CHAPTER 18

Mangrove Crabs

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I. INTRODUCTION

Mangrove crabs (known in different regions as mud, black, or Samoan crabs) belong to a group known as swimming crabs, which have characteristically flattened terminal segments on the last pair of walking legs. These paddle-like modifications enable the animals to swim with a degree of agility, although they typically remain in close contact with the substrate. Their size, high meat yield, delicate flavour and ease of capture mean that almost everywhere they occur mangrove crabs are highly sought-after as a quality food item. Their sedentary habits, accessible habitat and relative ease of capture also, however, make them susceptible to overexploitation.

During 1982-1988 the average annual production of all crab species (around 904,000 t) comprised between 25 and 30 per cent of the 3.3 million t of marine crustaceans produced throughout the world (FAO, 1989). More than half of this crab catch was taken from the north-west Pacific Ocean (FAO Statistical Area 61) which includes China, Korea, Japan and Taiwan. The bulk of the landings are attributable to a few large northern-hemisphere fisheries for species such as the king crab (*Paralithodes* spp.), snow crab (*Chionoecetes* spp.) and the swimming crabs *Portunus* spp. Annual crab landings in the Western central Pacific region (FAO Area 71) averaged about 66,000 t, approximately 7 per cent of the world total crab production over that period (Table I).

According to the FAO statistics and other estimates, around 80 per cent of the world catch of mangrove crabs (10,600 t) is taken in the western central Pacific and "inland waters" of the Philippines and Indonesia (Table I). The remainder comes mainly from the Indian Ocean shores of Indonesia and Thailand (both of which countries also contribute to the Area 71 total) and from the south-west Pacific region (New South Wales, Australia). Within the western central Pacific the major producers of *S. serrata* are Indonesia and Thailand (est. 4,000 and 2,700 t respectively in 1987). The combined 1987 reported mangrove crab production by the Pacific islands countries (Fiji, Palau, Federated States of Micronesia, and Papua New Guinea) amounted to about 500 t, about 4 per cent of the year's species total.

Table I. Mean annual production (metric tonnes) over the period 1982-87 of all crab species and *Scylla serrata* separately, in FAO statistical areas which lie at least partly within the known geographical range of the mangrove crab.

FAO Area	Description	All Crab Species	*S. serrata*
04	Asia - inland waters	1,393	1,380
51	Indian Ocean - western	1,488	1
57	Indian Ocean - eastern	10,155	1,871
61	Pacific Ocean - north-west	534,971	n.r.
71	Pacific Ocean - western central	66,205	7,183[a]
81	Pacific Ocean - south-west	464	150[b]

[a] includes an estimated 500 t from the Northern Territory and Queensland (Australia) evidently not reported to FAO.

[b] Estimated catch from New South Wales (Australia) evidently not reported to FAO.

II. BIOLOGY

TAXONOMY

Despite the widespread distribution and local economic value of the genus *Scylla*, to which the mangrove or mud crab belongs, its taxonomy is open to debate. Most authors recognise the existence of only one species - *Scylla serrata* (Forskal), but Estampador's (1949) revision of the genus is a source of periodic interest in whether the various "forms" or colour morphs seen in some populations do in fact represent different species. Estampador (1949) recognised three species - *S. serrata* (Forskal), *S. oceanica* (Dana), *S. tranquebarica (Fabricius)*, and one variety (*S. serrata* var. *paramamosain)* in Philippine waters, on the basis of differences in colour patterns, relative size, cheliped spination, chromosome "form", and gamete development. Serene (1951) agreed basically with this classification, except that he considered *S. tranquebarica* to be a variety of *S. oceanica*. Because of the rather qualitative nature of the criteria used in the above studies, Stephenson and Campbell (1960), in their revision of Australian portunids, rejected this classification, at least until further detailed quantitative taxonomic work yielded stronger supporting evidence.

Some authors, however, recognise *S. paramamosain* as a species co-occurring with *S. serrata* in a Papua New Guinea estuary (Quinn and Kojis, 1987) and in West Australian waters (R. George, as reported by Taylor, 1984). Joel and Sanjeeva Raj (1980), in a study of the portunid crabs of Pulicat

Lake in India, strongly supported a specific distinction between *S. serrata* and *S. tranquebarica*. Ong (1964) recognised four "forms" of *Scylla* in Malaysia, but agreed with Stephenson and Campbell (1960) in the need for further justification before subdividing *Scylla* into any more than a single species. The mud crab stock on Australia's northern and eastern seaboard has traditionally been considered monospecific (Anon., 1982; Hill, 1982; Mounsey, 1990), and despite Taylor (1984), the existence of two species in Western Australia has not been confirmed scientifically.

Perrine (1978) closely examined samples of mangrove crabs from Pohnpei (Federated States of Micronesia) and attempted to classify them according to the distinguishing features listed by Estampador (1949) and Serene (1951). The Pohnpei crabs were quite variable in colour and morphology, but these characteristics appeared to vary with age and moult stage. Perrine (1978) found that specimens from the local population sometimes corresponded to one "species", at times with another, sometimes with several, and sometimes with none. He therefore accepted only the single species *S. serrata* as being represented on Pohnpei.

In an attempt to rationalise the systematics of this group, a study of genetic inter-relationships within the *Scylla* population, using electrophoretic techniques, was initiated in Queensland in the mid-1980s (Walker, 1987). Unfortunately, the work was abandoned at an early stage, and no subsequent attempt has been made to revive it. The taxonomy of the group remains in a very confused state - even Forskal's original description of *S. serrata* is unreliable, because the type specimen was a poorly preserved male crab without claws (B.J. Hill, *pers. comm.*). Hill (*pers. comm.*) has also concluded, from examination of material in the British Museum, that cheliped spination is of little value in separating the "species" of *Scylla*. Just how many species there actually are remains to be determined, and the task of assigning valid scientific names to the various groups will be a major one for crustacean taxonomists in the future. In the meantime, extreme caution should be exercised in the use of names other than *Scylla serrata* for mangrove crabs in the Pacific region, and carefully documented evidence should be accumulated to support any decision to do so.

GEOGRAPHICAL DISTRIBUTION

The distribution of the mangrove or mud crab, *Scylla serrata*, is illustrated in Fig. 1, and described comprehensively, with supporting references, by Dickinson (1977) as follows:

> The natural range ... extends from Mossel Bay in South Africa (MacNae, 1968) along the East African coast including Mauritius and Madagascar (Barnard, 1950) to the Red Sea (Stephenson and Campbell, 1960). The

