

## CHAPTER 19

# Coconut Crabs

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### I. INTRODUCTION

The coconut or robber crab is the largest land dwelling crustacean and one of the most highly terrestrialised decapods. The species is distributed throughout the tropical Indo-Pacific, where its large size, strange appearance and habits along with a distinctive flavour, have made it a topic of special interest for scientists, naturalists and explorers for centuries.

Coconut crabs have excellent culinary properties and are a highly prized food item throughout their range. They often have special significance for ceremonies such as weddings and are reputed to have aphrodisiac properties in some areas (Brown and Fielder, 1988). More important, they are also served in restaurants, particularly those frequented by tourists who enjoy the novelty of the crab's folk-lore as much as the taste.

Because the crabs live on land, they can be caught easily using methods that require minimal investment; being relatively valuable they constitute a ready source of income for people in more remote areas where income generating opportunities are rare. The increase in tourism that has occurred in most countries where the crabs are present, together with the decline in copra production and prices in the past decade, has meant that the rates of exploitation on the crabs have increased greatly in certain areas.

There has been concern about an apparent decline in crab numbers in many regions for over 30 years (Holthuis, 1959), and in some places they are now virtually extinct (Amesbury, 1980). It is important that the scenario of declining abundances leading to local extinction does not repeat itself at all locations where the crabs are presently found. Thus, the rational management of this resource should be of vital importance to the governments of all countries with surviving populations of crabs.

The basis of any management policy is an understanding of the biology and life-history of a species. Much has been written about the coconut crab, they were reported as long ago as 1705 by Rumphius, and there have subsequently been over 200 reports and publications written about this species (Reyne, 1939; Davis and Altevogt, 1978; Wells *et al.*, 1983; Brown and Fielder, 1988). Most of these papers, however, are of an anecdotal nature and in many cases the

information reported has not been observed by the author. Relatively few have yielded significant new information about this species. Nonetheless, sufficient work has been done particularly in Palau and Enewetak by workers for the University of Hawai'i, and more recently by a study funded by the Australian International Centre for Agriculture Research (ACIAR) in Vanuatu to establish the basics of its biology and fisheries potential.

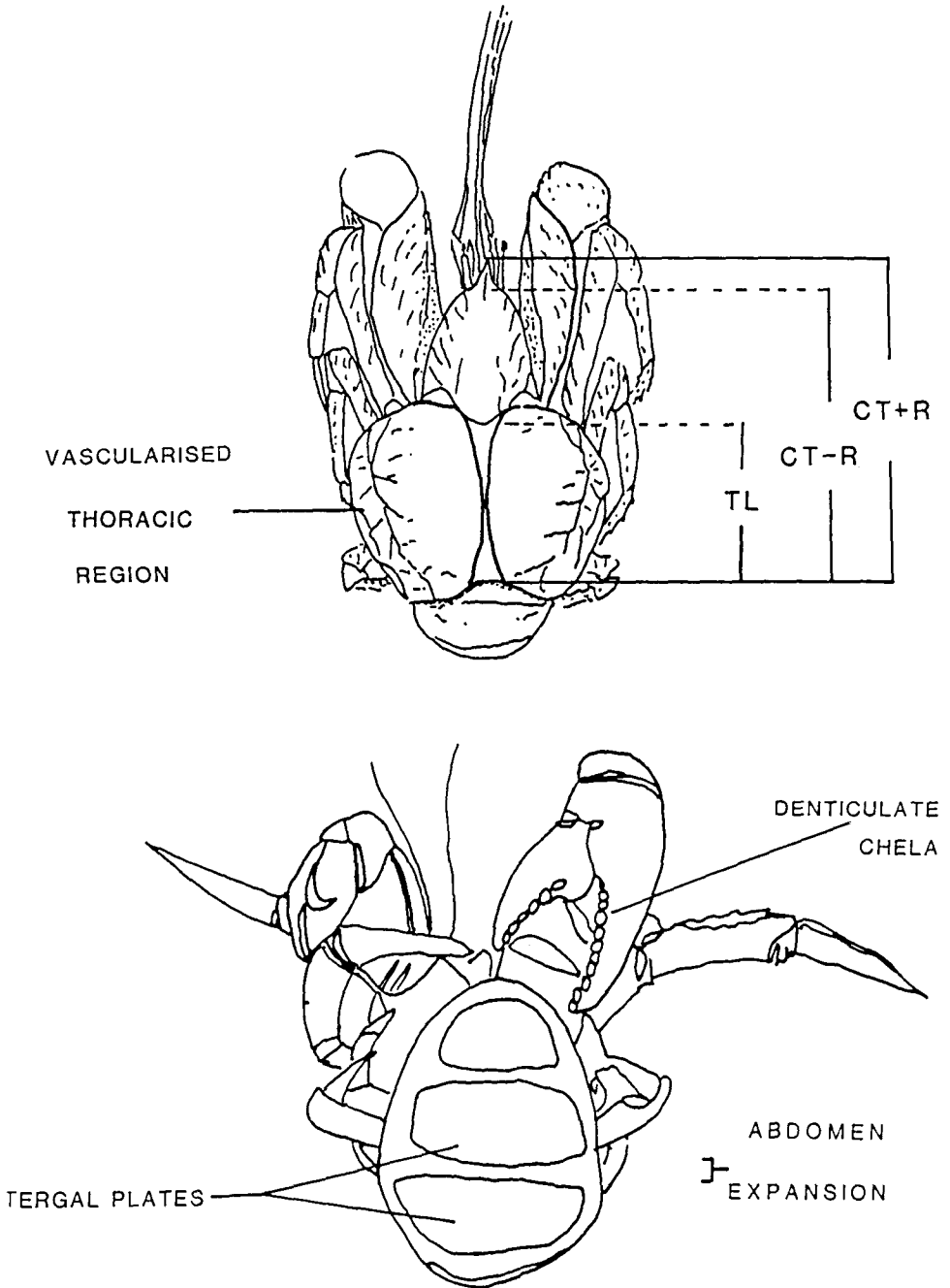
## II. TAXONOMY AND DESCRIPTION

The coconut or robber crab, *Birgus latro* (Linnaeus), obtained its name from a reputation for stealing nuts from coconut trees (hence the specific name *latro* which is Latin for "robber"). They belong in the Phylum Crustacea, Class Anomura, Family Coenobitidae, which includes most of the land-based hermit crabs. *Birgus* is a monospecific genus because *B. latro* is the only member of the group which, as an adult, dispenses with the general hermit-crab trait of protecting its abdomen with an empty gastropod shell. Instead, the abdomen is tucked partially underneath the body and is protected on the dorsal surface by a series of hardened tergal plates (Fig. 1a). The remainder of the abdomen is covered with a leathery skin bearing tufts of small bristles.

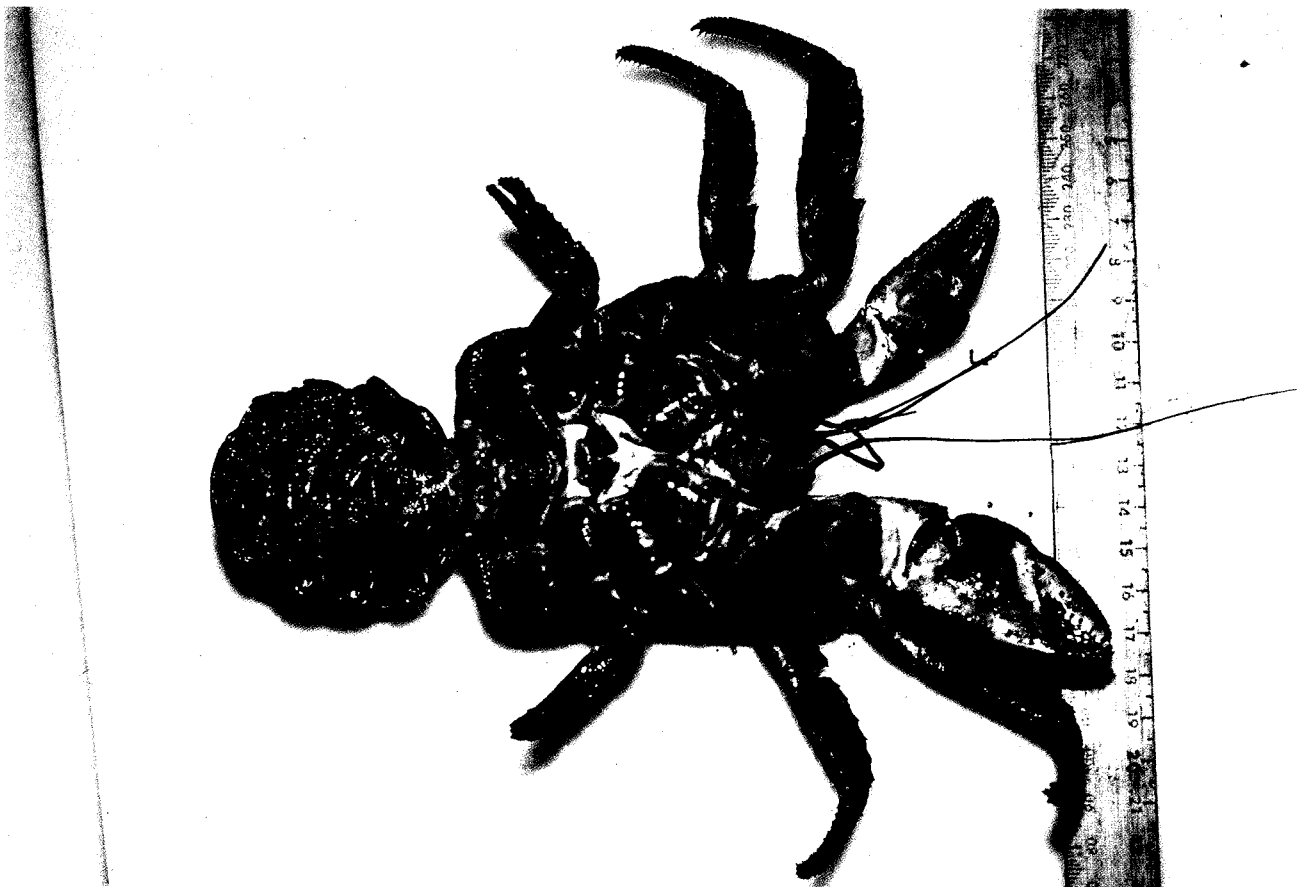
The color of the carapace varies between areas and among individuals within an area. Most crabs are a deep blue colour (e.g. Palau, Helfman, 1973; Guam, Amesbury, 1980; Vanuatu, Fletcher *et al.*, 1990b), although a few may be tinged with red (e.g. in Northern Vanuatu, *pers. obs.*). However, in some places such as the Seychelles, the crabs are all nearly completely red (Altevogt and Davis, 1975).

Coconut crabs have two chelae (claws), the large left claw and a smaller right claw both of which have a denticulate appearance (Fig. 1a). They have two pairs of long walking legs (peripods) and a smaller pair of appendages equipped with small claws. Female crabs use these clawed 'legs' to tend to their egg masses, and males probably use them to assist in the transfer of spermatophores. Female crabs are readily identified by the presence of three large, feathery pleopods on the ventral surface of the abdomen (Fig. 2) which are used to support their egg-masses.

