

FISHERY CHARACTERISTICS AND ABUNDANCE ESTIMATES OF THE MANGROVE CRAB *SCYLLA SERRATA* IN SOUTHERN TANZANIA AND NORTHERN MOÇAMBIQUE

D. K. A. BARNES*, N. K. DULVY†, S. H. PRIESTLEY‡, W. R. T. DARWALL‡, V. CHOISEL‡ and M. WHITTINGTON‡

The mud crab *Scylla serrata* is lightly exploited along the East African seaboard. This study reports on fishing practices and gives preliminary estimates of abundance and size structures of the mud crab populations in Utende, Chole Island and Juani Island, Tanzania, and west of Quirimba and Ibo Island, Moçambique. Estimates for three mangrove habitats (in Tanzania); open channel (<1 per 25 m²), mangrove fringe (3 per 25 m²) and inner forest (1 per 25 m²) were obtained using burrow density and from burrow occupancy from fisheries data. Mud crabs from Tanzania were significantly smaller (carapace width) and less abundant (in terms of mass) than those from Moçambique. This newly exploited resource provides a potential alternative source of income, but local management and monitoring plans need to be implemented early.

Key words: abundance, fisheries, Moçambique, mud crabs, Tanzania

The mud crab *Scylla serrata* is one of the largest portunids and is widely distributed throughout the coastal Indo-Pacific region. It is caught with traps, by commercial and artisanal fisheries (Chitravadivelu 1994, Overton *et al.* 1997). Because they are fairly ubiquitous and abundant in estuaries and mangrove swamps, mud crabs are readily available to coastal fishers (Macnae 1968, Hirata 1991, Overton *et al.* 1997). During low tides, individual crabs reside in elliptical burrows or tree holes above the upper mid-littoral zone (Nandi and Dev-Roy 1991). The burrows likely serve as refuges from predation, as well as reservoirs for water and food (Whitten *et al.* 1988). Mud crabs are active when the tide floods the mangrove area, feeding omnivorously and opportunistically (Kalk 1995).

Fisheries are commercially important in both Tanzania and Moçambique, and the landings are an order of magnitude higher than those in other mainland East African countries (Sanders *et al.* 1988). Although other invertebrate species tend to be overexploited in these countries, the crab fisheries appear to be underdeveloped (Horrill *et al.* 1996). Both Tanzania and Moçambique are believed to have substantial populations of mud crab, probably as a result of their extensive mangrove swamps (Semesi 1991).

The current crab fishery in both countries is relatively small and is geared towards the tourist industry (Andersson and Ngazi 1995, Barnes *et al.* 1998).

Tourism is growing in Tanzania, and it is expected to increase five-fold on Mafia Island in the near future (Horrill *et al.* 1996). The tourist industry in Moçambique (particularly in rural areas) may take longer to develop because of the problems created by the extensive conflict. However, as people move to the coastal from neighbouring countries, so the pressure on marine resources is likely to increase.

A marine park has been established at Mafia Island (Andersson and Ngazi 1995, Horrill *et al.* 1996), and one may be built soon around the Quirimba Archipelago. These protected areas have many purposes, including the provision of alternative sources of income for local residents, to offset the loss of income as a result of restrictions on unsustainable exploitation practices (Horrill *et al.* 1996). With good management, the crab fishery may represent one such alternative source of income.

The present study investigates the crab population structure, population density and their possible migrations at Mafia Island and the Quirimba Archipelago. Current fishing methods and pressure are also documented. An important objective is to provide a baseline estimate of abundance of mud crab. Pauly (1995) emphasized the importance of establishing baseline estimates early to avoid the shifting baseline syndrome, which has affected the perception of fisheries, and subsequent management, in many locations.