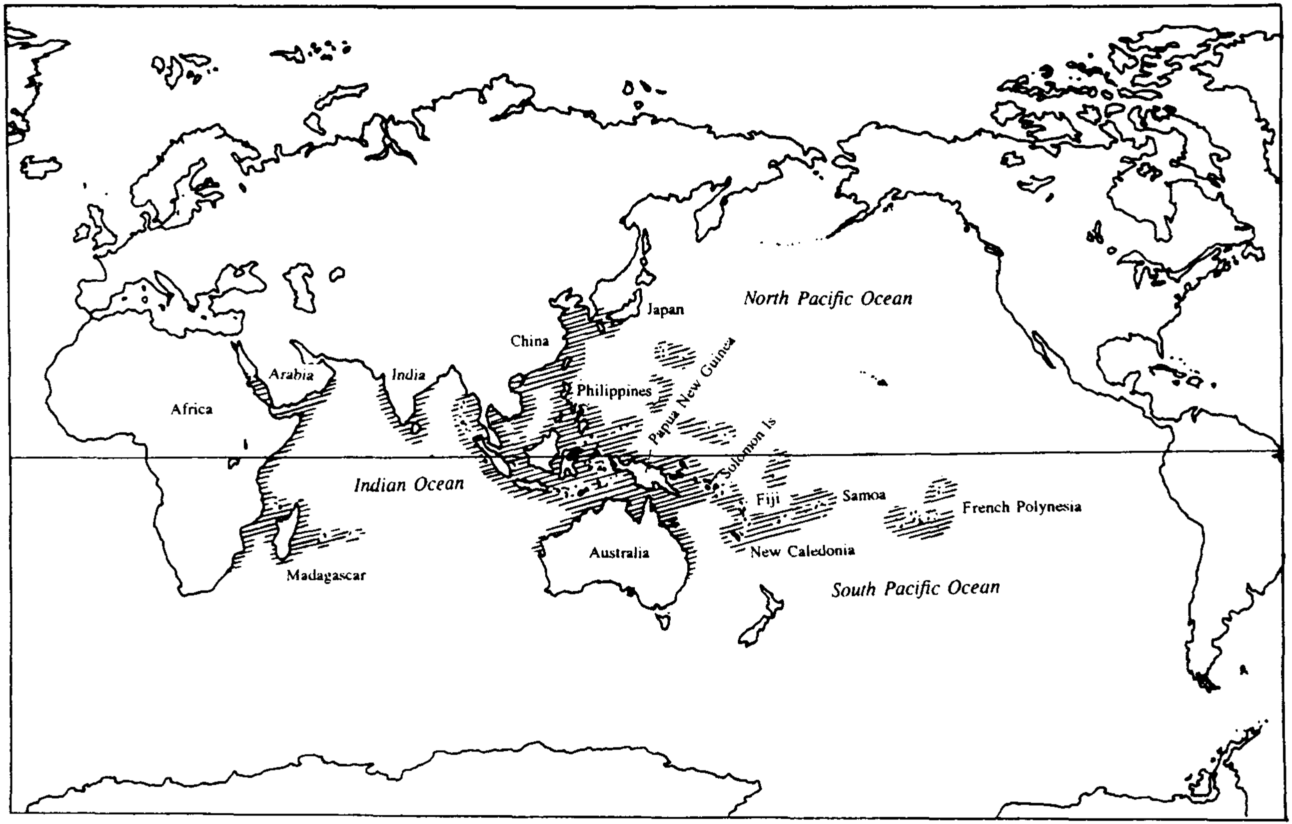
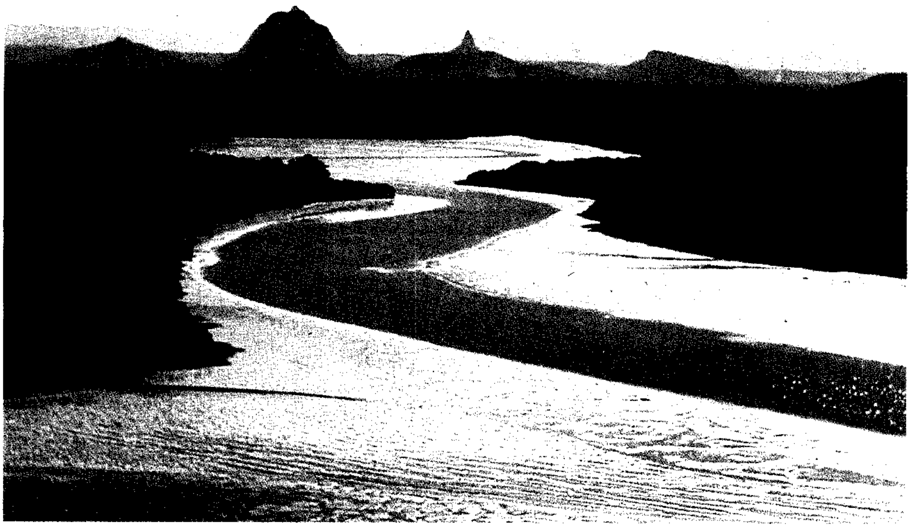
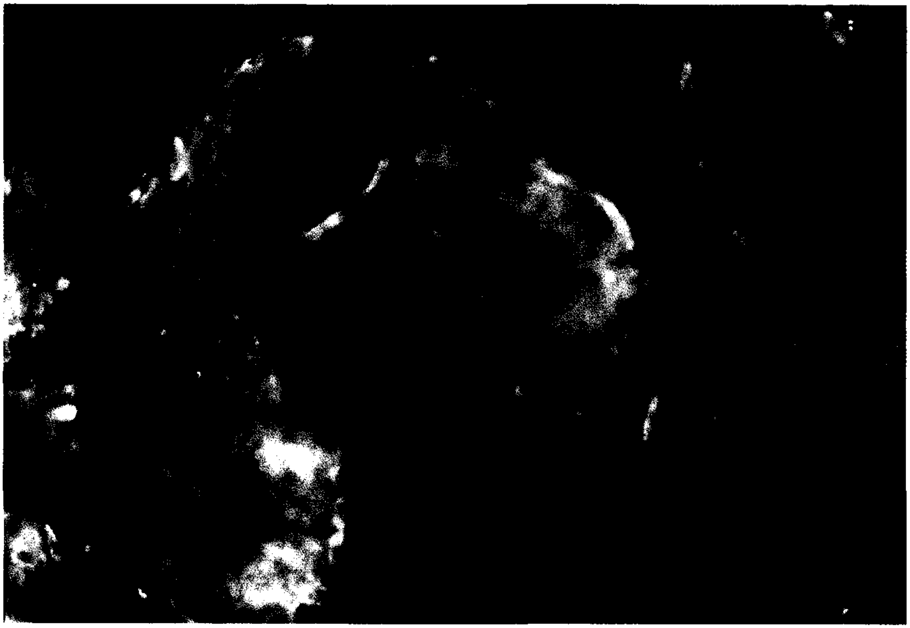


Figure 1. World geographical distribution of indigenous populations of *Scylla* species. Note that *S. serrata* was introduced into Hawaii from Samoa and has not become established in northern New Zealand.





range continues eastward to India and Sri Lanka (Jones and Sujansingani, 1952; Raphael, 1970; Chandy, 1973) and throughout Indonesia, the Philippines, and Malaysia (Arriola, 1940; Ong, 1966). Northward, it occurs in Thailand, China, and Taiwan (Tamura, 1966) and the northern limit is the mouth of the Tone River in Japan (Sakai, 1976). *S. serrata* is also found along the Australian coasts from Broome, West Australia, north and east to the Northern Territory and Queensland, and New South Wales to Port Jackson (Stephenson, 1972). It also occurs in New Zealand (Stephenson and Campbell, 1960) and the Pacific islands including the Caroline and Mariana Islands, Samoa, the Tuamotus (Bablet and Cayet, 1972), and Hawaii. It was successfully introduced into the latter from Samoa between 1926 and 1935 (Brock, 1960). This entire region encompasses an area referred to as the Indo-West Pacific (Ekman, 1953).

The occurrence of mangrove crabs in New Zealand is considered by Dell (1964) to have been a recent invasion, but according to Manikiam (1967) the population failed to become established. Although not mentioned by Dickinson (1977), *S. serrata* is also found in Papua New Guinea (Opnai, 1979; Quinn and Kojis, 1987), Solomon Islands (P. Nichols, *pers. comm.*), Vanuatu (A. Obed, *pers. comm.*), New Caledonia (Delathière, 1988) and Fiji (Anon., 1978). It seems very probable that any tropical Pacific island which is large enough to sustain a fluvial delta with associated mangrove forests will support a population of mangrove crabs.

HABITAT

As its common names suggest, *Scylla serrata* is frequently found in areas characterised by a muddy substrate associated with mangrove vegetation. It is the only portunid crab characteristically found in mangrove swamps (MacNae, 1968). This type of habitat is typical of sheltered tropical to subtropical estuaries, embayments and the lower reaches of rivers and tidal streams. Juvenile crabs tend to be found in the more protected areas; subadults feed preferentially in shallow water and adults are captured mainly in deeper subtidal waters (Hill, 1982). Mangrove crabs generally have a rather restricted home range, and Hyland *et al.* (1984) found that, although there was some exchange of crabs between a mangrove creek and the nearby bay, very little occurred between an estuarine system and the same bay, and none at all between neighbouring areas separated by a region of habitat unsuitable for *S. serrata*.

The crabs are sometimes found in the mud amongst mangrove roots (LeReste *et al.*, 1976), but more often in burrows which extend obliquely down into the mud at an angle of about 30° to the horizontal. Burrows may be up to 2 m in length and are used as general refuges by subadult and adult crabs, particularly when they are in the vulnerable soft-shell stage of the moult cycle and when mating (although it should be noted that moulting and mating also take place away from the protection of burrows). Because they normally extend below the low-tide water table, burrows always contain some water although the water is usually lower in dissolved oxygen, cooler and more saline than the surroundings (Fielder and Heasman, 1978).