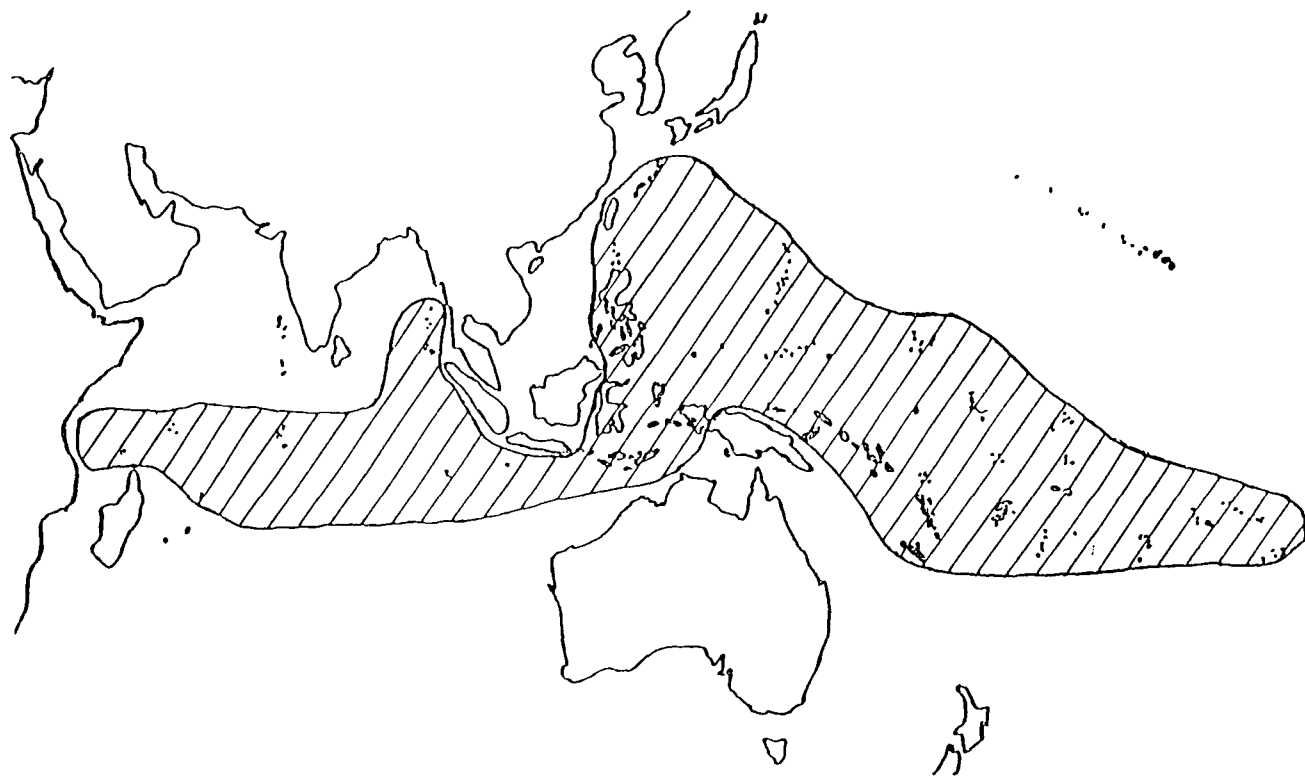
The crabs have only vestigial gills and will drown if left in water for more than an hour or so (Gross, 1955). The gills' respiratory function is greatly reduced (Smatresk and Cameron, 1981; Greenaway *et al.*, 1988) and has been taken over by the inner lining of the gill chamber located in the thoracic region (Fig. 1b). This highly vascularised tissue has a large surface area and a thin epithelium required for gaseous exchange (Storch and Welsh, 1984). Ventilation of these "lungs" is provided by the paddle like scaphognathites (part of the remnants of the gills) which draw air forward through the lung (Cameron and Mechlenburg, 1973; Storch *et al.*, 1979; Greenaway *et al.*, 1988).



**Figure 1.** Diagrams of coconut crabs showing major features and methods of measurement. TL thoracic length, CL - cephalothoracic length, R - rostrum.



**Figure 2.** Photograph of a female coconut crab showing the three feathery pleopods on the abdomen which are used for sex discrimination. These pleopods do not occur on the male crab. Photo: Warwick Fletcher.



**Figure 3.** Distribution of the coconut crab, from Reyne (1939) after Lavery and Fielder (1991) indicating the sites used in their electrophoretic study.

The length-weight relationship was calculated by Amesbury (1980) as  $W = 0.0077 TL^{3.008}$  where TL refers to the length of the thoracic region (Fig. 1b). In coconut crabs this measurement is preferred to the cephalothoracic length (CL) because the latter includes the rostrum (R) which is often broken. Helfman (1973) calculated the relationship between these two measurements as  $TL = CL/2.1$ , and the thoracic width is approximately the same as the cephalothoracic length.

### III. DISTRIBUTION

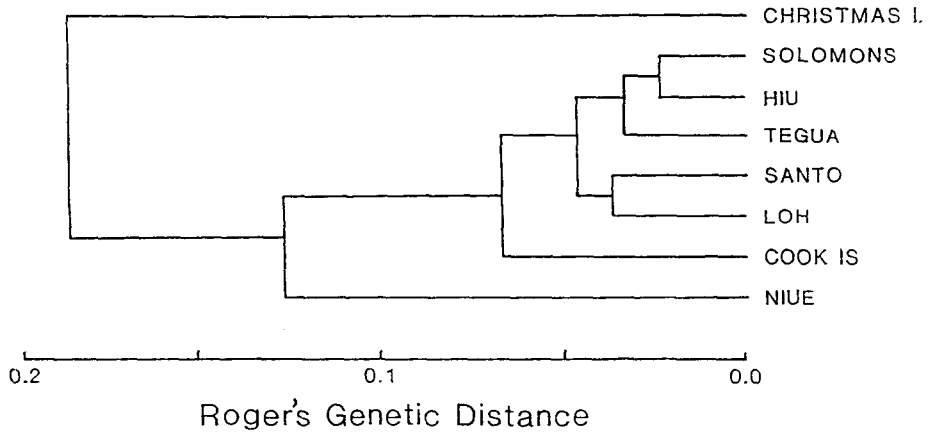
Reyne (1939) provided a detailed account of the world-wide distribution of the coconut crab (Fig. 3) from records of museum collections. Their distribution covers the tropical Indo-Pacific region, from Mauritius in the western Indian Ocean to the Tuamotu Archipelago in the eastern Pacific. The distribution of the crab is very similar to that of the coconut palm itself, an observation which has inspired a number of theories as to the possible means of migration of both species (*e.g.* Davis and Altevogt, 1978; Harries, 1983).

Coconut crabs are common only in island habitats; they have not been recorded from east Africa, the Indian sub-continent, mainland Asia or Australia (Brown and Fielder, 1988). Similarly, most crabs associated with larger islands such as New Guinea have come from off-shore islands rather than the main island. This pattern is thought to be due to the increased numbers of predators and competitors on larger land masses.

Subsequent to Reyne (1939), most data published on the distribution of the crab suggests that its range has already contracted (*e.g.* Holthuis, 1959; Horstmann, 1976; Amesbury, 1980). A mail survey of 28 countries, mainly in the Pacific and South-east Asia (Brown and Fielder, 1988), was conducted in mid-1984 prior to a recent ACIAR-funded study of coconut crabs in Vanuatu. The survey revealed that coconut crabs were at the time considered abundant only in six localities. They were regarded as being generally abundant in Solomon Islands, locally abundant in Vanuatu and Chuuk, Federated States of Micronesia, and generally common in Tokelau, Niue and the Marshall Islands. The remaining countries indicated that the species was either only locally common or rare. Significantly, none of the responses indicated that the crabs were unknown or completely absent.

### POPULATION SEPARATION

Recent studies by Lavery and Fielder (1991), using electrophoretic techniques, have investigated the genetic separation of populations throughout many parts of the crabs' range. They found little genetic differentiation between *Birgus* populations in Vanuatu and Solomon Islands, and they concluded that



**Figure 4. Dendrogram of Roger's genetic differences (relative degree of genetic isolation) found among sites (from Lavery and Fielder, 1991). Sites Loh, Tegua and Hiu are from the Torres Group in Vanuatu. Santo is another island in Vanuatu. Christmas Island is in the Indian Ocean.**

they probably constitute a single stock. There were, however, large differences in genetic characteristics between Indian and Pacific Ocean populations, suggesting two distinct stocks. Furthermore, in the Pacific, there was some indication that coconut crab populations in Niue and the Cook Islands are also separate independent populations (Fig. 4).

## HABITAT

Coastal habitats, particularly those with dense forest cover, are favoured by coconut crabs. The animals generally make use of some type of shelter, such as caves, crevices, tree roots, hollow logs or earth burrows during the day. They are usually found within a few kilometres of the ocean, but some individuals do make their way further inland where conditions are favourable. They are not often found in areas that have been cleared for agricultural purposes.

## HABITS

Unlike the normally gregarious hermit crab, the coconut crab is secretive, living a basically solitary existence (except for gravid females which have been observed at large densities, Schiller *et al.*, 1991). Coconut crabs can be nocturnal, diurnal or both, and it appears that their behavioural pattern is dependent upon local population density and possibly the level of human activity. In areas where they occur at high density and have not been hunted, the crabs are found out of their hiding places during both day and night. However, where their density is lower, especially as a result of harvesting activity, the crabs emerge from hiding only at night.

Daytime foraging may be a mechanism for reducing the number of intraspecific encounters in large populations. Helfman (1977a) showed that the crabs are highly aggressive. When they encounter one another they have a number of ritualistic responses, such as the raising and lowering of the walking legs and claws, which usually result in the smaller crab yielding to the larger. Sometimes these interactions can develop to the point of physical aggression, and one or both antagonists can be seriously injured. Cannibalistic behaviour has been observed, with larger crabs attacking and eating smaller individuals (Altevogt and Davis, 1975; Helfman, 1977a).

After foraging, the crabs often return to a particular crevice or sheltering site (Fletcher *et al.*, 1990a). Estimates of the frequency of foraging activity have varied between studies. Fletcher *et al.* (1990a) found during the dry season, foraging was infrequent (5-10 per cent of nights), in areas where the density was low. This frequency may increase at higher population densities because Helfman (1973) suggested that the crabs emerged every night in Palau, but this could also be due to differences in relative food availability or environmental conditions. Thus, for the same region Reese (1987) suggested that they emerged every night during the wet season and but only every fourth night in the dry season due to the adverse conditions.

Helfman (1973) calculated the home range of crabs in Palau to be 40 m<sup>2</sup>, whereas in Vanuatu it was 250 m<sup>2</sup> (Fletcher *et al.*, 1990a). Their home range may, however, include a number of distinct sites in different areas. On larger islands, the crabs appear not to remain in one area for long. In Vanuatu, few tagged crab released on the large island of Santo were recaptured, whereas on a small islet most of the tagged crabs were recaptured at least once (Fletcher *et al.*, 1990a). Radio tracking confirmed that the crabs on Santo moved away from the point of release after 1-3 months. Available evidence indicates that coconut crabs are basically nomadic but are capable of maintaining a home range (Helfman, 1973).

Some of the movements by the crabs may be due to the need occasionally to reach a source of seawater which is ingested to maintain osmotic balance. Crabs



may need to move away from the rocky cliff regions into the sandy areas in order to moult (Amesbury, 1980; Fletcher *et al.*, 1990b). Finally, females release their eggs in the ocean.

**Opening Coconuts:** One of the more interesting and controversial aspects of the crab's behaviour is its reputed ability to open coconuts. This has been a point of conjecture for many years, and, after a thorough investigation of the literature, Reyne (1939) concluded that, despite the many references to this behavioural activity, none of the authors had actually witnessed the event. The described techniques for opening the coconuts have also differed between the various accounts. The plausible ones include initial de-husking of the coconut by the crab, which then 1) carries the nut up a tree and drops it to crack open the kernel (*e.g.* Cropp, 1982), 2) bashes the nut open with its claw (*e.g.* Davis and Altevogt, 1978), and 3) pokes a hole in the kernel through one of the "eyes" and then snips open the nut (*e.g.* Reese, 1987). The latter method was adopted by captive crabs held in enclosures during the coconut crab study in Vanuatu. The entire sequence, for which a photographic record was made by this author, took several days to complete.