* Formerly Department of Zoology and Animal Ecology, University College Cork, Lee Maltings, Cork, Ireland; now Biological Science Division, British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK. E-mail: dkab@bas.ac.uk

† Department of Marine Sciences and Coastal Management, Ridley Building, University of Newcastle-upon-Tyne, Newcastle-upon-Tyne NE1 7RU, UK

‡ Frontier, The Society for Environmental Exploration, 50–52 Rivington Street, London EC2A 3QP, UK

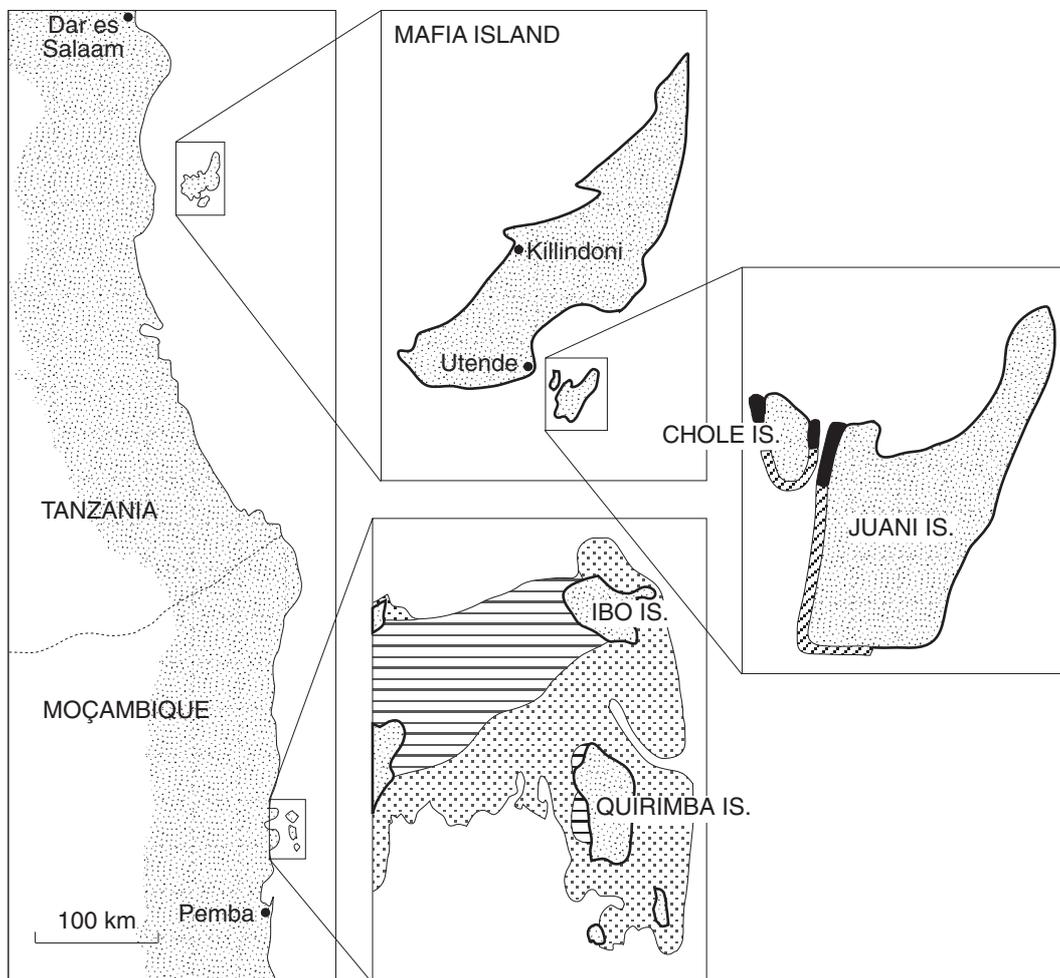


Fig. 1: Map of Tanzania and Moçambique showing the position of Mafia Island and the Quirimba Archipelago. Chole and Juani islands to the south of Mafia Island are also shown. The dotted area (in the Quirimba Archipelago) denotes shallows and intertidal zone and horizontal lines denote mangrove swamps. The oblique lines (off Chole and Juani islands) denote areas where crabs were marked and the thick line denotes areas of crab migration

MATERIAL AND METHODS

Study sites

The study sites on Mafia Island were within the boundaries of the National Park, in the vicinity of the villages of Kilindoni and Utende (Fig. 1). Data were collected in winter 1992 in the mangrove swamps at

Utende, which are of basin form and derive much of their freshwater input via land run-off. This contrasts with the swamp at Juani and Chole islands, where rivers provide most of the freshwater. The mangroves of the Utende stand consists mostly of *Avicennia marina* and *Sonneratia alba*, with some *Rhizophora mucronata* in the main stands. The mangroves of Juani Island consist mostly of dense *R. mucronata*, with some *S. alba*. Those at Chole Island are lower

in density, but higher in species richness, and are dominated by *R. mucronata*, *A. marina*, *S. alba* and *Bruguiera gymnorhiza*. The substratum in all locations is mainly sandy mud.