As the mangrove crab's intertidal and near-subtidal habitat is subject to considerable environmental variation, it is not surprising that S. *serrata* can tolerate a wide range of temperatures and salinities (Davenport and Wong, 1987). Adult crabs are able to survive salinities as low as 2 ppt for four months, and as high as 60 ppt (Hill, 1979a). This tolerance, however, is evidently dependent on the stage of the life cycle, as the pelagic zoeal larvae studied by Hill (1974) suffered high mortality at temperatures above 25° C and salinities below 17.5 ppt, and became inactive at temperatures below 10°C. The author concluded that the larvae of *S. serrata* are unsuited to estuarine conditions.

DIET AND FEEDING BEHAVIOUR

Arriola (1940) reported that *S. serrata* is both a scavenger and cannibalistic. In the natural environment large crabs will eat smaller injured or weak crabs of the same species as well as algae and decaying vegetable matter, and in aquaria they will seize and eat small live fish and shrimps. There is a great variety in the composition of mangrove crab diets reported in the literature, although most descriptions of the gut contents of wild-caught crabs feature crustaceans such as grapsid and hermit crabs (Dickinson, 1977; Hill, 1976) and barnacles (Dickinson, 1977), and bivalve molluscs such as the mud-burrowing edible clam *Geloina papua* (Dickinson, 1977) and mussels (Hill, 1976). Pillay (1954), Guinot (1966) and Thia-eng (1974) reported that *S. serrata* feeds extensively on fish, but evidence from other experimental studies (e.g. Hill, 1976; Perrine, 1978) indicates that large adult crabs, at least, are not agile enough to capture such fast-moving prey as healthy active prawns and live fish.

The mangrove crab is an opportunistic feeder, subsisting primarily on slow-moving or immobile prey organisms (Fielder and Heasman, 1978), and tends to live in parts of the estuarine system where prey is most abundant (Hill, 1979b). The main chelae or claws are dimorphic, *i.e.* of different shape. In a study of the feeding behaviour of *S. serrata* in aquaria, Williams (1978) showed that the larger claw, which is equipped with large molariform "teeth" on the propodus, is used for crushing hard-shelled prey (in this case the mussel *Trichomya hirsuta*). The other claw has smaller, conical teeth, and tends to be used more for biting and cutting and manipulating the food to within reach of the mouthparts.

Mangrove crabs usually remain buried during daylight hours and feed at night. Fielder and Heasman (1978) maintain that there are two main feeding periods - one in the early evening and one before dawn; Hill (1976) notes that the crabs emerge at sunset to feed intermittently throughout the night. Soft organic tissue is cleared from the foregut in a matter of 12 hr or so (Hill, 1976), but harder materials, such as fish bone and mollusc shell fragments, remain in the gut for rather longer (2-3 days and 5-6 days respectively). This highlights the need for care in interpreting the results of gut contents analysis in dietary studies. Feeding activity is greatly reduced, or ceases completely, during the late intermoult period of the moult cycle (Williams and Hill, 1982), during mating (Lavina, 1977) and when the water temperature falls below about 20°C (Hill, 1980).

REPRODUCTION

Size at maturity: Studies on the reproductive cycle of *S. serrata* in different latitudes indicate that there is considerable variation in both the size and age at which the crabs reach maturity. Fielder and Heasman (1978) suggest that the time difference could be as much as 18 months; in the tropics maturity may occur at 18 mo; in more temperate regions it may take up to 3 yr. Mangrove crabs in Moreton Bay (South Queensland), for example, take from 18 to 27 mo to reach maturity (Heasman, 1980), while aquarium-held crabs in Malaysia were recorded as undergoing the copulatory moult at around 12 mo (Ong, 1966). Table II (based on Table 7 of Quinn and Kojis, 1987) shows an increase in the maturity size of female crabs, from a carapace width of about 90 mm within latitudes 10° from the equator to more than 130 mm in the highest latitudes, towards the extremes of the species' natural range. These differences in size at first maturity suggest metabolic differences in reproductive as well as growth processes and strengthen the evidence supporting the existence of different species or at least genetically quite distinct stocks.

In some areas there is a belief that large female mangrove crabs lose their reproductive capacity. This is used to support the case for allowing the taking of large female crabs in fisheries where these are currently protected. However, most of the observations of mating crabs involve females which are being guarded by the male prior to moulting and copulation, and as Mounsey (1990) points out, the females can increase in size quite markedly (by as much as 30 mm CW) after moulting is complete.

Mating: The transfer of sperm from the male to the female crab can take place only when the female's carapace is soft, within a period of about 48 hr following a moult. However coupling between crabs is initiated well before the moult, when the female is cradled protectively by the male. Insemination involves the transfer of packets of sperm (spermatophores) into the female's sperm receptacle or spermathecum. This process begins as soon as the female has moulted and

Table II. Reported minimum sizes at maturity (carapace width) of female *S. serrata* in relationship to latitude. [Adapted from Quinn and Kojis 1987].

Country	C.W. (cm)	Latitude	Source
Malaysia	9.2	5°N	Ong (1966)
PNG	9.0	6°S	Quinn & Kojis (1987)
Philippines	8.5	8°N	Escritor (1970)
India	12.0	10°N	Pillai & Nair (1968)
Thailand	9.3	12°N	Varikul *et al.* (1972)
India	9.7	13°N	Raja Bai Naidu (1955)
Madagascar	10.2	13°S	Le Reste *et al.* (1976)
Philippines	10.0	15°N	Arriola (1940)
Queensland	13.8	28°S	Heasman (1980)
South Africa	13.7	34°S	Hill (1975)
South Africa	13.6	34°S	DuPlessis (1971)

may continue for several hours while her shell is still soft. The female crab subsequently remains in the protection of the male for several days until her new shell has become hard. Burrows provide shelter for mating crabs, but pre-copulatory coupling pairs are often caught in crab pots and dillies. Studies in Queensland involving the sampling of spermatophore contents by catheter have shown that very high rates of insemination (more than 90 per cent of mature females) are achieved in mid-summer (Moreton Bay) and in winter (Moreton Bay and Great Sandy Strait) (Hill, 1982).

The sperm cells can remain viable in their gelatinous packages for periods up to 7 months (DuPlessis, 1971) and still effectively fertilise ova as they pass along the female's oviducts to the exterior. After emerging, the eggs (which number from about two to six million, depending on maternal body size) are attached in a mass or "sponge" to a set of feathery pleopods beneath the abdominal flap where they are tended and aerated by the female. This part of the mangrove crab's life cycle is seen only rarely because the ovulating females migrate offshore (Arriola, 1940; Ong, 1966; Le Peste *et al.*, 1976; Hyland *et. al.*, 1984) to hatch their eggs in an oceanic environment more tolerable to the pelagic larval stages. The seaward migration is little understood, but there are numerous records of berried (ovigerous) mangrove crabs being caught by trawlers between 10 and 30 km offshore (up to 75 km), and in depths of 20-40 m (max. 300 m) (Hill, 1982), as well as inshore waters and even river mouths

(Mounsey, 1990). Multiple spawnings after a single mating (Ong, 1966; DuPlessis, 1971) may be a regular feature of the reproductive behaviour of larger crabs.

Early life history: The main events in the life cycle of the mangrove crab are illustrated in Fig. 2. Egg incubation (observed in captive crabs) takes from about 10 to 17 days, presumably depending on ambient water temperatures (Ong, 1966; DuPlessis, 1971; Arriola, 1940). At hatching, the planktonic zoea larva emerges from the egg, and over a period of about three weeks undergoes a series of up to five moults, during which time it is transported by tidal currents back to the estuarine environment. Delathière (1990) found that the zoeal series lasted for 16 days in New Caledonia at a salinity 31.75 ppt and temperatures between 28.5 and 29.0°C. The final zoeal stage ultimately changes into a megalopa which settles out on a suitable substrate if available and after about 5 to 12 days (Delathière, 1990 and Ong, 1964 respectively) becomes a juvenile crab. Hill *et al.*(1982) collected juvenile mangrove crabs (20 - 80 mm C.L.) using "habitat traps" on the estuarine mud flats of Moreton Bay, Queensland. The "traps" consisted of ceramic roofing tiles (330 x 415 mm) laid out in rows in the upper intertidal zone. Juveniles shelter naturally under stones in the same habitat (Heasman, 1980) and in estuarine reed beds and areas of aquatic macrophytes (Hill, 1979b).