Where coconut crabs live close to a source of coconuts, large quantities of husk and broken kernels are often seen near the entrances to the crabs' lairs (Reese, 1987). This, together with the fact that most of the kernels show evidence of having been broken through the eyes, is consistent with the method described by Reese (1987).

Coconut crabs are sometimes considered to be a pest of the coconut (Davis and Altevogt, 1978), but the most common physical damage done to coconuts in plantations is by rats which bore a hole through both the husk and nut.

**Diet:** The general conclusion of most studies is that the crab is omnivorous and probably a scavenger (*e.g.* Reyne, 1939; Altevogt and Davis, 1975). It is not dependent on the coconut; in fact, viable populations occur in many areas where there are no coconuts. Its major food items appear to be the fruits of pandanus, *Canarium* spp., *Barringtonia* spp. and the breadfruit, *Artocarpus* spp. They have also been cited as eating dead rats, birds and crabs (*Coenobitids*, *Brachyuran*), and occasionally other *Birgus*. In captivity they will eat a wide range of food including chicken-feed pellets (Fletcher *et al.*, 1989; 1990b), rice (Amesbury, 1980), dry cat-food pellets (Morris *et al.*, 1988), dog biscuits (Greenaway *et al.*, 1990) and even the remains of biological specimens fixed in formalin (Altevogt and Davis, 1975).

The crabs drink water of different salinity to maintain their osmotic balance (Gross, 1955). They have often been observed at the ocean shore, dipping their claws and drinking the sea water. They are able to survive for some time solely on either one by altering the volume of intake and by reabsorbing ions and water in the branchial chambers (Greenaway *et al.*, 1990).

## IV. REPRODUCTION

### SEXUAL MATURITY

Although Schiller *et al.*, (1991) observed one berried female which was only 21.8 mm thoracic length, coconut crabs of both sexes generally reach sexual maturity at a size of approximately 25 mm TL (Helfman, 1973; Fletcher *et al.*, 1990b), which is equivalent to an age of about five years (see below).

### COPULATION

Matthews (1956) compared the morphology of spermatophores of *Birgus* with those of aquatic hermit crabs and could find no evidence that coconut crabs have adaptations for non-aquatic sperm transfer. He concluded that copulation probably takes place in water. However in the one reliably documented case (Helfman, 1977b), copulation occurred at night on land with both crabs in the hard-shell condition. After a series of brief courtship displays, the male held the female's chelae with its chelae and pushed the female onto her back. The female held her abdomen flat against the ground and the male, using the modified coxae of the 5th periopod, deposited the white spermatophore over the gonopore at the base of the female crab's walking legs (Fig. 5).

Although other terrestrial hermit crabs are able to utilise a small reserve of sea-water kept in their shells to help with fertilization of the eggs (Matthews, 1956), this is clearly impossible for *Birgus*. Female coconut crabs with sperm packets were often seen partly submerged in shallow sea-water pools in Vanuatu (*pers. obs.*). In these circumstances, it is quite possible that the eggs are extruded through the sperm packet, and, as Matthews (1965) predicted, fertilization may, therefore, take place in sea water. The time interval between copulation and egg extrusion is still unknown, but is probably under two weeks.

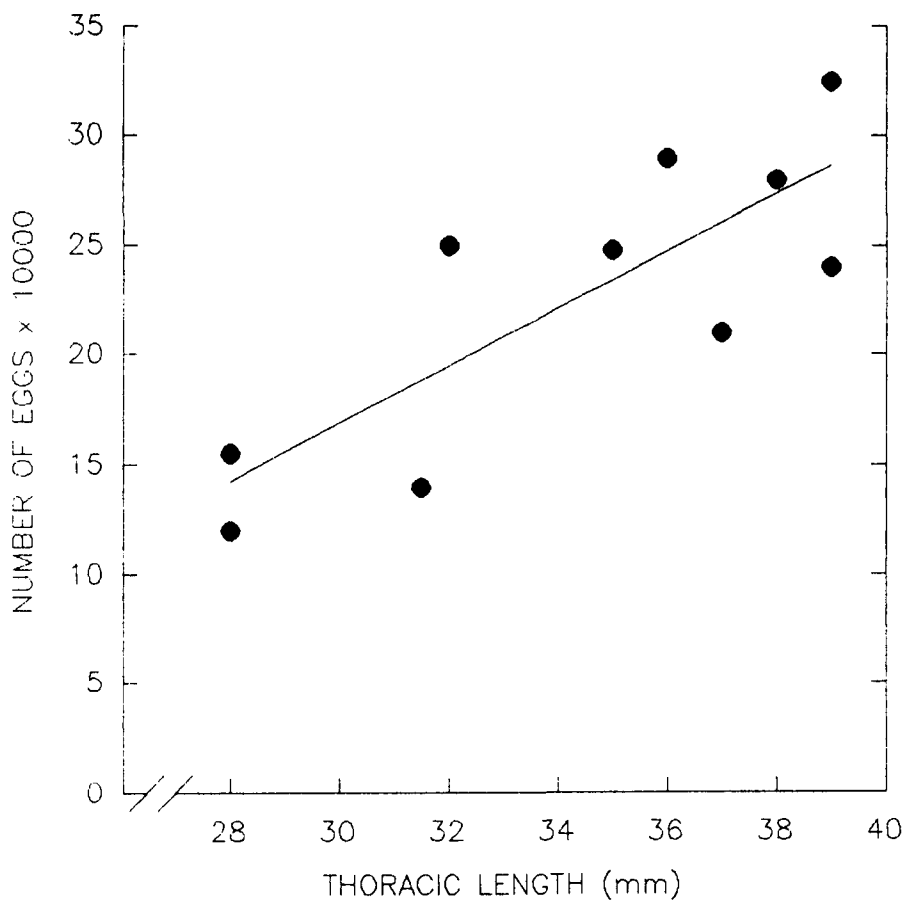
### SPAWNING

Coconut crabs appear to spawn during the summer period in both hemispheres (Reese, 1968; Reese and Kinsie, 1968; Reese, 1987; Schiller *et al.*, 1991). Ovigerous or "berried" females move down to the shore probably before the eggs are extruded. Immediately after extrusion, the bright orange fertilised eggs are attached "like bunches of grapes" to the three pleopods on the abdomen. There is a positive correlation between body size and the number of eggs extruded (Fig. 6; Helfman, 1973).

The gestation period was originally thought to be about three weeks (Reese, 1987), but Schiller *et al.*, (1991) found that egg maturation took between 25 and



**Figure 5. Photograph of position of spermatophore on the female after copulation. Photo: Warwick Fletcher.**



**Figure 6.** Fecundity of coconut crabs of different lengths (modified from Helfman, 1973).



**Figure 7.** Photograph of a berried female caught on her spawning walk. The egg sponge is dark and slushy in appearance. Photo: Warwick Fletcher.

45 days with the difference directed at synchronising the time of spawning. During this period the berried females usually remained in crevices within 100 metres from the shore, often at higher than normal densities (Schiller *et al.*, 1991). These authors used a six-stage classification to describe the development of the eggs. During development, their colour changes and darkens as the embryo's eyespots develop, and immediately prior to spawning they are a dark grey/grey-brown and the egg-sponge is "slushy" (Fig. 7). The osmolality of the eggs has changed from 800 to  $>1,100 \text{ mmol.l}^{-1}$  (Schiller *et al.*, 1991) which may assist with rapid hatching of the eggs.

Spawning takes place at night on rocky coasts, usually within 90 minutes of full darkness. The frequency of spawners in this habitat is greatest when high tide coincides with dusk (Schiller *et al.*, 1991). Thus, observers found a semi-lunar rhythm, with spawning concentrated about the periods of the first and last quarters of the moon. The berried female walks down to the waters edge, ensuring that the egg mass does not come in contact with the water. When it reaches the ocean it either reverses and places its abdomen in the water or waits for a wave to wash over it. Larval release occurs within a few seconds and is usually aided by a vigorous shaking of the abdomen (Hicks *et al.*, 1984; Reese 1987; Schiller *et al.*, 1991). Occasionally if the weather is rough, the females may become submerged briefly by waves, but they usually manage to return to dry land. After depositing the eggs in the sea, females have a white mass on their abdomens, which is merely the empty eggs cases, which the females themselves eat after a few days (Fletcher, *pers. obs.*).

Attempts to maintain berried or ovigerous females have not been successful (Amesbury, 1980; Schiller, 1989; Fletcher, *pers. obs.*). A female with a spermatophore was kept by Helfman (1977b) for one month, but no eggs were extruded and no advanced ovaries were found upon dissection although it may be significant that there was little sea water available in the enclosure. Females with newly extruded egg masses have been kept for up to 2 weeks, but they generally stop tending the eggs almost immediately which then become dirty and infected (*pers. obs.*) or they release the eggs before they are fully developed (Amesbury, 1980). Often the females attempt to destroy the eggs when being captured, and females that are caught on their spawning walk release the egg mass before the following morning. Even if these term crabs are bound to prevent them from physically damaging the eggs, the eggs appear to lose viability and are dead by the following morning (Schiller, *pers. comm.*). One possible explanation is that the eggs have been depleted of all yolk material and that they needed to have been fed to survive.

The only successful artificial hatchings have been performed within a few hours of catching the females on their spawning walk. Hatching these eggs merely involved immersing the egg-mass in seawater.

## LARVAL STAGES

The larvae of coconut crabs were first described by Borradaile (1900), and the first stage zoea have been described a number of times (*e.g.* Orlamunder, 1942; Daniel and Prem-Kumar, 1967; Amesbury, 1980). The complete description of all four larval stages was first made by Reese and Kinsie (1968; Fig. 8) who found that occasionally larvae passed through a fifth stage which may be a way of prolonging larval life. More recently information on the detailed time intervals for various larval stages has resulted from work in Vanuatu (Schiller, 1989). The duration of each larval stage is shown in Table I; and the complete larval series takes between 15 and 28 days, depending on ambient temperatures.

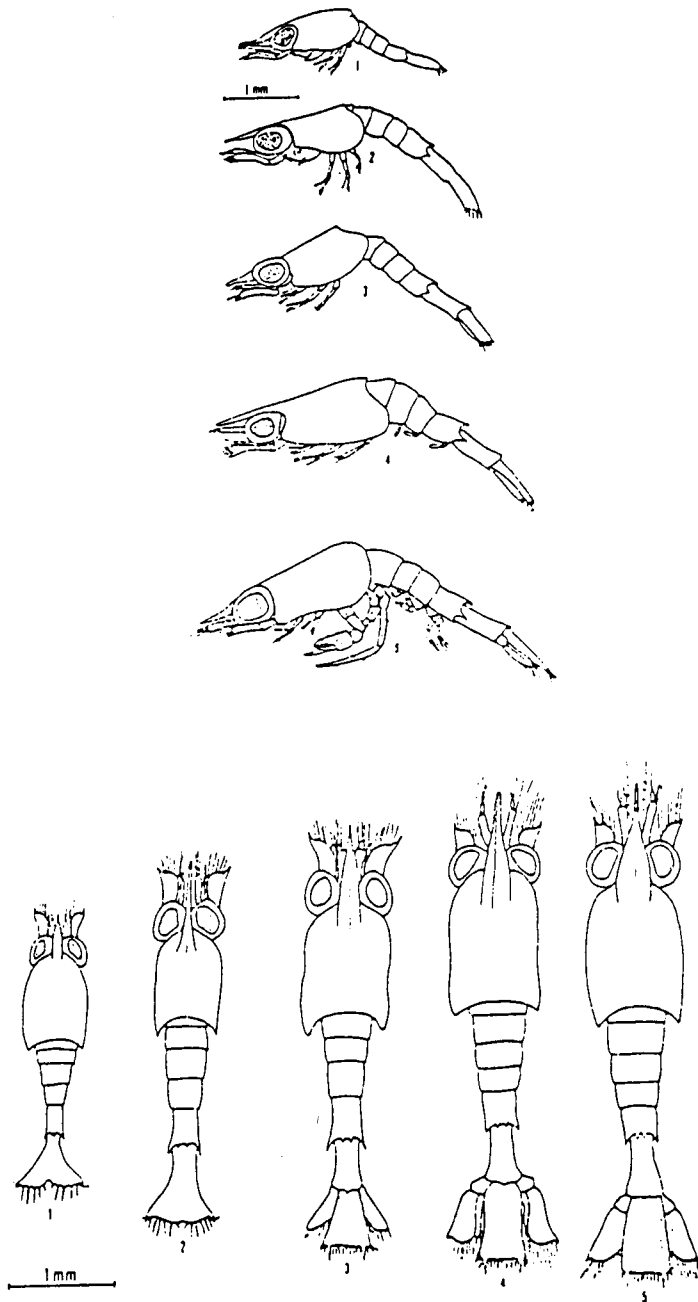
**TABLE I.** Duration of larval stage for the coconut crab, *Birgus latro* (from Reese and Kinsie, 1968).