The study sites in the Quirimba Archipelago were the mangrove swamps west of Quirimba and Ibo islands (Fig. 1). The mangroves on Quirimba Island are confined to a thin strip only 500 m wide, whereas those on Ibo Island are several kilometres wide. Both areas are dominated by similar species to those around Mafia Island, and *R. mucronata* is particularly abundant in the areas (see Barnes 1997).

Fisheries data collection

At Utende, Mafia Island, crab fishers were accompanied on fishing trips. Data were collected on the types of burrow searched, the sub-habitat of mangroves searched, and the fishing effort expended. The size (carapace width, *CW*), mass and sex of all crabs captured were recorded. Burrows were categorized as being either in sand or hollows at the base trees. Three sub-habitats of the mangroves were recognized. These included the bare riverine area between stands of trees (channel), and areas of either low tree density at the periphery of stands (fringe) or areas of high tree density towards the centre of stands (inner). Fishing effort was subdivided by total fishing time and by the length of time spent in each sub-habitat, as well as by the number of burrows of each type sampled in each habitat. At Juani Island, a different method of fishing precluded these measurements, and only fishing effort was recorded there. Estimates of fishing frequency, numbers of fishers and current markets and prices were determined from informal interviews with fishers conducted in Kiswahili. In the Quirimba Archipelago, data were recorded on fishing effort and crab morphometrics in a similar manner to that for Tanzania.

Population estimations

At Utende, the burrow density in each sub-habitat (channel, fringe and inner) was estimated using 20 random 25-m² quadrats. Burrow occupancy was then estimated from the number of crabs captured as a proportion of the number of burrows searched by fishers. From these data, crab density was estimated in each sub-habitat and extrapolated to provide mean population estimates for the whole mangrove forest. The areal coverage of each mangrove sub-habitat was calculated on the basis of a ground-truthed 1:2 000 scale.

Individuals were marked with small, coloured cable ties attached to one chela. In all, 56 crabs were tagged at Juani Island and a further 20 crabs were tagged (different colour cable ties) in east Chole Island. Animals were recaptured by intensive fishing, with the aid of local fishers, three times at each study site over a 12-day period following their release. Data were analysed as by Robertson and Piper (1991). Sites adjacent to the release areas were also fished to investigate possible movement of the crabs. During the short experimental period (July–September 1992) it was assumed that there would be little tag-shedding and that the tag did not affect catchability.

RESULTS

Fishery at Mafia Island

The methods of fishing differ between regions. At Utende, fishing is carried out during the day and involves searching burrows with hooked or curved sticks. When an occupied burrow is located, the crab is pinned down using the stick and the pincers removed prior to the extraction of the crab by hand. At Juani Island, free-swimming crabs are captured at night, using torches and racquet-like hand nets. Fishing takes place in water about 50 cm deep, on both ebb and flood tides on the sand flats adjacent to mangrove forests.

Only five areas of mangrove at Mafia Island were continually fished for crabs. These were north-east of Utende, west of Utende, south of Juani Island (Kitoni), west of Chole Island and between Chole and Juani islands. Interviews with fishers revealed that the east side of Juani Island and the west side of Jina Island were considered to be good fishing sites for mud crab, but that they were too far to travel for crab-fishing alone. The Chole Island mangroves were considered poor fishing grounds, apparently as a result of over-fishing. At Utende, five fishers fished only on order for the hotels, but there was occasional subsistence capture. The sole, permanent crab fisher at Chole Island made two trips per week, or more during the peak tourist season when the hotels required more crabs.