GROWTH

In common with all other crustaceans, mangrove crabs have an external rather than an internal skeleton. This confers obvious advantages in terms of protection from predators and insulating the animal from sudden changes in environmental conditions, but it does mean that in order to grow (*i.e.* increase in size) the rigid exoskeleton - the carapace or shell - must first be cast off. The process of moulting is followed by a brief period when the crabs is very vulnerable because its new shell, expanded by the intake of water into the muscular tissues, is still soft and pliable. It is at this point, of course, that the moult increment, or increase in body size, occurs. The complex process, under hormonal control, is described graphically and concisely by Fielder and Heasman (1978) as follows:

> Just prior to moulting the membranes joining the legs to the body swell and begin to form obvious bulges. A hair-line crack appears along the sides of the gill chambers. This rapidly opens around the back of the carapace and allows it to be lifted from the abdominal attachment. The crab can then back out of the old shell. The bulk of the body swells whilst fluids are reduced in the extremities to allow the legs etc. to be withdrawn. The outside walls of the gills, some of the gut lining, and the eye lenses are all part of the shell and are lost at this time. Once the crab

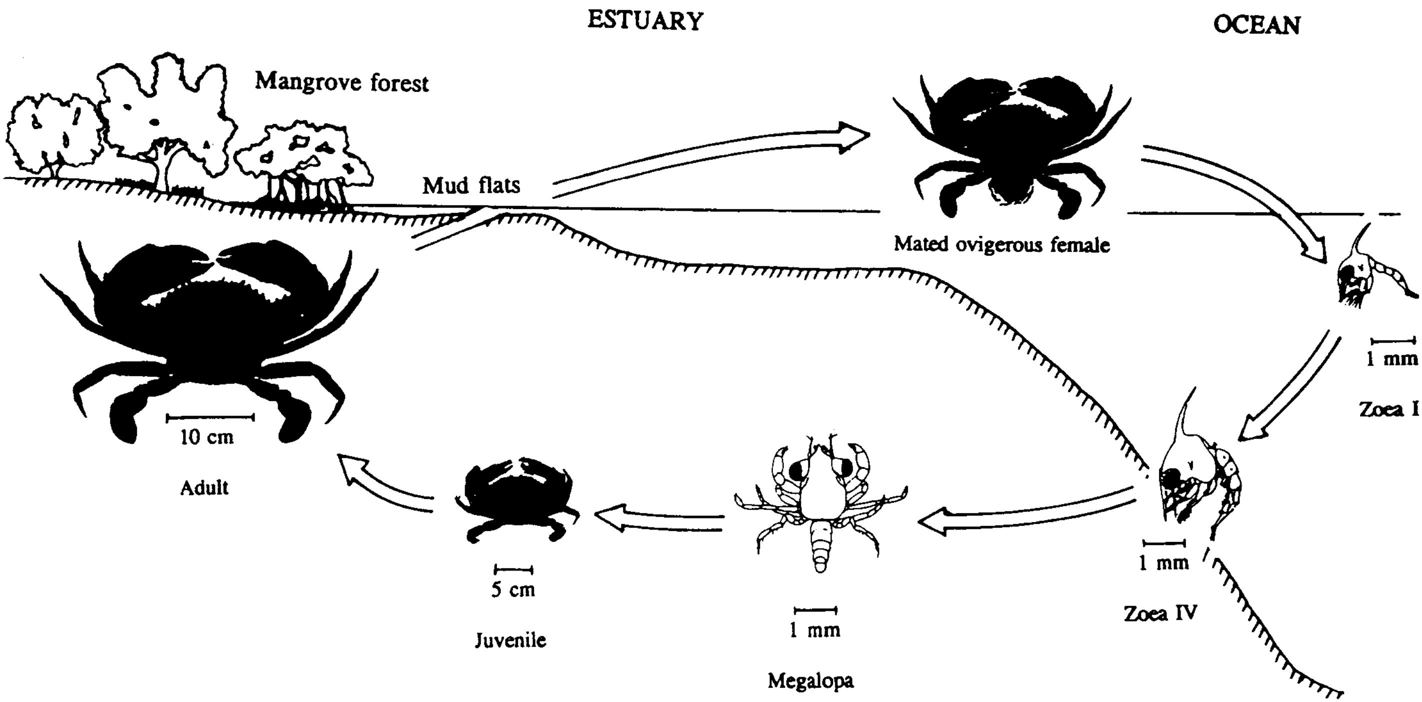


Figure 2. Schematic representation of the life cycle of the mangrove crab *Scylla serrata*.

is free of the old shell, fluid is taken up to expand the new larger shell while it is still soft.

Like most other decapod crustaceans mangrove crabs have the ability to regenerate appendages (claws, legs etc.) which may be lost in nature as a result of attack by predators. A membrane rapidly grows over the exposed part of the autotomised limb, and during the intermoult period a new limb or limb segment is produced beneath the membrane, forcing it out into a limb-bud. At moulting the folded, newly formed appendage is released, although it may take additional moults before it reaches a "normal" size and shape (Fielder and Heasman, 1978).

In Australian waters mangrove crabs can reach a carapace width of 24 cm, but the majority fall within the 15 - 20 cm size group (15 cm being the minimum legal size). In the lower tropical latitudes the crabs appear to attain a smaller final size than they do in otherwise comparable warm-temperate regions (Heasman, 1980). Wildman (1974) reported that crabs under culture in Hawaii attained marketable size (500 - 700 g) in 18 months at 24°C, while at 27°C they reached an equivalent size in only about 12 months. It may be that as crab stocks in localities closer to the equator mature earlier than their subtropical and temperate counterparts (Table II), it is biologically advantageous for animals which have become sexually mature to invest resources in producing gametes rather than increasing body size. Alternatively the smaller-sized tropical populations may, as authors such as Quinn and Kojis (1987) maintain, actually represent a different species or at least genetically distinct stocks of *S. serrata*.

In subtropical climates mangrove crabs attain a carapace width of between 8 and 10 cm in their first year, and between 13 and 16 cm in their second year (Heasman, 1980; Hill, 1982). In an extensive tagging study described in Hill (1982), 17 per cent of the 7,000 crabs tagged were recaptured, and almost one fifth of these had grown. Growth was strongly seasonal: 75 per cent of the crabs showing growth had been released and recaptured between September and January (spring to mid-summer in the southern hemisphere), indicating that this is the main moulting period for sub-adults.

The rate at which crabs grow depends on two factors - intermoult duration (an alternative way of expressing moult frequency), and moult increment (the size difference between the old and the new shell). A typical growth curve or "staircase" is shown in Fig. 3, which gives an indication of the number of times a mangrove crab moults throughout its life, the size of the moult increments, and the duration of the intermoult period. It also clearly demonstrates the effect that the time of settlement can have on population size structure. Crabs which settle early (around December, or the austral summer) can reach 80 mm CW by the following September, when postlarvae of only 3-4 mm CW are still being recruited into the population. After an initial burst of rapid growth (in the warmer months) involving about 10 to 14 frequent moults, the crab's growth rate stabilises as the intermoult period becomes longer. The absolute growth incre-

