The Coconut Crab

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The Coconut Crab:
aspects of the biology and ecology of
Birgus latro in the Republic of Vanuatu

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Introduction

THIS publication presents information generated during the ACIAR-sponsored project 'Growth and recruitment of coconut crab populations in Vanuatu'. It is in response to a request by the Government of the Republic of Vanuatu for information on the coconut crab *Birgus latro* which could be widely and easily disseminated throughout the region of the crab's distribution.

It is hoped that this monograph will enable non-scientists as well as scientists to appreciate the coconut crab as the valuable commodity we believe it to be, and that the work will stimulate everyone involved in the management of renewable natural resources (particularly in the small island countries of the Pacific) to become more active in conserving the remaining stocks of coconut crabs.

Details of the methods used and the important results obtained from the ACIAR study have been published in appropriate scientific journals. Summaries of (or at least reference to) these results are included in this volume, with relevant citation details. Other areas of investigation which were considered to have management importance, but for one reason or another did not entirely fall within the guidelines of the mainline journals, are also included.

The coconut crab (*Birgus latro*)

Typical of the crab's rainforest habitat in northern Santo, Vanuatu.

Typical crab coastal habitat at Hog Harbour, Santo, Vanuatu.

Bait trails are a successful method of assessing the potential yield of crabs at a site.

Dr Rick Fletcher using radio-tracking equipment to plot crab movements.

Collecting plankton samples.

Measuring the length of a mature crab.

Individual crabs were identified with felt pen and inscribed numbers on the carapace (below), heat branding (above) and freeze branding.
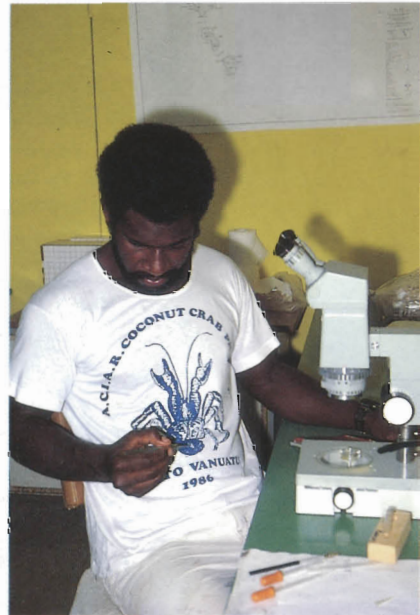
A female crab carrying an egg mass.

Mr Shane Lavery preparing crab tissue for electrophoretic analysis.

Mr Alsen Obed sorting samples.

1 Project Overview and Literature Survey

I.W. Brown and D.R. Fielder

Project Rationale and Development

THIS project stemmed from a request to the Australian Centre for International Agricultural Research (ACIAR) in September 1983 by the Ministry of Agriculture, Forestry and Fisheries in the Republic of Vanuatu to establish a collaborative project in Vanuatu aimed at studying certain aspects of the biology of coconut crabs, in order that the local resource might be managed more effectively. At the invitation of ACIAR a joint research proposal was developed by the Fisheries Branch of the Queensland Department of Primary Industries (QDPI), the University of Queensland (Zoology Department), and the Vanuatu Fisheries Department. For reasons of administrative efficiency QDPI was nominated as the commissioned organisation.

The coconut or robber crab *Birgus latro* is the largest of the land crabs, and the most highly terrestrialised decapod crustacean. It is widely distributed throughout the Indian and Pacific Oceans, primarily in island environments where predators are few. Although closely related to the hermit crabs, the adult coconut crab no longer requires the protection of a discarded mollusc shell, and has little need for access to the sea except to liberate its marine planktonic larvae. Adult crabs can grow to a weight of 4 kg; they possess powerful crushing claws and elongate, pointed legs which enable them to climb rocks and trees with comparative ease.

First described by Rumphius (1705), but known to Europeans at least since William Dampier's exploratory voyages around 1688, coconut crabs have attracted the attention of many naturalists visiting islands in the Pacific and Indian Oceans. Much of the early literature is anecdotal and concerns the creature's dubious reputation for removing and opening nuts from coconut trees. More rigorous scientific studies in latter years have contributed much to our understanding of the species' life-history, behaviour, reproduction, physiology and anatomy.

