1988 — Petersen and removal population size estimates: combining methods to adjust and interpret results when assumptions are violated. *Environ. Biol. Fishes* **21**: 293–307.

LE ROUX, L. 1994 — Stock assessment and population dynamics of the deep-sea red crab *Chaceon maritae* (Brachyura, Geryonidae) off the Namibian coast. M.Sc. thesis, University of Iceland, Reykjavik: 88 pp.

MELVILLE-SMITH, R. 1987 — Movements of deep-sea red crab (*Geryon maritae*) off South West Africa/Namibia. *S. Afr. J. Zool.* **22**(2): 143–152.

MELVILLE-SMITH, R. 1988a — The commercial fishery for and population dynamics of red crab *Geryon maritae* off South West Africa, 1976–1986. *S. Afr. J. mar. Sci.* **6**: 79–95.

MELVILLE-SMITH, R. 1988b — Comparative population size estimates for a portion of the red crab *Geryon maritae* stock off the South West African coast. *S. Afr. J. mar. Sci.* **6**: 23–31.

MILLER, R. J. 1990 — Effectiveness of crab and lobster traps. *Can. J. Fish. aquat. Sci.* **47**: 1228–1251.

RICKER, W. E. 1975 — Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Bd Can.* **191**: 382 pp.

STEFÁNSSON, U. 1991 — *Haffræði 1* [*Oceanography 1*]. Reykjavik; Prentsmiðjan Gutenberg: 413 pp. (in Icelandic).

ZAR, J. H. 1996 — *Biostatistical Analysis*, 3rd ed. New Jersey; Prentice Hall: 662 pp.