From staff interviews, it was estimated that the total demand by all hotels and lodges was about 420 crabs per month, with the Mafia Island Lodge demanding the most crabs (270 per month). Approximately 850 fishing trips were undertaken per year. Crabs were valued locally at between 100 and 200 Tanzanian Shillings (TS; in September 2000, TS470

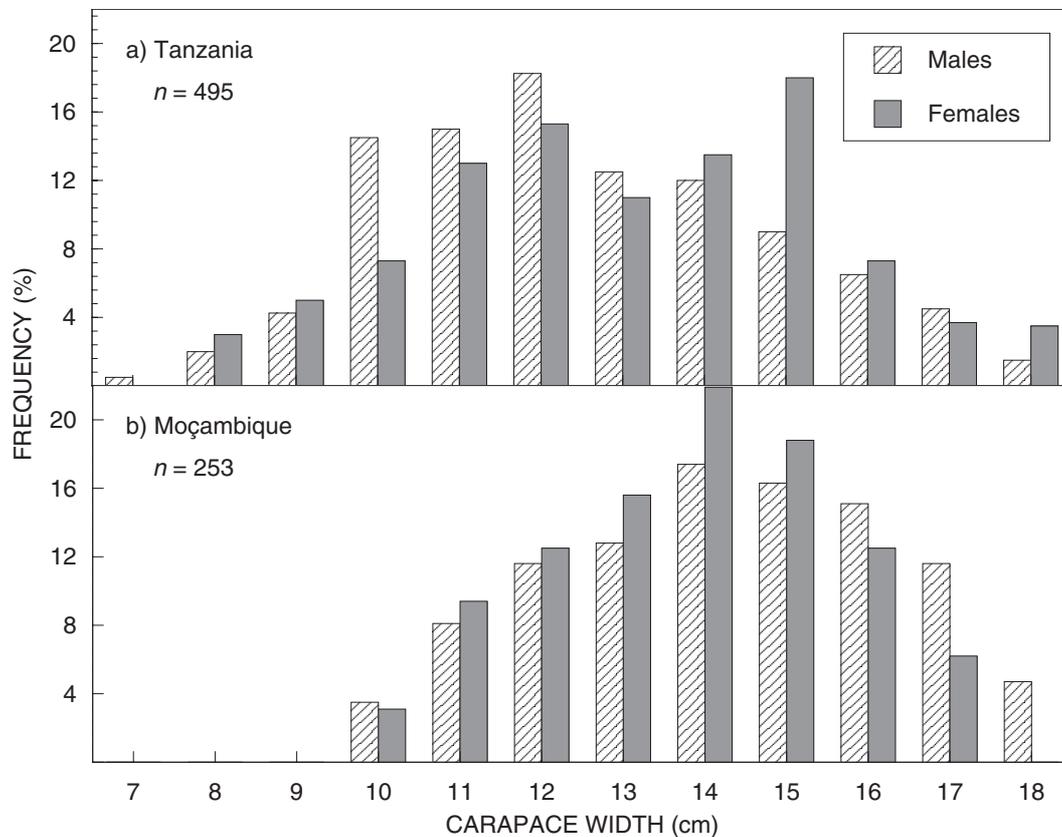


Fig. 2: Size composition of *S. serrata* in (a) southern Tanzania and (b) northern Moçambique fisheries

= 1US\$). In all cases, crab fishing represented a secondary income, supplementing that from agriculture.

The Chole Island fishers collected selectively, and ignored crabs smaller than about 110 mm CW. In Utende, fishers took crabs of all sizes. Fishing success was greater in the fringe areas than in the inner forest, because the proportion of burrows occupied in the former was higher (11 v. 5%). Four times the mass and number of crabs was caught (per unit time) at Juani Island compared to Utende (Table I). However, there was no significant difference between the mean mass or width of crabs caught at each location (Table I). Crabs caught at the Mafia Island sites ranged from 70 to 180 mm CW, peaking around 120 mm. Males were slightly larger than females (Fig. 2a).