Coconut crabs have excellent culinary properties and throughout their entire range are highly sought after as a food item. Almost every account mentions this fact. Coconut crabs are readily captured using methods which require no capital investment in equipment. In most cases they are caught by hand, having first been attracted to a staked bait, often a split coconut. Consequently a highly saleable, relatively valuable item can be harvested with minimum outlay in localities where opportunities for cash-flow are otherwise severely limited. Over the past decade an expanding tourist industry coupled with a downturn in local copra-based economies has significantly increased the socio-economic

value of coconut crabs (the crabs are offered as specialty dishes in tourist restaurants), and, as a consequence, increased harvesting pressure on coconut crab populations. Recognition of these factors by the Vanuatu Government was the main stimulus for this project.

Regardless of the stimulus for increasing demand, the amount of any natural resource available for harvesting is, by definition, regulated at least to some extent by factors beyond human control. Recruitment of juvenile coconut crabs into the exploited population depends largely on larval survival, which in turn is a function of the combined effects of oceanic currents, atmospheric conditions, natural predators, appropriate emergence substrates, food supply, and the availability of suitably sized protective mollusc shells. Until the technology for controlling larval survival (e.g. through artificial propagation and culture) is developed or at least identified, the resource will remain a natural one, fundamentally different from livestock herds and agricultural crops. Unless the problems of regulating the harvest of this valuable renewable natural resource are addressed and acted upon, there is little doubt that coconut crabs, to all intents and purposes, will become extinct. A trend in decreasing crab populations has become evident in many areas over the past few decades, and is attributed to uncontrolled exploitation, changing land-use patterns, and other man-made effects. A correct balance between conservation and exploitation may be achieved, but prior knowledge of how the resource functions in its natural state is essential. In some areas (e.g. Guam and Vanuatu) minimum legal size limits had been proclaimed as an interim management measure before the project started. However, these limits had been formulated on the basis of 'gut feeling' rather than on scientific evidence.

Several workers have already suggested that coconut crab production may possibly be enhanced either through artificial culture or some kind of husbandry or 'ranching'. Eggs had been cultured in vitro, and a complete larval series reared and maintained under laboratory conditions. Additionally, the 1973 Pacific Island Mariculture Conference in Hawaii listed coconut crabs in the 'second priority' group of invertebrates (along with mud crabs and giant clams) for potential culture, indicating a perceived capacity for market expansion. However, we agreed with Horstmann's (1976) assessment that this was still some time in the future, and important basic research had still to be done before ranching viability could be addressed.

Consequently a project was developed to address two broad objectives—

(i) to define the various aspects of coconut crab biology necessary to produce a strategic management plan for the resource, and

(ii) to investigate the feasibility of artificially culturing, ranching or farming coconut crabs for market.

A necessary prerequisite for any management plan is an assessment of the status of the resource and an understanding of its dynamic characteristics. Although some research had been done previously on coconut crabs, two specific aspects pertinent to resource status and

stock dynamics, namely, growth and recruitment, had not received adequate attention. Growth studies, including the development of new methodologies and the assessment of population sizes and mobility became the responsibility of Drs Ian Brown (Joint Project Leader) and Rick Fletcher (Vanuatu Research Team Leader), both from QDPI Fisheries Branch. Associate Professor Don Fielder (Joint Project Leader) and one of his M.Sc. students, Mr Craig Schiller (University of Queensland, Zoology Department) undertook to research the reproductive biology, including larval recruitment, and to assess the viability of providing hatchery-reared juveniles for farming or ranching. A local Vanuatu resident, Mr Alsen Obed, was recruited in Santo to act as a research assistant and liaison officer. Midway through the project (foreshadowed from the outset) Mr Shane Lavery was recruited as an additional M.Sc. student to study the population genetics of coconut crabs throughout their natural range.