Stage	Size TL (mm)	Range (days)	Mean (days)	Total (days)
1st Zoea	2.8	4 - 9	5 - 6	5 - 6
2nd Zoea	3.4	3 - 15	3 - 5	8 - 11
3rd Zoea	3.9	3 - 18	8 - 9	12 - 24
4th Zoea	4.3	6 - 18	8 - 9	17 - 38
5th Zoea	4.6	?		
Glaucothoe	4.0	21 - 28		50

Reese and Kinsie (1968) fed larvae a diet of *Artemia* nauplii supplemented with plankton, and obtained high survival rates. Schiller (1989) was successful in obtaining glaucothoe, but he believed that the increased mortality of the later stages in his study was due to the diet being solely *Artemia* nauplii.

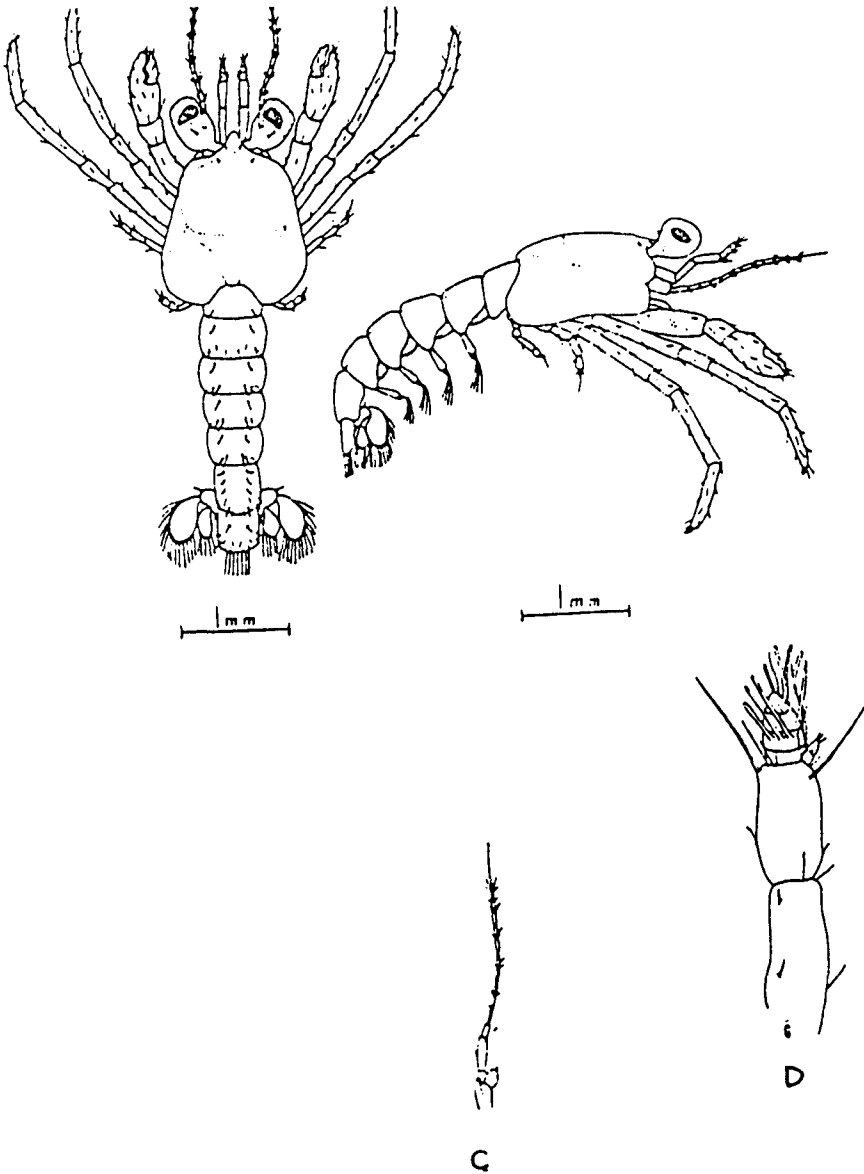
**Glaucothoe (amphibious) Stage:** After the four (or sometimes five) zoeal stages, the larva metamorphoses into a glaucothoe (Fig. 9). This is the benthic amphibious stage of the crab's life-history and one of the most critical in that it appears to be subject to the greatest rate of mortality of all the larval stages. The shrimp-like glaucothoe search for a small gastropod shell to inhabit, thus exhibiting a reversion of its hermit crab ancestry (Reese, 1968). The glaucothoe emerges from the ocean after 10 to 25 days, either with or without a protective shell, and takes up residence in the supra-littoral region of the beach. Reese (1968) demonstrated that unless the glaucothoe found a shell for protection against predators and desiccation, they failed to survive.

The glaucothoe of *Birgus* may be distinguished from other similar coenobitid



**Figure 8.** Zoea larval stages of the coconut crab (modified from Reese and Kinsie, 1968).





**Figure 9. Glaucothoe of the coconut crab, plus enlargements of the antenna (C) and antennule (D) (modified from Reese and Kinsie, 1968).**

glaucothoe by (1) a distinct rostrum, (2) the presence of a single terminal seta on the antenna which is considerably larger than any other setae and (3) the presence of 11 distal segments comprising the antennal flagellum, (other coenobitids have 7; Reese and Kinsie, 1968). Obviously a microscope is required for these criteria to be ascertained.

Rearing of the glaucothoe in captivity is extremely difficult and will represent the stumbling block to any attempt to mass rear these crabs for aquaculture. They are very susceptible to any fouling of the water or area they inhabit and require protection from dehydration (Schiller, 1989). Thus, it may be necessary, if culturing this species, to release the late larval stages into a natural area seeded with suitable small gastropod shells rather than attempting to get them through this stage artificially.

## V. RECRUITMENT

This is one of the least known aspects of the crabs' life-history because the glaucothoe are difficult to locate in their natural habitat (Reese, 1987). Despite extensive and intensive searches of likely habitats in Vanuatu, no *Birgus glaucothoe* were found (Schiller *et al.*, 1991). This stage continues for only one moult (28 days, Reese and Kinsie, 1968) when the crab metamorphoses into a juvenile coconut crab at a size of 5 mm CL. The juvenile continues the hermit crab's habit of using a shell for some time (as long as 2 years), under laboratory conditions (Reese, 1968; 1987). The largest crab seen by Reese (1987) in shell was 11.3 mm CL, and the smallest without a shell was 22 mm CL. In Guam, Amesbury (1980) found a 4.0 mm TL individual without a shell; in the Vanuatu study, a crab of 6.0 mm TL (15 mm CL) was found without a shell (Fletcher *et al.*, 1991). Reports of much larger individuals in shells are likely to have been the result of misidentification and are probably referable to *C. brevimanus*, which (like many *Birgus*) is blue in colour (Reese, 1987).

Juvenile coconut crabs are difficult to find due to their burrowing habit. Evidence from enclosure studies in Vanuatu suggests that small juveniles undertake relatively infrequent and brief foraging excursions, which explains why little information has been obtained on this stage (Fletcher *et al.*, 1991). Information on larger juveniles (> 15 mm TL), which appear less secretive, suggests that recruitment success is highly variable. Significant recruitment to an area may be a sporadic event, only occurring every 5-10 years possibly when inter- and intra-specific competition is minimised and oceanographic conditions are favourable.

Recruitment to an area is possibly affected by the density of adults. In areas of Vanuatu where the density of adults was high, only a few juvenile recruits (approximately 3-6 years old) were sampled. This situation remained even

when the density of the large crabs during one year was reduced ten-fold, indicating that the lack of juveniles was not merely a result of an inhibiting effect on their foraging by the large number of adults. In contrast, in many areas where the adult density had been low for some years, more small individuals were present. Thus, large numbers of big coconut crabs may inhibit recruitment.

Extrinsic factors such as the number of other coenobitids in the area may also affect recruitment. There was a negative correlation between the abundance of large coconut crabs with the density of other coenobitids in Vanuatu (Fletcher *et al.*, 1991). Amesbury (1980) postulated that higher densities of coenobitids may adversely affect juvenile *Birgus* survival. He warned of the potential threat of introducing the giant African snail to coconut crab areas because, among other dangers associated with the introduction of this gastropod in the Pacific, their shell provides a perfect shelter for coenobitids. Thus, a Ricker curve may be the most appropriate model of the stock-recruitment relationship for this species (Fig. 10).

In many areas, hydrodynamic and oceanographic conditions may conspire to make recruitment difficult. The typical steep, near-shore drop-offs may make it virtually impossible for the partly benthic late larval stages and completely benthic glaucothoe to reach shore. As a result, recruitment may only occur if weather conditions are such that the larvae are trapped close to a suitable shore at the time when they are ready to settle and metamorphose into glaucothoe. The life-history of the coconut crab is summarised in Fig. 11.

## VI. GROWTH

Estimation of growth in crustaceans such as the coconut crab is difficult because it is not only a function of the size increment at each moult but also the frequency of moulting. Both of these factors are difficult to measure due to the loss of the exoskeleton when the crabs moult (Fletcher *et al.*, 1989).

## MOULTING BEHAVIOUR

Coconut crabs have a special behavioural adaptation for moulting in the terrestrial environment, which they often accomplish in a subterranean burrow (Held, 1963; Amesbury, 1980; Fletcher *et al.*, 1990b). Before the crab moults, its abdomen becomes greatly enlarged (Amesbury, 1980; Fletcher *et al.*, 1990b) due to a rapid accumulation of fluid (Fig. 12). The process of moulting was described by Held (1963) for juveniles and for adults by Fletcher *et al.* (1990b).