The standing stock at Utende was calculated as a product of proportional occupancy and burrow density per 25 m². Occupancy was 10.7% in the fringe and 5.0%

in the inner mangrove forest (Table II). The mean number of burrows was 28.6 and 16.2 for the fringe and inner mangrove swamp respectively (Table II). Crab biomass per hectare was estimated at 604 kg for the fringe and 188 kg for the inner mangroves. Although the total area of the Utende mangrove stand is around 150 ha, a large section of it is salt pan, and only about 71 ha is inhabited by crabs. Of the habitable forest, channels consisted of approximately 37 ha, fringes 7 ha and inner forest 27 ha. Based on these habitat areas, the total standing stock was estimated to be 9 304 kg during the study period.

Population estimates based on analysis of mark-recapture data using the Petersen Method (see Robertson and Piper 1991) gave a mean value of 3 007 ($SE = \pm 677$) crabs for the Juani Island fishery and 193 ($SE = \pm 99$) crabs for the Chole fishery. There was no evidence to suggest movement of crabs between the two regions.

Table I: *Cpue* of *S. serrata* at Utende and Juani Island (Mafia Island), and at Ibo and Quirimba islands (Quirimba Archipelago). Crab morphometrics are shown as mean carapace width, and mass for males, females and combined sexes. The differences between sites and countries were compared using Student's *t*-test

Parameter	Tanzania (TZ)			Moçambique (MBQ)			TZ v. MBQ
	Utende	Juani	<i>t</i>	Ibo	Quirimba	<i>t</i>	<i>t</i>
<i>Cpue</i>							
kg h ⁻¹	1.96	8.23	4.40***	–	–	–	–
Number of crabs h ⁻¹	3.79	11.15	4.76***	–	–	–	–
Crab morphometrics							
Mean carapace width (mm)							
–male	126.0 (n = 99)	125.3 (n = 99)	0.41	–	147.9 (n = 98)	–	6.67***
–female	119.4 (n = 85)	129.0 (n = 99)	2.25*	–	135.7 (n = 74)	–	1.61
–combined sexes	124.7 (n = 184)	127.6 (n = 198)	0.72	154.8 (n = 81)	144.1 (n = 172)	2.37**	7.64***
Mean mass (kg)							
–combined sexes	0.516 (n = 184)	0.706 (n = 198)	0.75	0.791 (n = 81)	0.673 (n = 172)	2.38**	6.47***

**p* < 0.05

***p* < 0.01

****p* < 0.001

Fishery in the Quirimba Archipelago

The mud crab fisheries at Quirimba and Ibo islands employ similar burrow-searching methods to those used at Utende, Mafia Island. Crabs are caught opportunistically from burrows or while swimming on Quirimba Island, or by burrow-searching in the mangroves adjacent to Ibo Island. The abundance of mud crabs appears to have fluctuated at Quirimba Island, possibly because of the small size of the mangroves (Fig. 1) and overfishing. Only the periphery of the mangroves at Ibo Island is fished, and almost entirely for artisanal use. It is more productive (in terms of time and effort) for fishers to collect other crustaceans or molluscs during periods of low spring tides on the surrounding seagrass meadows or coral reef than to search mangrove burrows (see Barnes *et al.* 1998).

Both size and mass of crabs caught at Ibo Island were significantly larger than those caught at Quirimba Island (Table I). Males and females peaked at about

140 mm CW (Fig. 2b). The size range of crabs caught in Moçambique was narrower than in Tanzania, no crabs between 70 and 90 mm CW being caught (Fig. 2). Crabs caught in Tanzania were significantly smaller and lighter than those in Moçambique (Table I).

DISCUSSION

This study has provided preliminary estimates of the standing stocks of mud crab populations in some East African countries, and documents the practices of a potentially important income source. Although a large area of habitat was surveyed, relatively few fishers were involved in this developing fishery at both Mafia Island, Tanzania, and the Quirimba Archipelago, Moçambique, so caution must be used in extra-polation of this baseline study to a wider region.