All field studies were centred on the island of Espiritu Santo in the northern part of the archipelago, with some extensions to the Torres and Banks groups of islands to the north of Santo. Logistic and administrative support was provided through Mr Richard Kaltongga (Director, Fisheries Department, Republic of Vanuatu). Domestic administration was carried out by the Overseas Development Section of QDPI and the University of Queensland Research Services Section.

Biology and Life History of the Cocout Crab: A survey of the literature prior to 1983

The coenobitid anomuran *Birgus latro* is a close relative of the hermit crab group, and has evolved to become the largest and least marine-dependent of the land crabs. Its common name (coconut or 'robber' crab) reflects an unsubstantiated reputation for removing nuts from the tops of coconut palms. Because of its size (up to 4 kg), terrestrial habit, and the delicate flavour of its flesh, *Birgus* is highly regarded as a food item in those parts of the Indo-Pacific where it is still reasonably common. In times past, coconut crab meat was considered to have aphrodisiac properties, and quantities were exported dry to Hong Kong. Dried and lacquered crabs have also been marketed as curios to visitors in localities such as Christmas Island and Guam.

Viable populations of coconut crabs appear to be restricted mainly to island environments. Despite the species' wide distribution from the Seychelles (Western Indian Ocean) to the Tuamotu Archipelago in the eastern Pacific, it is virtually unknown in East Africa, the Indian sub-continent, mainland Asia and Australia, probably because of the distribution of large animal competitors and predators. Increases in human population density and changing land-use patterns in a number of areas have had an adverse effect on coconut crab resources and there are almost certainly some localities where the species is no longer found at all, either through habitat destruction, uncontrolled exploitation, or depredation by domestic and feral animals.

The most comprehensive published data on the coconut crab's

distribution appear in reports by Reyne (1939) and Wiens (1962), but subsequent authors such as Holthuis (1959, 1963), Horstmann (1976), Helfman (1973), Amesbury (1980), Wells et al. (1983) and Altevogt and Davis (1975) indicate that in the decades since Reyne's report the species' range appears to have contracted somewhat. To obtain some idea of the crab's current distribution, population density and utilisation patterns, a survey of representative countries and territories, primarily in the Pacific and southeast Asian regions, was conducted during May and June 1984. Questionnaires were mailed to appropriate research and/or management authorities in American Samoa, Cook Islands, Ponape (Eastern Carolines), Truk (Eastern Carolines), Yap (Western Carolines), Kosrae (Eastern Carolines), Fiji, Guam, Kiribati, Majuro (Marshalls), Saipan (Northern Marianas), Nauru, Niue, Koror (Palau), Papua New Guinea, Solomon Islands, Western Samoa, Tonga, Tuvalu, Tokelau, New Caledonia, Japan, India, Indonesia, Malaysia, Thailand and the Philippines.

Responses were received from all but five localities. Coconut crabs are considered generally abundant in Solomon Islands, locally abundant in Truk and the Republic of Vanuatu (other data sources), and generally common in the Tokelaus, Niue, and Marshall Islands. The remaining countries or territories suggested a population level within the range 'locally common' to 'rare'. None of the returned questionnaires indicated that the species was completely unknown or absent.

Recognition of the value of coconut crabs as a highly priced luxury food item, particularly in respect of tourist development in many of the areas where the animal is still abundant, has accompanied an increasing awareness of the need to ensure that the resources are adequately conserved and managed. The questionnaire also sought details of management strategies, either proposed or established. Some countries (Guam, Vanuatu and Tuvalu) have either introduced or are considering size limits, and commercial sale of coconut crabs is prohibited in Yap. Tuvalu discourages commercial harvesting and export. Tokelau finds it necessary periodically to prohibit the capture of coconut crabs for 2-3 months, not for stock management considerations, but to prevent people becoming ill through eating crabs that may have ingested rat baits. Several other countries (including Palau, Solomons, Kosrae, Majuro and Niue) are aware of the need for some management strategy, but do not have adequate resource assessment, biological or ecological baseline data.