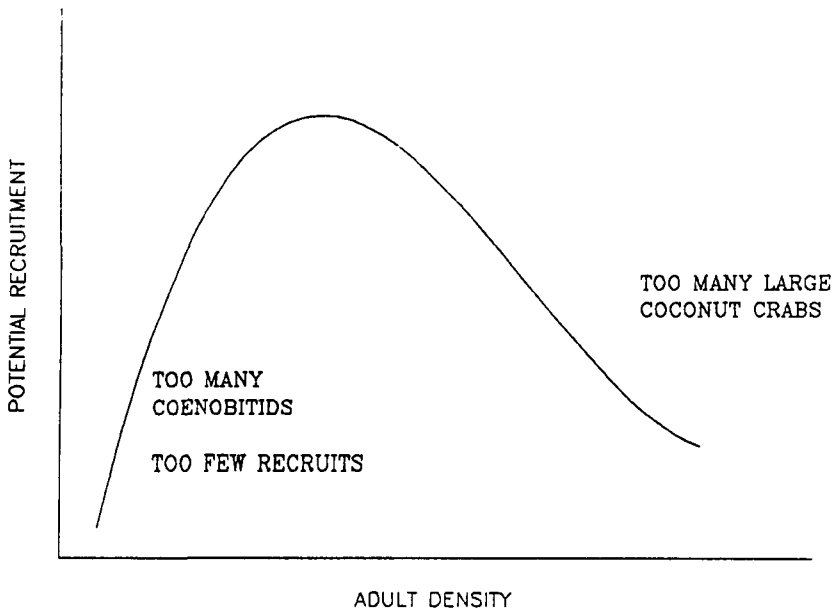
The crabs first dig a burrow in soft earth areas, away from their usual rocky habitats. The tunnels of adult crabs may extend for about 1 m and to a depth of 0.5 m. As the crab digs, it replaces the earth behind it so only a fan of disturbed soil is left to indicate the position of the entrance. The crab moults in a chamber



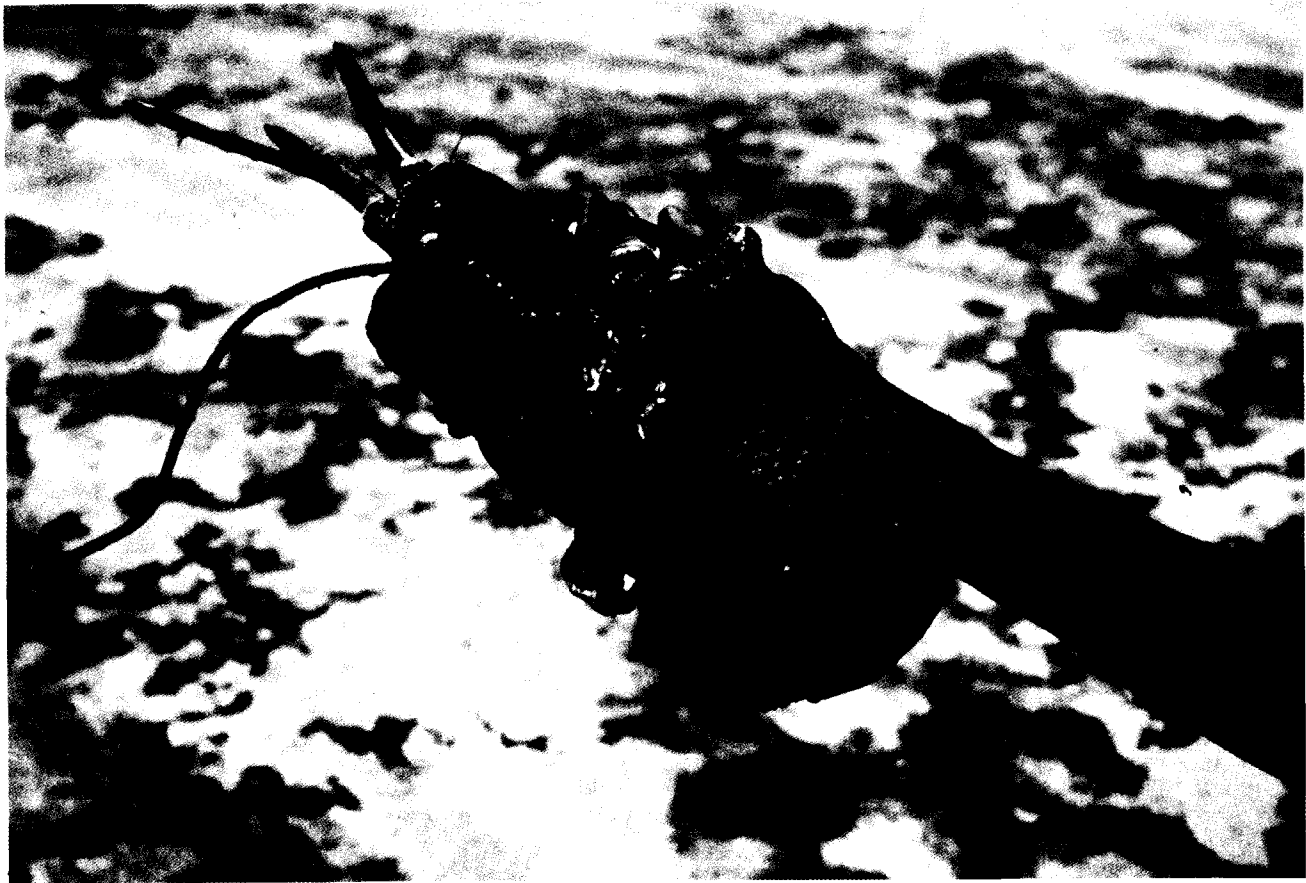
**Figure 10.** Suggested stock recruitment relationship for the coconut crab. Photo: Warwick Fletcher.

which is roughly circular and at least twice the crab's volume. Minerals are resorbed from the old exoskeleton which ultimately splits at the joint between thorax and abdomen due to an increase in internal hydrostatic pressure. The crab slowly pulls out of the old exoskeleton over a period of 1-2 hours, revealing the new soft, pale blue-white exoskeleton (Fig. 13). The crab remains immobile for some days while its new exoskeleton begins to harden. Subsequently, it consumes the old shell or exuvium, which enables minerals, such as calcium, to be recycled. This appears to contribute to the hardening of the new shell (Fletcher *et al.*, 1990b).

The time taken to complete the entire process is related to the size of the crab. Small crabs take only a few days (Held, 1963) larger crabs, however, may take as long as three to four weeks to finish eating the exuvium and for the exoskeleton to harden sufficiently for the crab to emerge (Fletcher *et al.*, 1990b). Thus, up to 1.5 months may be required to complete the entire moulting process in large individuals.



**Figure 11. Summary of the life-history stages of the coconut crab.**



**Figure 12.** Photograph of a crab dug up from its moult chamber prior to ecdysis. Note big abdomen. Photo: Warwick Fletcher.



**Figure 13.** Photograph of a crab which has just moulted. Note the white appearance of the new exoskeleton particularly near the distal regions of the legs. Photo: Warwick Fletcher.

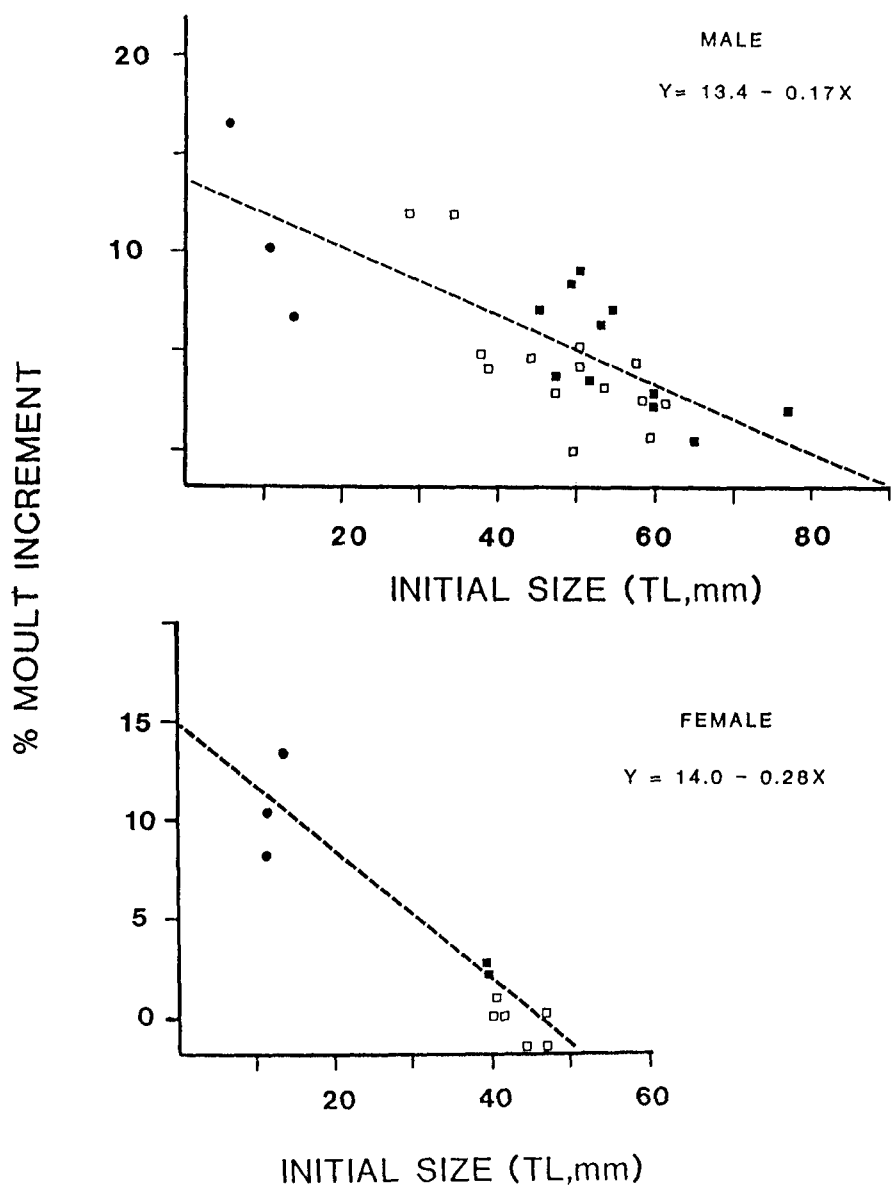


Figure 14. Relationship between the percentage moult increment and initial size for male and female crabs from Vanuatu (from Fletcher *et al.*, 1990b). Symbols indicate enclosure work ●, mark-recapture □, and post-versus pre-moult exoskeleton measurements ■.



## MOULT INCREMENT

The only successful laboratory studies on the growth rates of coconut crabs have been on juveniles (Held, 1963; Reese, 1968; Fletcher *et al.*, 1990b). One small crab kept in an enclosure for 18 months by Held (1963) moulted four times increasing from 20.8 mm to 30 mm during this time. Similar rates of growth for juveniles were found in Vanuatu (Fletcher *et al.*, 1990b).

In enclosure studies using adult *Birgus*, the crabs either did not moult (Hortsmann, 1976) or almost no increase in size occurred after moulting (Amesbury, 1980; Fletcher *et al.*, 1990b). Only Fletcher *et al.* (1990b) have studied the growth of the adult crabs successfully by using various branding techniques to provide mark-recapture estimates of the moult increment (see Fletcher *et al.*, 1989; 1990b). Additional data resulted from direct measurement of the growth increment of crabs excavated from their moulting burrows after moulting, but before they had eaten the exuvium. A total of 42 increments were measured during the Vanuatu study, providing a relationship between the proportional moult increment and initial size for both male and female crabs in Vanuatu (Fig. 14). The difference in increment between sexes is consistent with the size differences observed in natural populations (e.g. Helfman, 1973; Amesbury, 1980; Fletcher *et al.*, 1991).

## MOULT FREQUENCY

The moult frequency was assessed by Fletcher *et al.* (1990b) using monthly assessments of the moult stage of individuals from an index of abdominal expansion and from a subjective ranking of exoskeleton age. These both showed that adult crabs (> 30 mm TL) moulted only once per year, during the winter dry season. Crabs below this length moulted more frequently, with a maximum of about three moults per year. This is consistent with results of the enclosure studies (see above).