At Mafia Island, the Juani Island mangroves had a

Table II: Mean number and biomass of *S. serrata* per 25 m² and per hectare for the Utende mangroves. The mean crab biomass for the fringe is based on mean fringe crab mass (0.492 kg) and similarly the corresponding figure for inner is based on mean inner crab mass (0.580 kg). Standard errors are also given

Location	<i>n</i>	Mean number of burrows per 25m ²	% occupancy	Mean number of crabs per 25 m ²	Mean crab biomass (kg) per 25 m ²	Mean number of crabs per hectare	Mean crab biomass (kg) per hectare
Channel	20	1.0 ± 0.22	0	0	0	0	0
Fringe	20	28.6 ± 0.01	10.74 ± 0.68	3.07 ± 0.37	1.51 ± 0.26	1 228.0 ± 7.3	604.0 ± 5.1
Inner	20	16.2 ± 0.82	5.00 ± 1.26	0.81 ± 0.51	0.47 ± 0.39	324.0 ± 10.2	188.0 ± 7.7

higher density of mud crabs than Chole Island. It is difficult to compare these results with those at Utende, because of differences in the sampling methods. In the Quirimba Archipelago, the larger mangrove areas of Ibo Islands supported a greater density of mud crabs than the forests around Quirimba Island (DKAB pers. obs.). The mean and range of densities of mud crabs at both locations were comparable with regions in West Bengal, although burrow occupancy is much higher there than in the present study (Nandi and Dev-Roy 1991). The minimum and mean sizes of the crabs under study were larger, in each case, at the site of greatest crab density.

The importance of the crab fishery and the intensity of fishing at the Mafia Island locations seemed greater than at the Quirimba Archipelago, as evidenced by the larger size of the crabs caught in the latter area. Netting appeared to be the most time-efficient method of capture at Mafia Island, resulting in a higher *cpue* there. However, the burrow-search method was possibly more selective in only taking larger crabs. The *cpue* values are high, but it is difficult to compare them with those from other crab fisheries that use traps; e.g. 8 kg trap⁻¹ day⁻¹ in Sri Lanka (Chitravadivelu 1994).

Given the small proportion of the mangrove habitat fished, and the size of the crabs removed, it is likely that the Mafia Island crab fishery could be sustainable. However, the demand observed during the study period approximates half the estimated standing stock. The moderately high fecundity of the mud crab suggests that there may be high levels of variation in recruitment (Rickman *et al.* in press). This could lead to large inter-annual variations in mud crab abundance. If this is the case, then the mortality levels currently imposed may not be sustainable, so it is essential to examine the temporal dynamics of crab populations in order to assess long-term sustainability in light of recruitment variability. One approach would be to monitor burrow occupancy. Although Warren (1990) found that burrow occupancy was a good predictor of crab abundance, this depends on individual crabs having their own burrows and occupying them at sampling. Neither of these variables is known. Short time-scale mark-recapture methods are probably unsuitable for long-term monitoring of abundance. The present results show that the abundance estimates determined by both burrow density and occupancy at Utende, and by mark-recapture at Juani Island, are of the same order of magnitude. However, the error associated with population estimates made by the mark-recapture method is considerable. Mark-recapture studies conducted over longer time-scales could be used to provide more robust estimates of population size, and of rates of the interchange between areas (Robertson and Piper 1991).

There are a number of issues that need to be addressed in order to avoid overexploitation of this potentially important resource. The relationship between the tourist season and the breeding season would be an important issue in the Mafia Island fishery and possibly in the Quirimba Archipelago, because of the potential affect on recruitment from harvesting "berried" females. Options for management could include temporal or spatial restrictions to limit harvesting of breeding individuals. Elsewhere, these strategies have proved successful, when carefully planned, as management solutions to multispecies fin fisheries (Kennedy 1990, Roberts and Polunin 1993, Attwood *et al.* 1997). Data are required on the life history of the mud crab and their mating and breeding patterns, which appear to differ geographically. Breeding appears to be aseasonal in the tropical Pacific (Perrine 1978) and in the cooler waters off South Africa (Robertson and Kruger 1994). Heasman *et al.* (1985) found single peaks in breeding activity during November and December in Australia, and between May and October in Hawaii. Prasad and Neelakantan (1989) found a breeding peak during January and February and another in October in the tropical Indian Ocean, although Jayamanna and Jindasa (1993) found slightly different breeding patterns in Sri Lanka.