Before a specific resource can be managed effectively, knowledge of certain aspects of the species' life history and ecology is clearly essential. This applies particularly to attempts to propagate or culture the animal, because its natural biotic requirements must be emulated in an artificial environment. A search of the literature reveals that the life history of the coconut crab is reasonably well known. Like all other coenobitids (however well adapted the adults are to a terrestrial environment), their early stages are aquatic. Larvae emerge from the eggs as zoeae less than 3 mm in length, first described by Borradaile (1900) and subsequently

in greater detail by Orlamunder (1942). The most successful in vitro rearing of coconut crab larvae was done by Reese and Kinzie (1968), who described the four (occasionally five) zoeal stages, each of which has a duration of approximately one week. The final zoea metamorphoses into a glaucothoe post-larva about 4 mm long, which crawls rather than swims, and like other hermit crabs, adopts an empty mollusc shell for protection, and becomes amphibious (Harms 1932, Reese 1968). At this stage the species is morphologically very similar to glaucothoe of other coenobitids. During the next moult the post-larva metamorphoses into a juvenile (crab I). It continues to carry a mollusc shell for about nine months (Harms 1932), after which time the increasingly sclerotised tergal plates provide sufficient protection to its otherwise vulnerable abdomen. Partly because glaucothoal coconut crabs are difficult to distinguish from those of other common sympatric hermit crabs, the ecological requirements and behaviour of *Birgus* glaucothoe (and juveniles) are very poorly known.

As the juvenile grows (through successive moults), it presumably makes its way further inland through coastal scrub to the environment typically occupied by the adult population. The adult habitat may be quite variable, depending on the physiography of the island upon which the glaucothoe emerged, but its main characteristics are that it provides adequate food and burrow sites (Helfman 1973). Crabs are found in such diverse ecotypes as low coastal *Scaevola* scrub, stands of coconuts (Helfman 1973), and tropical rainforest (Abdulali 1971). However, Amesbury (1980) reports that they are rarely seen in the interior of high mountainous islands such as Guam.

Some accounts (e.g. Gibson-Hill 1947) suggest that adult crabs are inquisitive and will gather in groups to investigate unusual objects, but by and large the animals are rather secretive, avoiding potentially dangerous intraspecific conflict by using a repertoire of agonistic behaviour patterns (Helfman 1977a). Crabs tend to stay in a given area as long as food is locally available, rarely foraging more than 100 m or so from their burrow or hiding place (Harms 1937). However, they are equally capable of a nomadic existence (Helfman 1973) when food becomes scarce. Patterns of activity have been described in some populations as being nocturnal (Chapman 1948, Andrews 1900, Holthuis 1959, Amesbury 1980) and in others diurnal (Andrews 1900; Linsley 1934; Reyne 1939). The difference appears to depend on the presence of human activity—close to human habitation coconut crabs tend to be cryptic during the day and active at night (Reyne 1939).

Much of the early literature deals with the food and feeding habits of coconut crabs, particularly with respect to their ability (or otherwise) to cut down and open coconuts. Reyne (1939) summarised much of the evidence, concluding that *Birgus* is omnivorous, a scavenger, and probably incapable of actually cracking open an undamaged nut. Primary foods are coconut flesh and the fruits of the screw-pine (*Pandanus*), *Canarium* spp., sago palm (*Arenga listeri*), *Terminalia*, *Barringtonia*, and *Artocarpus*. The literature abounds with descriptions of

food items, from fruit and coconut husk to turtle hatchlings and dead rats. A more recent summary of the crab's food and feeding behaviour is provided by Davis and Altevogt (1978).