## GROWTH RATE

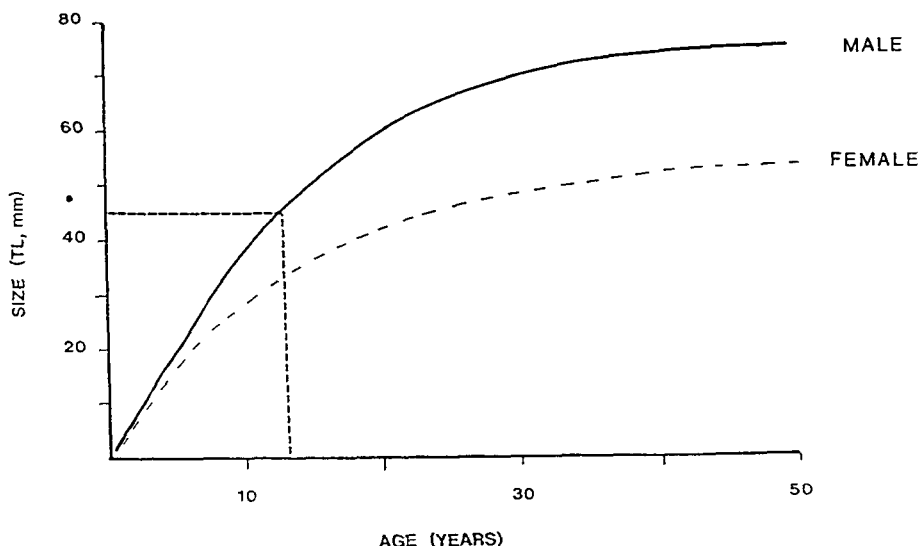
From the results of his enclosure studies on one juvenile, Held (1963) predicted that it would take five years for a crab to reach approximately 1 kg in size. Reese (1987), however, using the results of his earlier work on juveniles (Reese; 1968), concluded that large crabs may be 30 to 40 years of age.

Fletcher *et al.* (1990b) used a non-continuous model to construct a growth curve for the crabs in Vanuatu. The moult increment was obtained from the relationships given in Fig. 14. The size-related moult frequency was set at three per year for crabs up to 30 mm TL and one per year for adults. By integrating these two functions, the curves for male and female crabs was constructed

(Fig. 15). This indicates that a male crab weighing 1 kg may be more than 10 years old, and that the maximum size is not attained until an age exceeding 30 years.

The largest crab recorded in most studies have been in the range 74-76 mm TL (Helfman, 1973; Amesbury, 1980; Fletcher *et al.*, 1991) but a recent study in the Line Islands has found male crabs with a TL of approximately 100 mm TL (Garnett *et al.*, 1990), and Helfman (1973) found some "un-fished" islands where the maximum size was only 45 mm TL. Thus, there may be some environmentally caused variations in growth rate among areas, possibly related to the abundance of food.

The von Bertalanffy coefficient  $K$  for coconut crabs is 0.06, and longevity can exceed 50 years. The slow growth exhibited by this species suggests that the appropriate level of exploitation should be low; and that under high catch rates, declines in abundance can be expected.



**Figure 15.** Growth rates of male and female crabs from Vanuatu (modified from Fletcher *et al.*, 1990b).

## VII. POPULATION DYNAMICS

### METHODS OF CAPTURE

The most common method of capture for the crabs is the "baited trail". This involves setting a number of baits (usually opened coconuts), along a trail during the daytime and revisiting the baits after dark, collecting the crabs which are attracted to the baits (Fig. 16). The method of cutting and attaching the coconut varies between areas, as does the time of revisiting the baits. In general, when setting trails, the higher the crab population density, the fewer are the coconuts opened. Similarly, as coconut baits can be removed within an hour of sunset in high crab population areas, trails are checked shortly after dark.

In areas where the crabs are not plentiful, a more direct technique is used to catch the crabs. Coconut husk and other materials are set alight at the entrance to the crevice and the crab is smoked out of its hiding place. If the crab is hiding under a tree or in a hollow tree, then the tree itself may be set alight. The crab is caught when it emerges.

The third method of capture involves searching for the moulting burrows of the crabs. The place where the crab began burrowing can be identified by the telltale fan-like disturbance of earth. The path of the burrow is followed by probing the ground with a sharp stake locating the looser, disturbed earth within the burrow. The moulting chamber where the crab is located can be identified from the way the stake enters the open subterranean cavity. The crab is then excavated by hand. It may be in either a newly moulted "soft-shell" condition, or in the immediate pre-moult "swollen abdomen" condition, both of which are highly regarded in local diets

### SEASONAL DYNAMICS

There have been few assessments of the population dynamics of coconut crabs. Reese (1987) cites the results of a study of coconut crabs on Ikuren Islet, Enewetak Atoll, Marshall Islands from 1960 to 1976 using tag-recaptures. The population estimate ranged from 300 crabs in the April dry season to 1,200 in the wet season. He postulated that the differences were due to changes in foraging behaviour between the seasons. Fletcher *et al.* (1990c; 1991) also found variations in the crabs caught per coconut bait (catch per unit effort, CPUE) between months at a large number of locations throughout the Vanuatu Archipelago. The CPUE was at a maximum in the summer wet season and at a minimum in the winter dry season (Fig. 17). At least part of this cycle was considered to be due to a large number of the crabs being underground preparing to moult during the dry season, but changes in the frequency of foraging may also have contributed.



Figure 16. Photograph of a coconut crab attracted to a coconut bait. Number scratched on the back of crab indicates a recaptured crab. Photo: Warwick Fletcher.

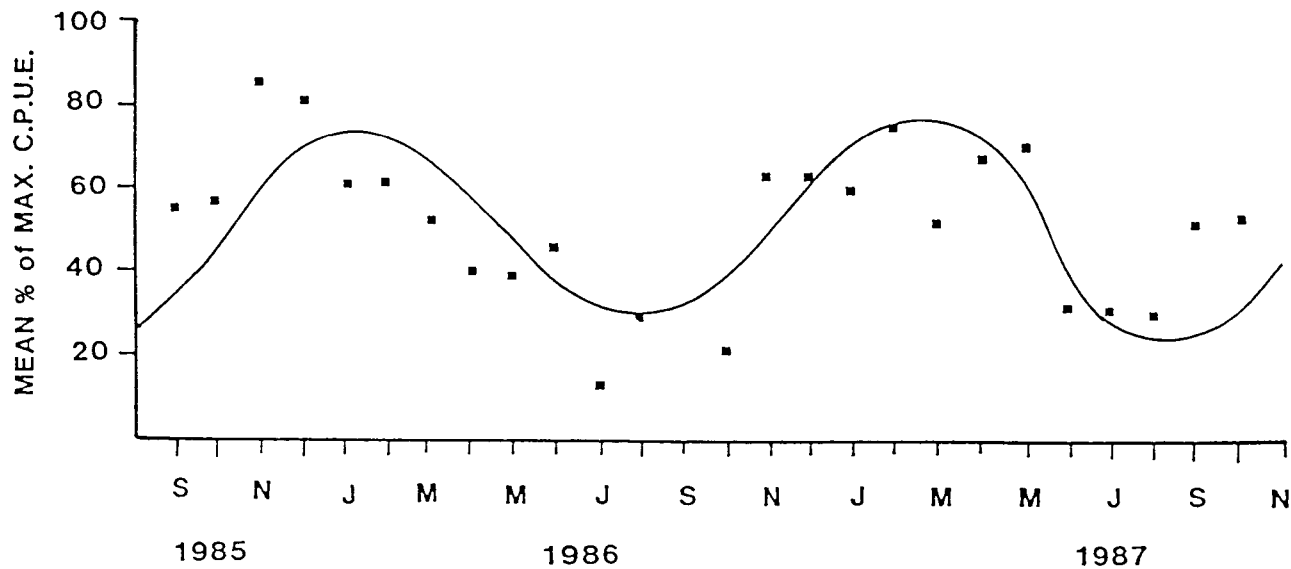


Figure 17. The pooled CPUE (crabs caught per coconut bait) indicating the seasonal cycle in Vanuatu (from Fletcher *et al.*, 1991).

## EFFECTS OF EXPLOITATION

Differences in the numbers of crabs among areas have usually been ascribed to variations in previous harvesting patterns (Amesbury, 1980). Only Fletcher *et al.* (1990c) have documented actual changes in the CPUE of crabs in an area over a number of years in relation to different rates of exploitation. Most of the 15 regularly sampled sites which were subjected to harvesting showed a decline in CPUE over the 30-month study. The most dramatic instance was at Tegua Island in the Torres Group where the CPUE fell from 4.2 in 1985 to 2.7 in 1986 following the removal of 4,000 crabs. It declined to 0.5 in 1988 after a further 10,000 crabs were removed during that year (Fig. 18). Less dramatic declines were seen at all sites on the island of Santo where collections occurred. In these cases, the CPUE of sites declined from about 0.29 to 0.05 during the study (Fig. 19). Significantly, at the one site where no collections were made (Mavea Island) the CPUE did not decline, but neither did it show any indication of a significant increase.

## INFLUENCES ON SIZE STRUCTURE

All studies have found differences in the size structures of the sexes, with males attaining much larger sizes than females (see section above). Observed differences in the mean size of individuals between areas have been attributed to variations in environmental conditions (Helfman, 1973) and harvesting patterns (Amesbury, 1980; Fletcher *et al.* 1990c; 1991). The dearth of small individuals in most studies was thought by Reese (1987) to have been due to sampling bias, but Hartnoll (1982) showed that for long-lived, slow growing species, relatively few juveniles should be expected even if the population was maintaining a stable age structure and assuming constant, low natural mortality at all ages.

In contrast to the changes in CPUE, Fletcher *et al.* (1990c) found no evidence of a decline in mean size of crabs in an area under intense exploitation in Vanuatu. The mean size of crabs at the Tegua site did not change despite the CPUE declining by 80 per cent (Figs. 18 and 20). Mean size is thus a poor indicator of the effect of exploitation in coconut crab populations. When recruitment of juveniles occurs at a lower rate than the exploitation of the population, size structure will be less affected. Obviously, at Tegua there was almost no recruitment of smaller crabs to the population during the study period so the overall size structure remained static. This scenario suggests grave consequences for the future of this islands' stock.

## VIII. STOCK ASSESSMENT

An estimate of biomass usually assists management of the exploitation of a

species. For coconut crabs the direct estimation of numbers is generally impossible. Mark recapture estimates have been made on a number of small islands (Helfman, 1973; Reese, 1987; Fletcher *et al.*, 1990a) but on large islands the rates of recaptures are too low for reasonable estimates to be made (Fletcher *et al.*, 1990a).

To overcome this problem, Fletcher *et al.* (1990c) determined the relationship between the relative abundance measure (CPUE, number of crabs caught per bait set) and the absolute stock size through the calculation of the catchability coefficient ( $q$ ). This was determined from depletion and addition experiments in Vanuatu where a CPUE of 1 crab per bait corresponded to a population density of  $1,200 \text{ ha}^{-1}$ . This coefficient only relates to CPUE data collected during the wet season, using baits set at locations where crabs are likely to be found. The area measurement obviously should only encompass areas of suitable habitat for coconut crabs.

The catchability coefficient has been used to estimate the remaining stocks of crabs in various parts of the Vanuatu Archipelago (Fletcher *et al.*, 1991), and it is likely that it could be applied equally, but with caution, to crab stocks in any area.

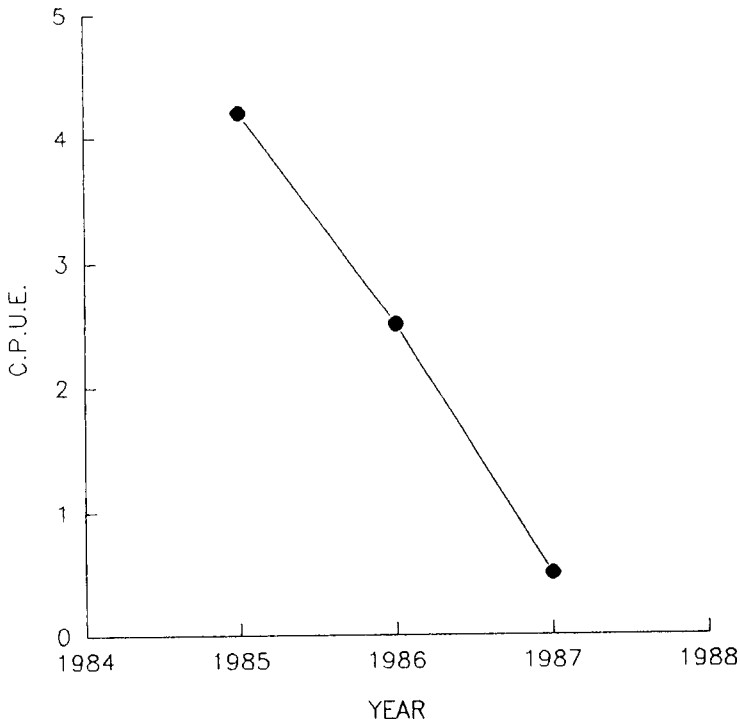


Figure 18. The CPUE at Tegua Island, Vanuatu (from Fletcher *et al.*, 1990c).