Size limits on harvestable crabs have been used as a management measure in South Africa. There, the legal harvestable size limit for *S. serrata* was recently raised to 140 mm CW. In Queensland, Australia, *S. serrata* moult to adult body form at 140–160 mm CW, and females reach sexual maturity at >80 mm CW (Heasman 1980) and males at 90–110 mm (Knuckey 1996). Along the coast of Karwar, India, the size-at-50%-maturity of females was estimated at 91–100 mm CW (Prasad and Neelakantan 1989). Those authors also found that sexual activity peaked at 120–180 mm CW and declined in individuals >190 mm. Size-at-50%-maturity of *S. serrata* is 120 mm CW in Sri Lanka (Jayamanna and Jinadasa 1993), 123 mm CW in South Africa (Robertson and Kruger 1994) and 150 mm CW in the Northern Territory of Australia (Knuckey 1996). As maturation parameters are geographically variable, similar studies would need to be conducted in Tanzania and Moçambique in order to determine the size at sexual maturity.

Summarizing, the newly exploited mud crab resource in Mafia Island and the Quirimba Archipelago could provide a suitable alternative source of income to offset that lost because of management procedures to reduce or partially restrict destructive fishing techniques and exploitative practices such as dynamite-fishing and coral-mining (Dulvy *et al.* 1995, Horrill *et al.* 1996). However, local management and monitoring plans need to be implemented early, because

tourism in both these areas is expected to develop rapidly. Ultimately, any management plan would need to fit in with the regional integrated coastal zone management ideas for East Africa in general (Linden 1993, Coughanowr *et al.* 1995).

ACKNOWLEDGEMENTS

We thank the members of the FRONTIER research stations at Mafia Island and the Quirimba Archipelago. The collaborative venture between the Society for Environmental Exploration (SEE) in the UK and the Ministério para a Coordenação de Acção Ambiental (MICOA) in Moçambique was partly funded by the Darwin Initiative for the Survival of Species (Department of the Environment, UK). We are also grateful to Dr D. P. Stanwell-Smith (Society for Experimental Exploration, UK) for being instrumental in facilitating travel to Moçambique and all the volunteers who contributed to data collection.