Being arthropods, coconut crabs can grow only by moulting. Crabs are exceptionally vulnerable to predation during the moulting process and immediately afterwards while their new shells are very soft. Coconut crabs cast off their exoskeletons underground, in shallow burrows dug in loose earth or sandy soil (Gill 1876; Helfman 1973; Held 1963; Amesbury 1980). The burrow entrances are plugged with earth, which often forms a small but visible mound on the surface (Amesbury 1980). Crabs removed from burrows are characterised by a swollen abdomen which is probably the result of the accumulation of food reserves in the hepatopancreas to tide the animal over the ecdysis period, which may last a month or more (Held 1963). Apart from Held's observations on the moulting and growth of one small crab captured on Rongelap Atoll and maintained in a laboratory at Washington University for about 18 months, there are no published data on coconut crab growth. Gibson-Hill (1947) states that coconut crabs '... are said to reach maturity in their fourth year, after the eighth moult', but provides no supporting data. On the basis of his work with a small captive crab, Held (1963) estimates that animals with cephalothoracic lengths exceeding 10 cm (which are common) could be about five years old. According to Helfman's (1973) conversion factors and Amesbury's (1980) length-weight relationship, a CTL of 100 mm would correspond to a weight of about 720 g. As individuals at least four times this weight have been observed (e.g. Amesbury 1980) the inference is that, compared with other crabs, *Birgus* is characterised by a rather slow growth rate. From the resource management point of view it is very important that the growth parameters be established with some degree of precision. It is known, however, that males grow to a larger size than females (Reese 1965, Helfman 1973, Amesbury 1980).

Mating between sexually mature adults is believed to occur in the summer months (Horstmann 1976), and there is but a single published report of the copulatory act which is brief, occurs on land, and is not preceded by elaborate courtship behaviour (Helfman 1977b). After an as yet undetermined period, mature ova are extruded by the female and presumably fertilised simultaneously by sperms from the spermatophore mass deposited on the crab's undersurface. The egg 'sponge' which contains about 100 000 eggs is attached to the ventral surface of the abdomen by means of three feathery pleopods (Alexander 1979, Helfman 1973).

Reported observations of ovigerous females suggest that the reproductive period is mid-year in the northern hemisphere (Reese and Kinzie 1968, Helfman 1973) and around January–March in the southern hemisphere (Andrews 1900, Reyne 1939, Gibson-Hill 1947). As one approaches the equator seasonal differences become less pronounced, so in equatorial regions reproductive activity may be less restricted to a particular time of the year, and be influenced by factors other than temperature and photoperiod.

There is little available information on the length of time that the females carry the egg 'sponge', but Reese and Kinzie (1968) reported that as embryonic development progresses the eggs change from a bright orange-red to a dull yellow-grey colour. When the embryos are mature, the female crab makes its way to the water's edge to release the larvae (Gibson-Hill 1947, Chapman 1948, Schultz 1948), possibly in response to lunar cues (Helfman 1973). Reese and Kinzie (1968) described the crabs' behaviour thus: '.... always at night, the female walked onto the rocks of an intertidal area so that breaking waves periodically washed over her. Upon contact with sea-water, the eggs hatched and the zoeae were liberated into the sea'.

An extensive account of the agonistic behavioural repertoire of *Birgus* is given by Helfman (1977a), and the same author describes the species' copulatory behaviour in another paper published the same year. Behavioural patterns associated with moulting are reported in Held (1963), and some aspects of the activity of glaucothoe have been examined in an experimental situation by Reese (1968). General observations on adult behaviour (feeding, climbing trees, escaping from confinement, movement, etc.) are prolific, especially in the earlier literature (e.g. Wilson 1913, Linsley 1934, Daniel and Prem-Kumar, 1967, Gibson-Hill 1947, 1948, Wiens 1962, Chapman 1948, Johnson 1965, Altevogt and Davis, 1975, and Motoh 1980).

Anatomical studies have been conducted on the ultrastructure of the male reproductive system and spermatophores (Matthews 1956), antennular olfactory organs (Harms 1932, Altevogt and Davis, 1975), and gills, lung and hepatopancreas (Storch et al., 1979). Massaro and Cohen (1978) examined the electrophoretic patterns of several enzymes in *Birgus* using vertical starch-gel techniques, and Lawrence (1970) analysed the lipid content of the hepatopancreas, intestine, gills, testis, thoracic muscle and claw muscle.

Occasional instances of poisoning resulting from the ingestion of coconut crab viscera have been reported from the Tuamotu Archipelago and atolls in the Ryukyu Islands south of Japan (Bagnis 1970, Hashimoto 1979, Fusetani et al. 1980). In these cases certain plant materials (e.g. *Diospyros*, *Hernandia* and *Ceodos*) in the crabs' diet have been implicated.