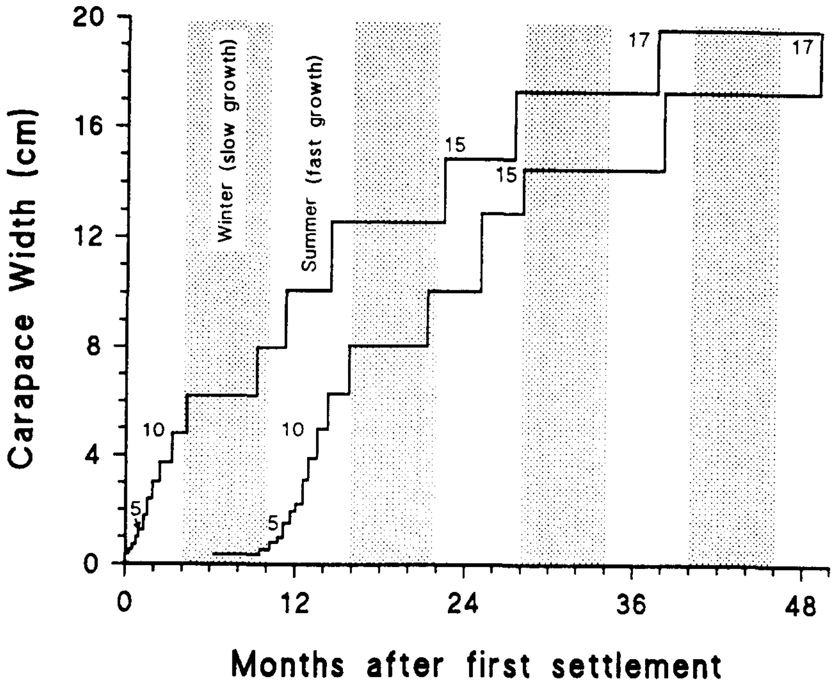


Figure 3. **Growth patterns of *S. serrata* in southern Queensland (after Fielder and Heasman, 1978; re-drawn with permission of the Queensland Museum).**

ment increases, although as a proportion of pre-moult size it falls, and ultimately growth tapers off with a single moult - the "terminal moult" - in the final year of life. Heasman (1980) concluded that environmental temperature has a more pronounced effect on intermoult duration than moult increment: at temperatures of 27° ± 0.5°C the relationship between carapace width and intermoult duration is described by the equation:

$$Y = 2.996 + 2.747\ X + 0.254\ X^2$$

where Y = intermoult duration (days) and X = carapace width (cm). Robertson (1989) developed a slightly simpler model:

$$Y = 1.74\ X^{0.87}$$

with similar parameters except that carapace width is given in millimetres. The latter predicts significantly longer intermoult periods than the former over a range of carapace widths, which may be due to the lower ambient temperatures (20°-27° C) experienced during the experiment. Robertson (1989) also gives the relationship between premoult (X) and postmoult (Y) carapace widths as:

$$Y = 1.86 + 1.16\ X.$$

On average about 15 moults are required for a mangrove crab in Queensland to reach 150 mm CW, the size at which it matures sexually and may legally be taken according to local fishery regulations (Fielder and Heasman, 1978).

Le Peste *et al.* (1976) concluded that it is not possible to estimate the growth rate of mangrove crabs from analysis of length-structured data (*i.e.* length-frequency mode progression), presumably because of asynchrony in settlement and moulting. However from an analysis of mean sizes of crabs sampled each month they believed they could detect the same "cohort" recruiting to the estuarine environment that was present in the mangrove environment some eight months previously. This led them to conclude that between the sizes of 6 and 15 cm CW male crabs grow at a rate of about 2.7 cm mo^{-1}, and females grow 2.3 cm mo^{-1}. This is a considerably higher rate of growth than has generally been derived from other more conventional methods such as tagging (Hill, 1982) and repeated measurement over time of crabs in aquaria or pond culture situations (Ong, 1964; Raphael, 1970; Tamura, 1970), thus should be treated with caution.

MORTALITY

Very little work has been done on the estimation of rates of natural, fishing or total mortality in mangrove crabs. The only published mortality estimates for *S. serrata* are by Hill (1975), in an unexploited crab population in Kleinemond Estuary (South Africa), which, during the period of the study, was open to the sea only intermittently, after heavy rain. Because of this, recruitment was presumably nonexistent or at best minimal. On the basis of a time-series of monthly catch-per-unit-effort research trapping data over a 2.5 yr period, Hill (1975) calculated a natural mortality rate of 41 per cent (M = 0.53) during the crabs' second year of life, and 60 per cent (M = 0.92) during their third year. These estimates of natural mortality were derived from an unusually simple biological system, with no fishing mortality (apart from that due to the sampling process), and no recruitment. For this reason the figures should be used only as a general guide to possible mortality rates in mangrove crab populations at other locations, where predator-prey relationships and environmental conditions might be substantially different.

Care is needed when attempting to derive mortality figures for any animals whose ages are impossible to determine directly, and whose populations are being replenished by recruitment. Crabs lack the scales and bony structures used to age vertebrates, and often stop growing when they have undergone a certain number of moults, so that body size (particularly in larger animals) is not a good measure of age. The use of tag release-recapture methodologies to estimate mortality in crabs also requires careful evaluation, because reliable estimates of tag mortality and the effect of tagging on moulting have not been adequately documented.

Natural predators of the mangrove crab's planktonic larval stages have not been identified, but presumably comprise zooplanktivorous fish and possibly nektonic coelenterates. In the estuarine mangrove "nursery" habitat the post-settlement megalopae and juvenile crabs are subject to predation by wading birds such as herons (Mukherjee, 1971) and a variety of demersal fish and other crustacean species. Larger mangrove crabs have been recorded in the diets of tiger sharks (Crosnier, 1962), and Taylor (1979) found crab remains in one of the 289 crocodile stomachs examined. Large fish and possibly turtles may also be natural predators of *Scylla* (Fielder and Heasman, 1978).

The parasitic barnacles *Octolasmis, Loxothylacus* and *Sacculina* may have an adverse effect on survivability of severely infested crabs. Hashmi and Zaida (1964) believe that *Octolasmus,* a commensal cirripede which grows upon the gills of the crab, may increase mortality by reducing respiratory efficiency. Quinn and Kojis (1987) argued that this should be reflected in indicators of general biological function such as the gonosomatic index (GSI), but these authors found no significant differences in GSI between parasitised and "clean" mangrove crabs. In any case, as Mounsey (1990) points out, the crabs rid themselves of these unwelcome intruders each time they (the crabs) moult. *Sacculina* and *Loxothylacus* are rhizocephalid barnacles which cause the host to behave as an ovigerous female but, through a process known as "parasitic castration", render it incapable of reproduction (Hill, 1982). The parasite forms a large sac, which is often mistaken for an egg mass, beneath the crab's tail flap. Mounsey (1990) found about 10 per cent of undersize females, but no large females, were infested by the parasite. About 1 per cent of legal sized females (>130 mm CW in the Northern Territory) showed signs of having been infested previously (they were sterile and exhibited male morphological characteristics), and he concluded from this that the parasite causes a high level of mortality amongst the females it infests. An alternative explanation, however, is that the "females" were in fact parasitised males which retained some of the male characteristics but exhibited a female-like broadening of the tail flap.

RECRUITMENT

The absence of a reliable quantitative method of estimating the size of populations of post-settlement and juvenile mangrove crabs means that it is difficult to estimate rates of recruitment of small crabs to the habitat in which they become vulnerable to exploitation.

Hill (1982) reported a plankton sampling programme in southern Queensland estuarine waters designed to measure the rate and seasonal pattern of recruitment of the megalopa stage. While megalopae of the related sand crab *Portunus pelagicus* were quite abundant (sometimes numbering more than 1,000 individuals per 10-min plankton tow), mangrove crab megalopae were rarely caught. Those that were captured appeared in samples collected between November and June (*i.e.* from early summer to early winter). The reason for the small numbers is unclear, but may be a function of larval behaviour in relation to the sampling device. Hill (1982) concluded that more work is needed to clarify the relationship betweeen spawning areas and inshore settlement zones.

Mounsey (1990) reported the occurrence of large numbers of small (2 - 7 cm CW) juvenile crabs aggregating on the seaward margins of sandbars at the mouth of the Roper River, Northern Territory, during May 1988 (*i.e.* in the middle of the northern tropical dry season). This observation fits in with the timing of megalopa appearance in more southerly latitudes reported by Hill (1982). Few attempts have been made to quantify the recruitment of post-settlement crabs, but the sampling system of uniform artificial habitats used by Hill *et al.* (1982) may be an appropriate starting-point.