LITERATURE CITED

- ANDERSSON, J. E. C. and Z. NGAZI 1995 — Marine resource use and the establishment of a marine park: Mafia Island, Tanzania. *Ambio* **24**: 475–481.
- ATTWOOD, C. G., HARRIS, J. M. and A. J. WILLIAMS 1997 — International experience of marine protected areas and their relevance to South Africa. *S. Afr. J. mar. Sci.* **18**: 311–332.
- BARNES, D. K. A. 1997 — Ecology of tropical hermit crabs at Quirimba Island, Mozambique: distribution, abundance and activity. *Mar. Ecol. Prog. Ser.* **154**: 133–142.
- BARNES, D. K. A., CORRIE, A., WHITTINGTON, M., CARVELHO, M. A. and F. GELL 1998 — Coastal shellfish resource use in the Quirimba Archipelago, Mozambique. *J. Shellfish Res.* **17**: 51–58.
- CHITRAVADIVELU, K. 1994 — Aspects of fishery and species composition of edible crabs in the Jaffna Lagoon. *J. nat. Sci. Coun. Sri Lanka* **22**: 43–55.
- COUGHANOWR, C. A., NGOILE, M. N. and O. LINDEN 1995 — Coastal zone management in Eastern Africa including the island states: a review of issues and initiatives. *Ambio* **24**: 448–457.
- DULVY, N. K., STANWELL-SMITH, D. P., DARWALL, W. R. T. and C. J. HORRILL 1995 — Coral mining at Mafia Island, Tanzania: a management dilemma. *Ambio* **24**: 358–365.
- HEASMAN, M. P. 1980 — Aspects of the general biology and fishery of the mud crab *Scylla serrata* (Forsk.) in Moreton Bay, Queensland. Ph.D. thesis, University of Queensland: 506 pp.
- HIRATA, K. 1991 — Benthic fauna in the Nagura Lagoon and vicinity, Igshigaki Island, Okinawa Prefecture, Japan. *Reps. Fac. Sci. Kagoshima Univ.* **24**: 121–173.
- HORRILL, C. J., DARWALL, W. R. T. and M. NGOILE 1996 — Development of a marine protected area: Mafia Island, Tanzania. *Ambio* **25**: 50–57.
- JAYAMANNA, S. C. and J. JINADASA 1993 — Size at maturity and spawning periodicity of the mud crab *Scylla serrata* (Forsk.) in the Negombo Estuary. *J. nat. Sci. Coun. Sri Lanka* **21**: 141–152.
- KALK, M. 1995 — *A Natural History of Inhaca Island, Moçambique*. Johannesburg: Witwatersrand University Press: 395 pp.
- KENNEDY, A. D. 1990 — Marine reserve management in developing nations: Mida Creek – a case study from East Africa. *Ocean Shoreline Mgmt* **14**: 105–132.
- KNUCKEY, I. A. 1996 — Maturity in male mud crabs, *Scylla serrata*, and the use of mating scars as a functional indicator. *J. crustacean Biol.* **16**: 487–495.
- LINDEN, O. 1993 — Resolution on integrated coastal zone management in East Africa signed in Arusha, Tanzania. *Ambio* **22**: 408–409.
- MACNAE, W. 1968 — A general account of the fauna and flora of mangrove swamps and forests in the Indo-West-Pacific region. *Adv. mar. Biol.* **6**: 73–270.
- NANDI, N. C. and M. K. DEV-ROY 1991 — Burrowing activity and distribution of *Scylla serrata* (Forsk.) from Hooghly and Matla estuaries, Sundarban, West Bengal. *J. Bombay nat. Hist. Soc.* **88**: 167–171.
- OVERTON, J. L., MACINTOSH, D. J. and R. S. THORPE 1997 — Multivariate analysis of the mud crab *Scylla serrata* (Brachyura: Portunidae) from four locations in Southeast Asia. *Mar. Biol.* **128**: 55–62.
- PAULY, D. 1995 — Anecdotes and the shifting baseline syndrome of fisheries. *Trends Ecol. Evol.* **10**: p. 430.
- PERRINE, D. 1978 — *The Mangrove Crab on Ponape*. Ponape, Eastern Caroline Islands; Marine Resources Division: 88 pp.
- PRASAD, P. N. and B. NEELAKANTAN 1989 — Maturity and breeding of the mud crab *Scylla serrata*. *Proc. Indian Acad. Sci.* **98**: 341–349.
- RICKMAN, S. J., DULVY, N. K., JENNINGS, S. and J. D. REYNOLDS (in press) — Recruitment variation predicted by fecundity in marine fishes. *Can. J. Fish. Aquat. Sci.*
- ROBERTS, C. M. and N. V. C. POLUNIN 1993 — Marine reserves: simple solutions to managing complex fisheries? *Ambio* **22**: 363–368.
- ROBERTSON, W. D. and S. E. PIPER 1991 — Population estimates of the crab *Scylla serrata* (Forsk., 1755) (Decapoda: Portunidae) in two closed estuaries in Natal, South Africa, from mark-recapture methods. *S. Afr. J. mar. Sci.* **11**: 193–202.
- ROBERTSON, W. D. and A. KRUGER 1994 — Size at maturity, mating and spawning in the portunid crab *Scylla serrata* (Forsk.) in Natal, South Africa. *Estuar. coast Shelf Sci.* **39**: 185–200.
- SANDERS, M. J., SPARRE, P. and S. C. VENEEMA 1988 — Proceedings of the workshop on the assessment of fishery resources of the Southwestern Indian Ocean. **FAO/UNDP: RAF/79/065/WP/41/88/E**: 357 pp.
- SEMESI, A. K. 1991 — Management plan for the mangrove ecosystem of mainland Tanzania. Ministry of Tourism, Natural Resources and Environment, Forestry and Beekeeping Division, Dar Es Salaam. Vols 1–10: 292 pp.
- WARREN, J. H. 1990 — The use of open burrows to estimate abundances of intertidal estuarine crabs. *Aust. J. Ecol.* **15**: 277–280.
- WHITTEN, A. J., MUSLIMIN, M. and G. S. HENDERSON 1988 — *The Ecology of Sulawesi*. Gadjah Mada University Press.