Several physiological studies have been published in recent years, mostly with respect to the coconut crab's adaptation to a terrestrial environment. Air breathing and gas exchange have been examined by Cameron and Mecklenburg (1973a and b) and Cameron (1981a). Papers by Harris and Kormanik (1981), Kormanik and Harris (1981), Smatresk and Cameron (1981), Cameron (1981b), Burggren and McMahon (1981) and McMahon and Burggren (1981) deal with salt, water and acid-base balance in various land crabs including *Birgus*. Blood and tissue nitrogen compounds have been researched by Henry and Cameron (1981), and Towle (1981) investigated the use of transport-related enzyme activity as an indicator of tissue function in three of Palau's land crabs.

Finally, a few authors have referred to the possibility of artificially culturing coconut crabs. Horstmann (1980) concluded that the successful cultivation of coconut crabs will depend upon controlled moulting, inferring the need for more research into growth characteristics. In 1973 a group of Vanuatu islanders constructed a compound which was stocked with 800-1000 reasonably-sized crabs in an attempted breeding venture (Anon. 1973a, b), but the operation was evidently unsuccessful, and no further attempts appear to have been made. An assessment of the potential for culturing coconut crabs in the Philippines was published by Horstmann (1976), who included some useful and relevant information on techniques used during the brief study. He felt that 'there might be a possibility of culturing *Birgus* in farms', but recognised the need for additional research. A similar operation in Guam showed some promise (Amesbury 1980), but unfortunately a cyclone destroyed the enclosure facility after only a couple of months, and the results were inconclusive.

Because of the potential economic value of *Birgus latro*, and the fact that it can quite easily be transported live, delegates at an aquaculture conference in Hawaii during 1973 nominated the species as a probable candidate for culture in the Pacific (Anon. 1973c). While there is considerable general interest in the potential for farming *Birgus*, most scientists directly involved in researching the species believe that because of the lack of critical data it will be some time before the artificial culture of coconut crabs becomes a reality.

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2 Reproduction, Early Life-History and Recruitment

C. Schiller, D.R. Fielder, I.W. Brown and A. Obed

ALTHOUGH it is the most terrestrial of the crustaceans, the coconut crab *Birgus latro*, like all other coenobitids, has aquatic larvae, and adults must return to the ocean to hatch their eggs. Development is indirect and mature eggs hatch immediately upon contact with seawater, liberating first stage zoeal larvae approximately 2.5 mm long.

The larval life history of the coconut crab has been well documented. First stage zoeal larvae were initially described by Borradaile (1900a) and later by Orlamunder (1942). Reese and Kinzie (1968) carried out extensive laboratory studies and described in detail the duration and morphology of each larval stage. Larvae remain in the ocean as pelagic planktotrophs for 3–4 weeks, passing through 3 to 4 moults. The fourth or, less commonly, fifth zoeal stage metamorphoses into an epi-benthic post-larval glaucothoe which remains in the ocean for another 2–3 weeks. After inhabiting a suitable vacant gastropod shell, the glaucothoe becomes amphibious, emerges from the ocean and adopts a terrestrial existence (Harms 1932). The post-larval glaucothoe metamorphoses into a juvenile coconut crab which continues to carry a gastropod shell, like other hermit crabs, for a further 12 months (Harms 1932) to 24 months (Reese 1987). Sexual maturity is thought to be attained at between 3.5 years (Harms 1932) and 5 years (this study).

Apart from the coconut crab's larval development, little specific information is available concerning its reproductive biology. This chapter presents the results of research carried out over a four-year period (1985–1989) in Vanuatu, Christmas Island (Indian Ocean) and Niue with the intention of providing a detailed overview of coconut crab reproductive biology. For convenience, coconut crab reproductive activity has been divided into six categories, each forming a section for discussion within this chapter. The categories are:

Timing of the reproductive period

Reproductive migrations

Egg extrusion and incubation periods

Egg hatching/larval release cycle and possible zeitgebers

Methods of egg hatching/larval release

Recruitment.