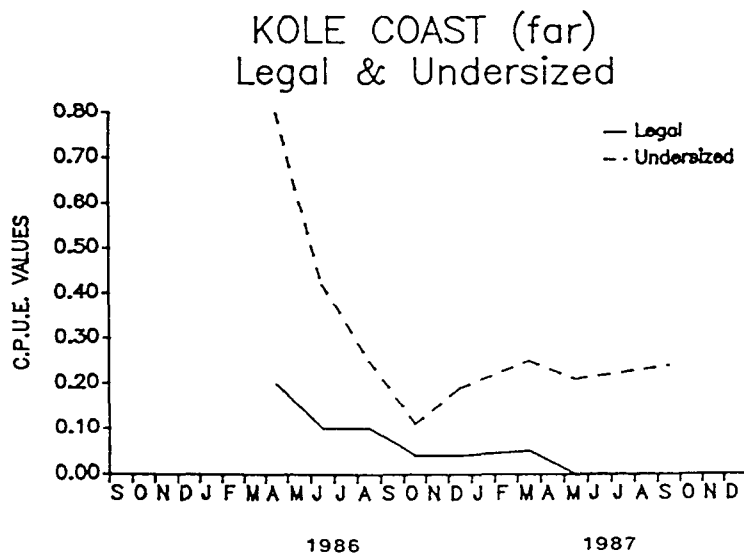
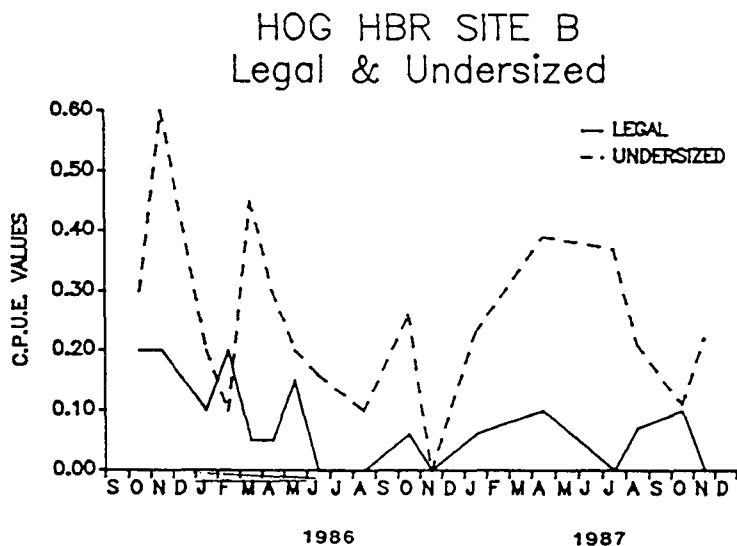
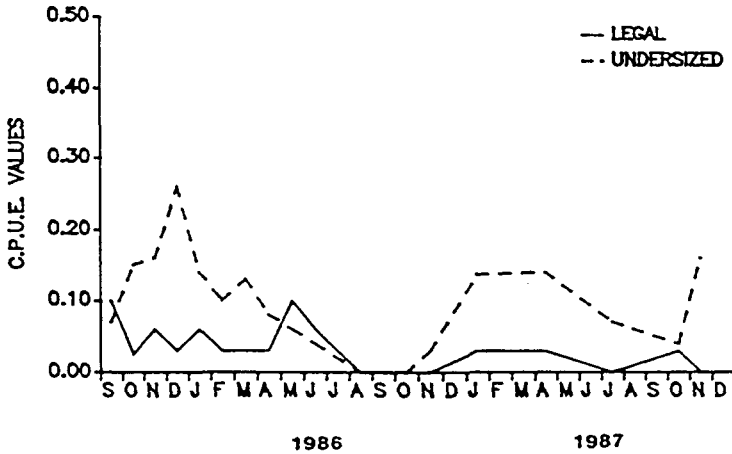


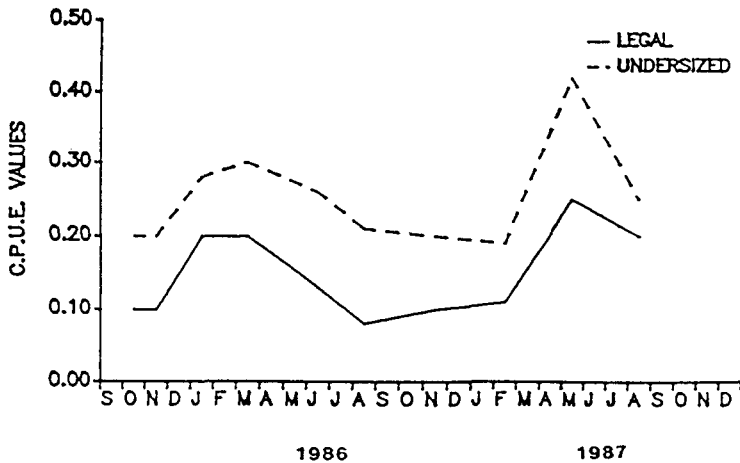
Figure 19. The CPUE at sites on the island of Santo, Vanuatu (from Fletcher *et al.*, 1991). A and B were fished heavily whereas C and D were fished lightly or not at all.



# HOG HBR SITE A Legal & Undersized



# MAVEA (CLIFF) Legal & Undersized



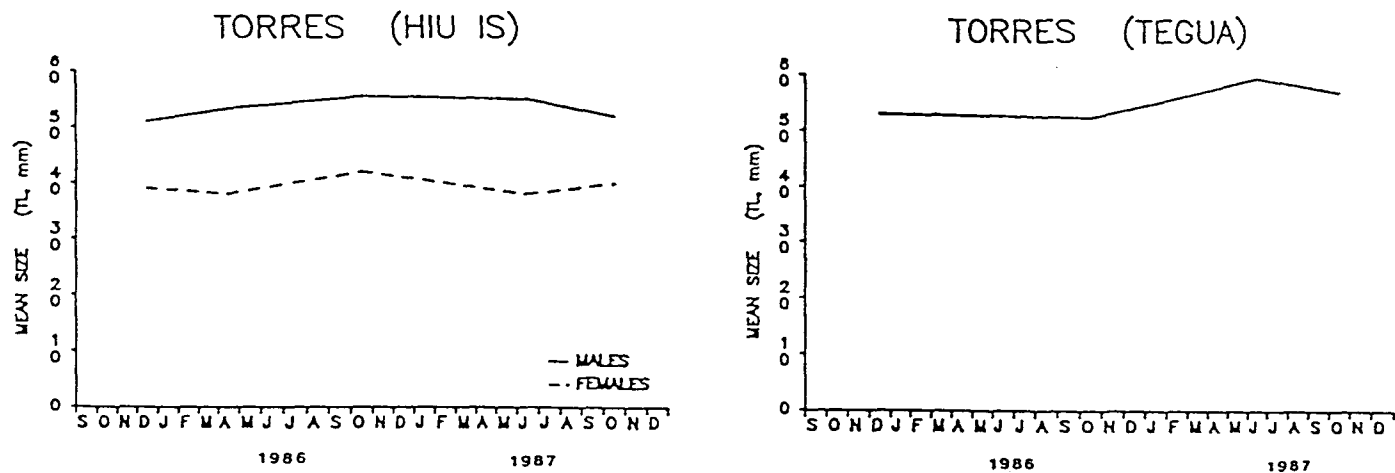


Figure 20. The mean size (thoracic length) of crabs from Tegua Island, Vanuatu (from Fletcher *et al.*, 1991).

## IX. MANAGEMENT

There have been few serious attempts to manage the stocks of coconut crabs in any part of its range. In Guam, Vanuatu and Tuvalu some regulations relating to the capture of the crabs have been implemented (Brown and Fielder, 1989). Guam and the Federated States of Micronesia (FSM) have set a minimum size limit of 3" (76 mm) across the carapace and banned the capture of ovigerous or berried females. Other proposals for FSM included a closed season between 15 June and 15 August (to protect spawning crabs) and setting up specified areas which would be permanently closed to the capture of the crabs (Knott, 1971, Amesbury, 1980). These closures were, however, only to operate for between 1 and 3 years.

Prior to the recent ACIAR study, the only regulations in place in Vanuatu were a size limit of 9 cm cephalothoracic length (not including the rostrum), and a restriction on the capture of berried females.

Although intending exporters of coconut crab in Solomon Islands are required to apply to the government for an export permit, no other regulations apply to harvests in that country. Concern over the status of the resource in Solomon Islands and a recent increase in overseas demand for coconut crab, have led to the suggestion that Solomon Islands government legislate to protect local stocks and regulate exports (Skewes, 1990).

The slow growth and poor recruitment of the crabs, however, result in a situation where these measures may be inadequate to prevent the populations of crabs being reduced over short periods of time. Thus, for some populations, prior to exploitation a large percentage of the crabs may be greater than the size limit. The accumulation of these older adults represent a non-renewable stock, which under heavy exploitation will never return. Furthermore, if all adult crabs are removed, it is possible that little or no subsequent recruitment will occur. Even if it does, it would take 10 years to re-establish an adequate number of legal sized individuals. Therefore, the danger with these types of populations is that the rates of exploitation increase rapidly due to initially high catch rates, the expectation of the fishermen are corresponding high, and the consequent intense pressure on the stock inevitably leads to a fall in catch rates as the accumulated stock is reduced. This pattern has occurred in a number of fisheries which target long-lived sedentary species (*e.g.* deep water snapper; Polovina, 1987).

Consequently, the only way to keep a viable long-term fishery for this species is by restricting the rate of exploitation. At maximum, it must not exceed the rate of natural mortality of the crabs, which is about 5 per cent of the adult population size per year.

An example of the type of management required is that suggested for Vanuatu. The approximate numbers of crabs remaining in the various regions were estimated using the methods cited above (Fletcher *et al.*, 1991). From

these, yearly quotas for each region were set according to the standing stock of the area. Given that the methods for calculating standing stock are crude, this quota should be subject to review following a yearly reassessment of the current stock size in each area.

This policy should be linked to a restriction on the methods of disposal of the crabs. Originally, in Vanuatu, the crabs were sold at a large number of outlets including local municipal and major markets, as well as direct to restaurants and local wholesalers. Such a situation meant that it was almost impossible to determine how many crabs were coming from any given area. Sale of the crabs was to be restricted to the government-controlled fish markets which would be able to monitor the number and origin of crabs bought, and to set a base price. This will probably be amended to have restricted number of licensed vendors, preferably co-operatives of the fishermen who could then maximize the price obtained for each crab caught.

The price to the crab collectors in Vanuatu before regulation varied greatly but in general it was poor, between 200 and 400 Vatu/kg (US\$2-4). This was an unrealistic price in comparison to the value of the crab at the point of retail sale; for example, on the restaurant table it could fetch 2-3,000 Vatu/kg. Thus, the crabbers needed to sell many crabs to make a reasonable amount of money. An increase in the base price to 500 Vatu/kg was part of the trade-off for temporarily closing the markets for coconut crabs and restricting the numbers that could be collected. Thus, most collectors should not experience a drop in income, despite a restriction on the numbers of crabs they are permitted to catch.

In areas where the abundance has been reduced to very low levels (less than 0.3 crabs per bait), it would be wise to prohibit all collecting. Consequently, in many areas of some countries (and in some cases, the entire country), large scale collecting may have to be banned altogether for some time to allow the crab population to rebuild.