Recruitment success has been estimated by Le Peste *et al.* (1976) through an examination of changes in the mangrove crab catch at a time when the crabs would have been 5 - 6 months old. These authors presented evidence that recruitment (at least at the latitude of their sampling area in Madagascar) is seasonal and inversely related to rainfall. They argued that the latter may be due to strong seaward surface currents generated by river flow, which carries the larvae out towards the open sea, away from their nursery habitat. Forbes and Hay (1988) however found that a major cyclone, with associated flood-scouring of the intertidal habitat, sustained strong outflow currents and reduced salinity levels, had little measurable effect on either the resident population of adult mangrove crabs or recruitment of megalopa larvae to the St Lucia estuary in Natal, South Africa.

In latitudes closer to the equator recruitment appears to have little seasonal component and, for example in the Labu estuary of PNG, is nearly continuous throughout the year (Quinn and Kojis, 1987). This is attributed to the non-seasonal nature of reproduction (Arriola, 1940; Perrine, 1978), which also contributes to the lack of any distinct year-class structure in the population (Quinn and Kojis, 1987).

III. EXPLOITATION AND DISTRIBUTION OF STOCKS IN THE SOUTH PACIFIC

FISHING METHODS

Techniques for capturing mangrove crabs vary between localities, and their effectiveness depends to a large extent on operator skill and local knowledge. The simplest method, described for the Purari Delta (PNG) fishery by Opnai (1979), involves villagers walking through the mangrove forest and collecting crabs by hand, or with the aid of a crab hook. The use of a suitably-shaped hooked stick or metal rod can facilitate the removal of mangrove crabs from their burrows as well as from beneath their log and mangrove-root shelters, and is also described as a capture technique in India (Hora, 1935; Premkumar and Daniel, 1971), Australia (Stephenson and Campbell, 1960; Fielder and Heasman, 1978), and Pohnpei (Perrine, 1978). Considerable expertise is required to avoid damaging the crab with the hook, and, as careless hooking can also damage the burrows (making them unoccupiable for other prospective tenants), Fielder and Heasman (1978) suggested that the use of this gear should be discouraged.

Nets of various types are used to catch crabs in lower intertidal and subtidal areas. Motoh (1979), Perrine (1978) and Yamakawa (1978) describe the use of gill nets, which are set at the edge of the mangrove swamp to catch crabs as they move into deeper water on the falling tide. Circular baited "dillies" up to 1 m in diameter with a mesh bag attached are used in Australia (Stephenson and Campbell, 1960; Fielder and Heasman, 1978) and Mozambique (Piatek, 1981). An inverted version of the dilly, known as the "witch's hat" or suicide dilly (Fielder and Heasman, 1978), consists of a cone of fine-mesh net supported at its apex by a small float, and with a bait in the centre of the circular frame. In attempting to reach the bait, the crab becomes tangled in the mesh. Widespread use of this sort of gear is also not recommended, as the mesh can easily be damaged by large crabs and small crabs are frequently injured or killed during removal.

In more highly developed mangrove crab fisheries, crab traps or pots are the standard unit of fishing gear (Fielder and Heasman, 1978; Motoh, 1979; Jones and Sujansingani, 1952; Hill, 1982; Robertson, 1989). Numerous designs have been tried, including a compact collapsible model described in detail by Hill (1982). Typically, however, the trap is a circular or rectangular box covered with mesh (plastic, wire-netting or welded mesh) with two simple horizontally flattened entry funnels projecting a short distance into the interior. Access for removing the catch and rebaiting is via a small hinged door, which may be secured by a wire hook at the end of a length of innertube rubber.

Other less common catching techniques include spearing (Premkumar and Daniel, 1971), hunting at night with torches amongst turtle-grass clumps and stands of macrophytic algae on semi-exposed sandy reef flats during very low tides (Perrine, 1978), stringing baited lines across creeks (Hora, 1935), using dip nets (Premkumar and Daniel, 1971) and long-handled scoop-nets at night with the aid of torches. Fielder and Heasman (1978) consider the latter rather unproductive in Queensland, Australia, because it yields mainly undersized and female crabs which must legally be returned to the water.

MANGROVE CRAB FISHERIES IN THE SOUTH PACIFIC

Stock Distribution: The largest populations of mangrove crabs are found in areas where silty riverine deltas have dense tropical to sub-tropical mangrove forests. The most productive and important fisheries for *Scylla* tend therefore to be located on the coastal fringes of large land-masses which, because of their size, support a catchment area sufficient to feed substantial permanent rivers. For this reason it is not surprising that relatively few Pacific islands rank mangrove crabs amongst their most important marine resources. The general absence of reliable catch data for mangrove crabs in the South Pacific makes it difficult to determine the importance and development potential of the primarily artisanal fisheries in various localities. The annual catches of *Scylla* in those countries of the western Pacific able to provide estimates of production are shown in Table III.

Despite the apparent low levels of production of mangrove crabs in most of the smaller countries the fishery is frequently regarded as being quite important. The animals can be kept alive out of water for periods up to 6 or 7 days under optimum conditions of humidity and temperature (J. Burke, *pers. comm.*), which is an important consideration in areas where post-harvest processing and transportation facilities may be less than adequate. Setting up a crabbing operation requires a minimal capital investment in plant or equipment, and, as the product is highly regarded in the tourist and restaurant trade, it commands a high price.

One serious gap in our knowledge of mangrove crab populations relates to

Table III. Estimated current annual catches of mangrove crabs (*Scylla* spp.) in south and central western Pacific countries.

Country	Estimated catch (t)	Source
Fiji	80	Market surveys
New Caledonia	<15 ?	S. Delathière (*pers. comm.*)
Solomon Islands	5	A. Wright (*pers. comm.*)
Australia (Queensland)	365 +	Commercial logbooks
(New South Wales)	150 +	S. Kennelly (*pers. comm.*)
Pohnpei	4	M. Gawel (*pers. comm.*)
Kosrae, Yap and Chuuk	<1 ?	M. Gawel (*pers. comm.*)

the question of stock delineation. Systematic relationships within the genus *Scylla* need to be clarified so that researchers and fisheries managers know with some degree of certainty how many species they are dealing with. This will require the use of current technology in population genetics, meristic analysis, and expertise in taxonomic protocol and procedures. It will also require the co-operation of research workers in many countries to ensure that adequate and representative samples are obtained from the whole distributional range. Thorough documentation of the species relationships will be very important for future investigation and analysis of mangrove crab stocks.

Stock assessment: The existence of several comprehensive bibliographies on *Scylla serrata* (*e.g.* Matilda and Hill, 1980; Anon. 1985 and 1989) indicates the considerable amount of literature which has been published on this species. Matilda and Hill (1980) divided their list into 51 topic categories, including biology, life history, ecology, physiology, fisheries and aquaculture, but only four of the 172 annotated references in the bibliography relate to the dynamics of mangrove crab populations. By far the great bulk of published work involves topics which at best provide information of only peripheral value to the assessment and management of mangrove crab resources. It should therefore be of interest to those concerned with managing *Scylla* stocks that the one major mangrove crab research programme presently underway in the South Pacific region (S. Delathière, New Caledonia) is investigating recruitment and mortality processes, predation, and the dynamics of the local crab population.

Fisheries authorities in a number of places (*e.g.* Fiji, Pohnpei, and New Caledonia) recognise the value of their mangrove crab stocks and are concerned about the possibility of overexploitation. However, because of limited resources few have been able to establish the data-gathering programmes essential for even the most basic stock assessment and population trend analyses. The collection of reliable catch and effort statistics presents problems in fisheries which operate basically at an artisanal/subsistence level with geographically dispersed fishing units and diverse marketing avenues.

Landings of fisheries products (including mangrove crabs) in Fiji are monitored by regular surveys of the main municipal markets and periodic random surveys of other seafood outlets (hotels, restaurants, etc.). General marketing and export information is collected in New Caledonia, and in Queensland logbooks covering all commercial fishing activities have been compulsory since early 1988. With the exception of Queensland there is very little corresponding information on fishing effort, and almost none on the size of the recreational or subsistence components of the fishery. In other areas (*e.g.* Solomons, Papua New Guinea) mangrove crab stocks may well be underexploited, and survey work is needed to determine the extent to which an expansion of fishing effort should be promoted. *Scylla* is known to exist in parts of the Vanuatu archipelago, but no data are available to indicate whether the stocks are large enough to support a commercial fishery.