In this chapter much reference is made to research carried out on Christmas Island in the Indian Ocean. It should be pointed out that Christmas Island research was a logical extension of research conducted during a two-year ACIAR coconut crab project based on the Island of Espiritu Santo in the Vanuatu archipelago. This project examined egg release/hatching and larval recruitment in the coconut crab and, among other things, established the presence of an egg hatching/larval release

rhythm, identified several methods of egg release by females, and developed a standard research methodology used during later Christmas Island and Niue studies[1].

Timing of the Reproductive Period

Coconut crab reproductive activity, as indicated by the presence of ovigerous (egg-bearing) females in a population, tends in most geographical regions to be seasonal, occurring in the warm summer months of both the northern and southern hemispheres. It is probable that *Birgus* females produce only one batch of eggs a year.

Ovigerous coconut crabs have been observed in May (late spring) at Palau (Helfman 1973) and in the Philippines (Borradaile 1900a) while Reese (1965, 1987) observed ovigerous females at Eniwetok from April (mid spring) through to August (late summer). Literature concerning reproductive activity of the coconut crab in the southern hemisphere lacks concise information on the extent of the reproductive season. Ovigerous females in the southern hemisphere have been observed in the Loyalty Islands in January (mid summer) (Borradaile 1900a), on Christmas Island (Indian Ocean) from mid-November (late spring) to February (late summer) (Gibson-Hill 1949) and on Great Nicobar Island in March (early autumn) (Daniel and Prem-Kumar 1967).

In Vanuatu the earliest sighting of ovigerous females was mid-November and on Christmas Island, 5 November 1987. However on Christmas Island in 1988 freshly spent females (whose eggs had hatched) were observed on 4 November, suggesting that the onset of reproductive activity was between late September and early October (mid spring). On the island of Munda, Solomon Islands, Chapman (1948) observed ovigerous females in July and August (winter), while in Vanuatu, ovigerous females were observed as late as June (early winter), albeit in very small numbers.

For the sub-tropical southern hemisphere at least, it appears that coconut crabs are reproductively active for approximately nine months each year, from late September or early October through to early June of the following year. In the tropical areas of both the northern and southern hemispheres the seasonality of reproductive activity may lose definition, effectively giving a non-seasonal reproductive period. Although data on coconut crab reproductive activity in Solomon Islands is incomplete, extrapolation of available information (using Christmas Island and Vanuatu data as a guide) suggests that coconut crab reproduction in these islands is non-seasonal, occurring throughout most of the year. However, as discussed later, reproductive activity tends to be concentrated over a much shorter period (December to February in Vanuatu and Christmas Island), with low to very low levels of reproductive activity in the months before and after this reproductive 'peak'.

Reproductive Migrations

Although reproductive migrations are an integral component of coconut crab reproductive strategy, they have received scant attention from researchers, with the result that available information is primarily anecdotal and lacking in detail. Important questions concerning the timing and nature (individual or group) of the seaward migration, residence time of migratory females in coastal areas, and the timing and nature (individual or group) of the return (landward) migration have not been investigated until now.

During the breeding season, female coconut crabs migrate from inland areas to the coast for the purpose of releasing larvae into the ocean. Unlike many other terrestrial crab species in which both males and females migrate, e.g. *Gecarcoidea natalis* (Gray 1981), only *Birgus* females participate in the reproductive migration (Borradaile 1900b; Chapman 1948; Gibson-Hill 1949, this study). Shortly after arriving on the coast gravid females extrude their eggs. Egg maturation requires on average 4–5 weeks, after which time the ovigerous females move to the ocean to hatch the eggs and release the larvae. The hatching process is restricted to a few days each month and occurs in a discernible rhythm.

It is suggested that the coastal migrations of female crabs occur in a series of rhythmic 'waves' having a periodicity the same as that of the egg hatching rhythm. Migration from inland areas is timed so that crabs arrive on the coast between four and five weeks prior to an egg-hatching/larvae-release period.