A further option is the provision of a number of sanctuary areas where all collecting is prohibited (as suggested for Guam). This is an attractive idea but suffers from the difficulty of surveillance in remote areas. Furthermore, depending upon local hydrography, this "bank" of crabs may not increase the potential for recruitment elsewhere, even on nearby islands. The results of a population genetics study by Lavery and Fielder (1991) do suggest that larvae are transported among islands and island groups, but having one high density area may be insufficient to supply all the other regions with larvae. Moreover, in areas where the density of crabs is very low, recruitment is probably adversely affected by competition or predation by coenobitid hermit crabs even if larvae reach the shore (Section V). Thus, a sanctuary should not be imposed in isolation from more general controls over exploitation rates.

Artificial propagation of *Birgus* has also been suggested as a way of conserving stocks of the crab (Anon., 1973; Brown and Fielder, 1988). There

are, however, problems associated with rearing the larvae and particularly the glaucothoe (see Section V). It appears unlikely that large scale rearing can be done without considerable financial investment and further research, even in areas where spawning females can readily be found.

This species appears to be very susceptible to both overexploitation and the influences of urbanisation through habitat alienation and the introduction of exotic predators. It can become locally extinct in a matter of a few years, and its continuing presence in many areas of its range is in serious doubt.

In conclusion, if an industry based on the collection of coconut crabs is to be established or continued, it is imperative that an accurate assessment of the status of the stock is obtained and appropriate measures to regulate collections are imposed immediately. If this is not enacted, few countries can expect to have any coconut crab resource by the next century.

## REFERENCES

- Altevogt, R. and Davis, T.A. (1975). *Birgus latro*, India's monstrous crab: a study and an appeal. *Bull. Dept. Mar. Sci. Univ. Cochin* 7, 11-24
- Amesbury, S.S. (1980). Biological studies on the coconut crab (*Birgus latro*) in the Mariana Islands. *University of Guam Technical Report No. 17*. 39 pp.
- Anon. (1973). Pacific Mariculture Conference. Univ. Hawaii Inst. Mar. Biol. February. 1973. Kaneohe, Hawaii. 21 pp.
- Bagnis, R. (1970). A case of coconut crab poisoning. *Clin. Toxicol.* 3, 585-588.
- Borradaile, L.A. (1900). A note on the hatching-stage of the Pagurine landcrabs. *Proc. R. Soc. Lond. (B. Biol. Sci.)*, pp. 937-938.
- Brown, I.W. and Fielder, D.R. (1988). Annotated bibliography of the coconut crab *Birgus latro* (L.). *ACIAR Working Paper No. 17*. Canberra, Australia. 38 pp.
- Cameron, J.N. and Mecklenburg, T.A. (1973). Aerial gas exchange in the coconut crab *Birgus latro* with some notes on *Gecarcoidea landalii*. *Respir. Physiol.* 19, 245-261.
- Cropp, B. (1982). Coconut cracking crabs. *Oceans* 15, 14-15.
- Daniel, A. and Prem-Kumar, V.K. (1967). The coconut crab *Birgus latro* (L.) (Crustacea: Paguridae) in the Great Nicobar Island. *J. Bombay Nat. Hist. Soc.* 64, 574-580.
- Davis, T.A. and Altevogt, R. (1978). Is the coconut crab a pest of coconut? pp. 157-162. *World Crops*. July/August 1978.
- Darwin, C. (1845). *The Voyage of the Beagle*. Dent, London.
- Fletcher, W.J., Fielder, D.R. and Brown, I.W. (1989). Comparison of freeze and heat branding to mark the coconut crab, *Birgus latro* L. *J. Exp. Mar. Biol. Ecol.* 127, 245-251.
- Fletcher, W.J., Brown, I.W. and Fielder, D.R. (1990a). Movement of coconut crabs (*Birgus latro* L.) in a rainforest habitat in Vanuatu. *Pac. Sci.* 44, 407-416
- Fletcher, W.J., Brown, I.W. and Fielder, D.R. (1990b). Growth of the coconut crab *Birgus latro* in Vanuatu. *J. Exp. Mar. Biol. Ecol.* 141, 63-78
- Fletcher, W.J., Brown, I.W. and Fielder, D.R. (1990c). Use of standard and inverse Leslie experiments to estimate the density of coconut crabs (*Birgus latro* L.) in Vanuatu. *Fish. Res.* 9, 317-324

- Fletcher, W.J., Brown, I.W. and Fielder, D.R. (1991). Structure and dynamics of populations of coconut crab in Vanuatu. In: *The Coconut Crab: Aspects of the Biology and Ecology of Birgus latro in the Republic of Vanuatu*, (I.W. Brown and D.R. Fielder, eds). pp61-86. *ACIAR Monograph 8*. Australian Centre for International Agriculture Research, Canberra, Australia.
- Garnett, M.C., Kepler A.K., and Wragg, G. (1990). ICBP 1990. Line and Phoenix Island Expedition Report. 12pp.
- Gibson-Hill, C.A. (1947). Field notes on the terrestrial crabs (Christmas Island). *Bull. Raffles Museum* **18**, 43-52.
- Greenaway, P., Morris, S. and McMahon, B.R. (1988). Adaptations to a terrestrial existence by the robber crab *Birgus latro*. II. *In vivo* respiratory gas exchange and transport. *J. Exp. Biol.* **140**, 493-509
- Greenaway, P., Taylor, H.H. and Morris, S. (1990). Adaptations to a terrestrial existence by the robber crab *Birgus latro*. VI. The role of the excretory system in fluid balance. *J. Exp. Biol.* **152**, 505-519
- Gross, W.J. (1955). Aspects of osmotic regulation in crabs showing the terrestrial habit. *Amer. Nat.* **LXXXIX**, 205-222.
- Harms, J.W. (1937). Lebensablauf und Stammesgeschichte des *Birgus latro* L. von der Weihnachtsinsel. *Zeitschr. für Naturwissen (Jena)* **71**, 1-34.
- Harries, H.C. (1983). The coconut palm, the robber crab and Charles Darwin: April fool or a curious case of instinct. *Principes* **27**, 131-137.
- Hartnoll, R.G. (1982). Growth. In *The Biology of Crustacea*. Vol 2 (L.G. Abele, ed.). pp. 111-197. Academic Press, New York.
- Held, E.E. (1963). Moulting behaviour of *Birgus latro* L. *Nature* **200**, 799-800.
- Helfman, G.S. (1973). The ecology and behaviour of the coconut crab *Birgus latro* (L.). *Unpubl. MSc thesis*. University Hawaii. Honolulu, Hawaii. 158 pp.
- Helfman, G.S. (1977a). Agonistic behaviour of the coconut crab, *Birgus latro* (L.). *Birgus latro* (L.). *Z. Tierpsychol.* **43**, 425-438.
- Helfman, G.S. (1977b). Copulatory behaviour of the coconut or robber crab *Birgus latro* (L.). *Crustaceana* **33**, 198-202.
- Hicks, J., Rumpff, H. and Yorkston, H. (1984). Robber and hermit crabs. In *Christmas Crabs*. Christmas Is. Nat. Hist. Assoc. pp. 24-34.
- Holthuis, L.B. (1959). Contributions to New Guinea carcinology. III. The occurrence of *Birgus latro* (L.) in Netherlands New Guinea. *Nova Guinea (Zool.) new ser.* **10**, 303-310.
- Horstmann, U. (1976). Some aspects on the culture of the coconut crab (*Birgus latro*). 3rd Regional Seminar, Univ. San Carlos, Philippines.
- Knott, N.P. (1971). *Meet Birgus latro: Mrs Coconut crab*. Land Res. Brch., Div. Lands and Surveys, Dept. Resources and Develop. (Saipan, TTPI). Extension publication. 5 pp.
- Lavery, S. and Fielder, D.R. (1991). Genetic characteristics. In: *The Coconut Crab. Aspects of the Biology and Ecology of Birgus latro in the Republic of Vanuatu*, I.W. Brown and D.R. Fielder, eds.), pp. 87-98 *ACIAR Monograph 8*. Australian Centre for International Agriculture Research, Canberra, Australia.
- Matthews, D.C. (1956). The probable method of fertilization in terrestrial hermit crabs based on comparative study of spermatophores. *Pac. Sci.* **10**, 303-309.

- Morris, S., Greenaway, P. and McMahon, B.R. (1988). Adaptations to a terrestrial existence by the robber crab *Birgus latro*. I. An *in vitro* investigation of blood gas transport. *J. Exp. Biol.* **140**, 477-491.
- Orlamunder, J. (1942). Zur entwicklung und formbildung des *Birgus latro* L. mit Besonderei berucksichtigung des x-organs. *Zeitschr. wiss. Zool.* **155**, 280-316.
- Polovina, J.J. (1987). Assessment and management of deepwater bottom fishes in Hawaii and Marianas. In: *Tropical Snappers and Groupers: Biology and Fisheries Management*. (J.J. Polovina and S. Ralston, eds.), pp 505-532, Westview Press, Boulder, Colorado, 659 pp.
- Reese, E.S. (1968). Shell Use: an adaptation for emigration from the sea for the coconut crab. *Science (Wash.)* **161**, 385-386.
- Reese, E.S. (1987). Terrestrial environment and ecology of Enewetok Atoll. In *The Natural History of Enewetok Atoll*. (D.M. Devaney, E.S. Reese, B.L. Burch and P. Helfrich, eds.), Chapter 11, pp. 187-202. Vol. I The ecosystem: environment biotas and systematics. U.S. Dept. of Energy, Oak Ridge, Tennessee.
- Reese, E.S. and Kinsie III, R.A. (1968). The larval development of the coconut or robber crab *Birgus latro* (L.) in the laboratory (Anomura, Paguridae). *Crustaceana Suppl.* **2**, 117-144.
- Reyne, A. (1939). On the food habits of the coconut crab (*Birgus latro* L.) With notes on its distribution. *Arch. Neerl. Zool.* **3**, 239-247.
- Schiller, C. (1989). Reproduction and larval biology. Final report to ACIAR (unpub. m.s.).
- Schiller, C., Fielder, D.R., Brown, I.W. and Obed, A. (1991). Reproduction, early life-history and recruitment. In: *The Coconut Crab: Aspects of the Biology and Ecology of Birgus latro in the Republic of Vanuatu*, (I.W. Brown and D.R. Fielder, eds.) pp. 13-34. *ACIAR Monograph 8*. Australian Centre for International Agriculture Research, Canberra, Australia.
- Skewes, T. (1990). Marine Resource Profiles : Solomon Islands. *South Pacific Forum Fisheries Agency Report 90/61*, Forum Fisheries Agency, Honiara, Solomon Islands, 52 pp.
- Smatresk, N.J. and Cameron, J.N. (1981). Post exercise acid-base balance and ventilatory control in *Birgus latro*, the coconut crab. *J. Exp. Zool.* **218**, 75-82.
- Storch, V., Cases, E. and Rosito, R. (1979). Recent findings on the coconut crab *Birgus latro* (L.). *Philipp Sci.* **16**, 57-62.
- Storch, V. and Welsh, V. (1984). Electron microscope observations on the lungs of the coconut crab *Birgus latro* (L.) (Crustacea: Decapoda). *Zool. Anz. Jena* **212**, 73-84.
- Vogel, H.H. and Kent, J.R. (1970). Life history, behaviour and ecology of the coconut crab, *Birgus latro*. *Amer. Zool.* **10**, 289-290.
- Wells, S.M., Pyle, R.M. and Collins, N.M. (1983). Coconut or robber crab. In *I.U.C.N. Invertebrate Red Data Book*. I.U.C.N.; Gland, Switzerland. 632 pp.
- Wiens, H.J. (1962). *Atoll Environment and Ecology*. Yale Univ. Press, New Haven and London. 532 pp.