The greatest information need in the area of mangrove crab fishery management generally is for time-series of reliable catch and effort data, including locality information and a realistic measure of fishing effort which can be used to calculate a CPUE or index of population density. Without such a means of monitoring changes in the size of the stock in different geographic areas regular resource surveys are required, with attendant problems of cost, continuity of personnel, sampling design and fishing technique. If there is no established fishery, surveys may need to be carried out to determine whether there is an exploitable resource available, and to provide a measure of the size of the virgin stock.

Table IV shows trends during the last decade in South Pacific countries and states where some comparative crab production data or estimates are available. It should be borne in mind that, because these figures are not weighted by any measure of effort, they may not necessarily reflect trends in population density. This data set also demonstrates the problems associated with only partial coverage of the fishery. For example, the steady decline in mud crab landings at the Queensland Fish Board between 1980 and 1986 would suggest a serious depletion of the stocks, but in fact resulted to a large extent from a diversification of markets, with a progressively smaller proportion of the total catch being sold through the Board. The 1988-1989 figures obtained from commercial logbooks are far more accurate, but they still provide no information on the size of the recreational catch. Fisheries authorities and researchers are concerned that mangrove crab stocks in southern Queensland may already be fully exploited (Hyland, 1986). Delathière (*pers. comm.*) also points out that a period of heavy exploitation in the early 1980s to supply mangrove crabs for export to Tahiti may have had a detrimental effect on the New Caledonian stock. After a peak probably exceeding 30 t in 1983, catches dropped to around 18 t in 1986, and, although official data are not yet available, there is some evidence that the decline has continued in the last few years. The absence of effort data, however, makes it difficult to interpret the wide variations in landings data collected by New Caledonian fisheries staff (Delathière, 1988 and [in part] Table IV).

Table IV. Annual trends in mangrove crab landings in selected western Pacific fisheries. Quantities indicated are in metric tonnes, and nd = no available data.

Country	1980	81	82	83	84	85	86	87	88	89	90
Fiji[a]	46	40	47	111	85	78	138	131	124	80	nd
Queensland[b]	54	46	41	25	22	11	4	14	278	361	364
New Sth Wales[c]	150	125	60	70	100	70	75	est	nd	nd	nd
N. Territory	nd	8	nd	nd	28	nd	105	129	88	96	128
N. Caledonia[d]	1	13	15	30	19	20	17	nd	nd	nd	nd
Pohnpei[e] [4.8 t in 1977]											4

[a] Includes sales at municipal markets and other outlets, but no subsistence catch (A.D. Lewis & S. Sharma, *pers. comm.*)

[b] Queensland Fish Board sales (1980-87); compulsory logbook data (1988-89), with pro-rata estimate for 1990.

[c] Sydney Fish Market sales data (S. Kennelly, *pers. comm.*).

[d] Voluntary monthly declarations of catches (presumably underestimating actual landings) to New Caledonian Fisheries Dept. personnel (S. Delathière, *pers. comm.*).

[e] 1977 figure from Perrine (1978); 1990 figure, which includes 3.2 t estimated subsistence catch, from M. Gawel (*pers. comm.*).

A few studies have estimated production rates and numerical density which could provide a guide to the size of a potential crab resource in a mangrove habitat of known area. Hill (1975) used tag-release-recapture methods on a population in the unexploited 25.5 ha Kleinemond Estuary (South Africa), estimated population density at 1 crab/124 m^2 (= approx. 80 individuals ha^{-1}), a standing stock around 4.5 g m^{-2}, and (assuming an average age of 16 mo), a production rate of 3.4 g m^{-2} yr^{-1}. Estimates by Williams and Hill (1982) of the size of the adult mudcrab population in Pumicestone Passage (Moreton Bay, Queensland), again using tagging methods, yielded densities of between 2 and 12 individuals ha^{-1}, while in the St Lucia Estuary, South Africa, Hill (1979) estimated a total population of 180,000 individuals (presumably adults), at a density of between 4 and 34 individuals ha^{-1}.

A series of brief tagging experiments on various parts of the Queensland


Scylla serrata (Mud crab)

coast (Hill, 1982) produced density estimates ranging from 2.0 crabs ha^{-1} (upper Coochin Ck, Bribie Passage) to 11.0 crabs ha^{-1} (Garden Is., Great Sandy Strait), with an average of about 5 crabs ha^{-1}.

If commercial capture methods (such as trapping or potting) are used to monitor populations of mangrove crabs, it is essential that sources of variability in the data be identified. Seasonal (temperature-related) cycles of feeding activity, which influence trapping behaviour and therefore catch rates, are well known. Williams and Hill (1982) showed that size-frequency distributions of the catches from crab pots are biased towards larger animals and that the presence of a crab in a pot reduces the probability of further captures. Water temperature and the incidence of recently-moulted crabs in the population account for a large part (66 per cent) of the variation in monthly catches, and the authors were able to fit the following regression catch model

$$\text{Catch (numbers)} = -23.189 + 3.688\ T - 1.199\ M$$

where T = ambient water temperature (°C) and M = percentage of recently moulted crabs. Williams and Hill (1982) concluded that the catch-per-unit-effort can be used as a measure of relative abundance provided allowance is made for temperature and moult state, but they did not recommend the use of mark-release-recapture methods because of cost involved, and bias in data collection.

In a more recent study of the influence of various factors on pot catches and population estimates, Robertson (1989) demonstrated that traps which were cleared every two hours over a 24 hr period yielded higher overall catches than those which were not cleared. This was attributed to a trap saturation effect. There was no significant difference between night-time and day-time catches, nor was there any noticeable increase in the catch if the trapped crabs were prevented from eating the bait. Estimated saturation levels varied widely (from 0.8 to 6.1 crabs $trap^{-1}$) within traps of identical design. Robertson (1989) argues that, because CPUE (*i.e.* catch per trap-hour) decreases with soak time, it is not a good index of population abundance, and he recommends investigating either the use of the asymptotic catch of regularly cleared traps, or the rate at which this asymptote is approached, as an index of abundance.

Hill (1978) and Hyland (1984), using ultrasonic transmitter tags and conventional Floy T-bar anchor tags respectively, have shown that while *Scylla serrata* is essentially non-territorial, it moves only modest distances (<500 m $night^{-1}$, and <4 km over a 36-week period). This suggests that a carefully planned local depletion experiment using traps might be an alternative to tag recapture methods as a means of estimating absolute population density and catchability coefficients provided catch rates are reasonably high. Density figures derived this way could then be related to measurements of habitat area (e.g. from aerial photographs or satellite imagery) to obtain an estimate of total stock size. Knowledge of the catchability coefficient (*i.e.* the proportion of the stock removed by one unit of fishing effort) is clearly very useful, as it provides a means of estimating total stock size from CPUE data.

Tags of various types have been used to mark and identify mangrove crabs in several studies. In a study designed to estimate the growth rates and density of crabs in a closed South African estuary, Hill (1975) used numbered Floy FD67 anchor tags applied with a Dennison tagging gun. The tags were inserted into the posterior region of the crabs at the junction between the carapace and abdomen. To avoid damaging the dorsal abdominal artery, the tags were located slightly off-centre. The advantage of applying the tag in this position is that when the animal moults , the thoracic part of the carapace separates from the abdominal part along this suture. This allows the tag to remain embedded in the flesh and minimises snagging on the exuvium. Hill (1975) reported that of the 2,100 crabs released in the estuary, 140 (6.7 per cent) were recaptured and that the tagging procedure caused little behavioural disturbance.

Hyland *et al.* (1984) used the same technique for marking mangrove crabs in a Queensland estuary to determine the extent of their movement between Morton Bay and the adjacent intertidal mangrove habitat. Recapture rates after the first week of liberty ranged from 9.3 per cent to 14.4 per cent at the various sites within the study area. Including first-week recaptures, the overall recapture rate was 18.9 per cent. Williams and Hill (1982) also used Floy FD67B anchor tags to determine the effectiveness of tag release-recapture studies for estimating population abundance. These authors concluded that while tagging methods provided little more information on relative population size than CPUEs (sample trap catches), they did indicate the absolute size of that part of the population vulnerable to pot or trap capture as well as providing valuable information on the degree of bias in the capture method.

Hill (1978) used ultrasonic transmitter tags (K-Dan Systems, Tucson, Arizona, USA) to track the movements of mangrove crabs in the Kowie Estuary, South Africa. These tags consisted of a miniature transmitter housed in a 55 mm x 60 mm plastic cylinder which was clamped to the crab's dorsal surface. The tags emitted a pulsed (1-2 Hz) signal of a frequency between 70 and 80 kHz. Directional hydrophones fitted with magnetic compasses were used to determine the location of the tagged crab by triangulation. The maximum distance over which the signal could be transmitted was about 350 m.

No attempt has yet been made to establish a stock-recruitment relationship for mangrove crabs. There is a general attitude (*e.g.* Perrine, 1978) that because of their high fecundity and the migratory behaviour of ovigerous female crabs, the stock could be reduced to a very low level before there was a measurable effect on recruitment. Studies of various crab fisheries in the United States (*e.g.* More, 1969) have failed to demonstrate significant relationships between recruitment and parent stock size and concluded that factors such as salinity, temperature, food supply and natural predation are more important than the number of eggs produced in determining population levels. This may well be true at modest levels of exploitation, but in any population there is a stock size below which recruitment will be adversely affected. Detection of this critical point will be difficult, as it may well change substantially depending on prevailing environmental conditions. If, for example, ocean currents in a particular year are unfavourable for the shoreward transportation of the crabs' pelagic larvae, recruitment could be severely limited regardless of the numbers of spawners in the parental stock.

Development of a stock-recruitment relationship in mangrove crabs would require not only accurate catch and effort statistics from the entire fishery (recreational as well as commercial), and a sufficiently flexible management system to provide the necessary year-to-year contrast in fishing effort, but also the exploitative capacity actually to reduce the stock size to within the critical region so that a response may theoretically be observed. Even if these conditions are met, system "noise" due to undocumented environmental changes would make any estimate imprecise. To derive even a basic understanding of how factors such as ocean current patterns, larval dispersal mechanisms and behaviour interact and influence recruitment success in a quantitative sense would require a major research effort.

An important aspect of this relationship concerns the spawning success of the parental stock. The early estuary-based phases of the reproductive cycle are reasonably well documented, but further study is needed 1) to determine the proportion of potential spawners which migrate offshore and what happens to them after their eggs hatch, and 2) to characterise spawning areas in terms of geographical location and the stratum of the water column in which spawning occurs. Consideration might also be given to investigating the environmental conditions which favour postlarval settlement and developing techniques for enhancing the "settlement potential" of estuarine areas where for one reason or another recruitment success is low. In its simplest form, this might merely involve the deployment of artificial shelters to reduce mortality amongst post-settlement juvenile crabs.

Resource management: Perrine (1978) reviewed management regulations relating to mangrove crab fisheries in various parts of the world. (1) No regulations existed in the Philippines or American Samoa. (2) Fiji had introduced a minimum legal size of 5" (127 mm) carapace width. (3) Certain areas of Palau had legislated a minimum legal size of 5" (127 mm) CW, and closed seasons. (4) There was a minimum legal size of 6" (153 mm) in Hawaii, and a prohibition on taking mangrove crabs by spear. (5) Although no commercial fishing for mangrove crabs was permitted in South Africa, recreational crabbers were entitled to a bag limit of two crabs per day with a minimum carapace width of 120 mm. (6) The Queensland regulations provided for protection of mangroves and burrows, protection of male crabs under 150 mm CW and all females, prohibition on the use of explosives, noxious substances and tangle nets, and licensing of persons selling crabs.

In Pohnpei the only fishery restriction relating to mangrove crabs was a prohibition on commercial export, although *Scylla* was temporarily exempted from this in 1977. Perrine (1977) cited a survey carried out at about the same time by K. McHugh, who found that, of the fisheries organisations in 16 places contacted, only Australia and Mauritius had introduced legislation aimed at the conservation of mangrove crabs. No such management controls existed in Tanzania, New Zealand, India, Sri Lanka, American Samoa, Chuuk, Thailand, Brunei, Western Samoa, Kiribati, Yap, Solomon Islands, or Hong Kong. Prohibition of the commercial export of *Scylla* remains the only mangrove crab legislation in Pohnpei, and additional research following on from Perrine's (1977) programme has been proposed but not yet funded (M. Gawel, *pers. comm.*).

Since the work of Opnai (1979) in the Purari Delta, no research or monitoring work has been carried out on mangrove crabs in Papua New Guinea, and no legal restrictions have been placed on the fishery (J. Natera, *pers. comm.*). It would appear that the PNG stock is still generally underexploited, as is probably the case in Solomon Islands where attempts have been made to establish a commercial crab fishery to supply the Honiara market. These attempts have evidently met with little success. Proposed resource surveys in Solomon Islands emphasising *Scylla* have not received funding support (P. Nichols, *pers. comm.*), and, not surprisingly, no specific legislation has been introduced (A. Wright, *pers. comm.*).

In New Caledonia there is a closed season during the reproductive period (October - March inclusive), a prohibition on the sale of soft-shelled (post-moult) crabs, and a minimum legal size of 130 mm CW (S. Delathière, *pers. comm.*). As a result of Delathière's (1988) work on the population biology of New Caledonian mangrove crabs, an increase in the minimum size to 150 mm is currently being considered. Recreational crab fishermen are permitted to use a maximum of two pots or traps, but there are no restrictions on the numbers used by commercial crabbers.

The habitat value of the mangrove crab burrow is widely known, and, according to Perrine (1978), "... knowledge of the location of burrows is a [Pohnpei] crabber's most prized possession. If a burrow is not damaged crabs may be removed from it for years." Hill (1982) demonstrated the importance of mangrove and seagrass areas for juvenile mangrove crabs, and argued that protection of these habitats may be essential for maintaining the crab resource. Current legislation in Queensland provides for the conservation of coastal mangrove ecosystems, prohibits unauthorised removal of mangrove trees and the damaging or destruction of mud crab burrows. The effect on the population of removing the protective burrows from an otherwise unchanged habitat has not been investigated, but it may expose the animals to increased natural mortality, or for behavioural reasons reduce their availability to the fishery.

Female mangrove crabs may not be taken by either commercial or recreational fishermen in Queensland, and the minimum legal size for male crabs is 150 mm CW. These possibly conservative measures are designed to ensure the maintenance of the spawning stock by allowing crabs to reproduce before being exposed to fishing mortality and prevent the possibility of gamete limitation which could conceivably occur if, through heavy exploitation, the sex ratio became severely imbalanced.

Although not explicitly stated, many effort-restricting management devices have been applied to mangrove crab fisheries to minimise the risk of recruitment overexploitation. Containment of fishing effort is an important component of mangrove crab management in Queensland, and is addressed through restricted entry to the fishery, by limiting the number of pots, traps or dillies to 50 (for commercial crabbers) and four (for recreational crabbers), and by a year-round recreational bag-limit of 10 crabs.

The value of coastal wetland habitats to various life-history stages of many important marine fishery resources is becoming more and more widely recognised. Mangrove habitats are of particular interest, as they appear to be an essential component of the life cycle of species such as *Scylla serrata*, and it might well be argued that similar effort should be applied to the assessment and management of the animal's habitat as to the mangrove crab resource itself.

ACKNOWLEDGMENTS

Sincere thanks are due to the fisheries officers who responded so promptly to my requests for information on the status of crab fisheries in various parts of the Pacific. The Southern Fisheries Centre editorial committee provided useful comments on the manuscript, and I am particlarly indebted to Dr Burke Hill and Mr Stuart Hyland for reviewing the document and giving their valuable technical advice.

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The following list of references is not meant to be representative of the literature on *Scylla serrata*. It refers, for instance, to few papers on mud crab aquaculture or experimental physiology, for both of which fields there is an abundant literature. It does, however, provide most of the important biological and management-oriented references, as well as related material cited in the text. The availability of comprehensive annotated bibliographies on mangrove crabs (e.g. Matilda and Hill, 1980, and the regularly updated SEAFDEC compilations, Anon., 1985 and 1989) makes the production of another exhaustive bibliography unnecessary.

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