Field observations indicate that females migrate primarily as individuals, not as part of a concerted mass (cf. *Gecarcoidea natalis*), and congregate in areas within a few hundred metres of the ocean. This migration pattern may be influenced by local topographical features. The natural habitat of the coconut crab is often extremely rugged, with coastal areas usually characterised by jagged limestone pinnacles. Where 'natural pathways' to the coast exist, they tend to be utilised by migrating females. The tendency to access the ocean using 'paths of least resistance' may become manifest on a large scale, giving the impression of a concerted mass migration. Such a situation has been reported on Niue (Schiller 1988) and in Solomon Islands (Chapman 1948). On Christmas Island there is generally good access from inland areas to coastal regions and group coastal migrations of coconut crabs are not common.

Arrival of migrating crabs along the coast is not random, rather there appear to be distinct areas of congregation with certain coastline types being preferred over others. The combination of a 'natural pathway' leading to a preferred coastline type can result in very high local densities of female crabs in near-shore habitats.

Soon after releasing their eggs, females from inland areas depart the coast on their return migration. In Vanuatu two crabs with freshly extruded eggs were fitted with radio tags and their movements monitored. Both crabs remained on the coast for a month, one departed four days after egg release, and the other after eight days.

There is qualitative evidence to support the suggestion that coconut crabs returning inland migrate in groups. On Christmas Island (1987–88 and 1988–89) a total of six close-knit groups of 20–50 freshly spent females were observed crossing a road (2 km inland) from seaward to landward. All such observations were within 5 to 11 days of a major egg-hatching/larval-release period. It appears that the return migration, like the coastal migration, occurs in waves having a periodicity similar to that of the egg-hatching/larval-release rhythm, with each wave commencing 4 – 10 days after an egg-hatching/larval-release period. It is also suggested that the return migration initially is in groups, which later break up with increasing distance from the coast.

To summarise, it is proposed that both seaward and landward reproductive migrations occur in rhythmic 'waves' with a periodicity the same as the egg-hatching/larval-release cycle. Seaward migration is most likely an 'individual' event, with each migratory wave timed to commence such that crabs arrive on the coast approximately 4–5 weeks prior to an egg hatching/larval release period. Egg extrusion occurs soon after the crab arrives on the coast. Females remain on the coast for approximately 5–6 weeks, forming dense transient groups along restricted coastline types. Females depart the coast and return inland 4–10 days after egg hatching/larval release. The return migration is initially in groups which disperse as the crabs move further inland.

Copulation and Egg Extrusion

On the basis of the morphology of coconut crab sperm, Mathews (1956) concluded that both copulation and fertilisation in *Birgus* occur in the sea. This theory was proved untenable by Helfman (1977b) who observed two coconut crabs copulating on land. Coconut crabs mate in the summer months prior to extrusion of eggs by the female (Horstmann 1976 and this study). Unlike other coenobitids, copulation in *Birgus* is brief (approximately three minutes) with little in the way of pre- or post-copulatory courtship behaviour. The male holds the female's chelipeds with its claws and walks forward until the female is on her back, their legs interlaced and abdomens extended straight back behind them with the female's abdomen curved distally over that of the male. The male uses modified coxae of the fifth pair of pereiopods (walking legs) to transfer a spermatophore mass to, and around, the female's oviducts, which open at the base of the third pair of pereiopods.

Female coconut crabs do not possess a seminal receptacle and so it is assumed egg 'laying' takes place soon after copulation (Barnes 1980). Fertilisation of eggs is presumed to occur as they pass through the spermatophore mass during extrusion from the oviducts. The female attaches the newly extruded eggs to setae of the endopodites and exopodites of the three pleopods originating on her left ventral surface, the eggs forming a sponge-like mass which is held beneath the abdomen. *Birgus* extrudes from 51 000 to 138 000 (mean of 100 000) micro-lecithal (low yolk volume) eggs, with a positive correlation between the number of eggs produced and the size of the female (Helfman 1973).

The smallest sexually mature (i.e. egg-carrying) female recorded had a thoracic length of 19.7 mm and was observed on Niue in 1988. Helfman (1973) and Fletcher (1988) both recorded a minimum thoracic length of 25 mm for sexually mature females.

Egg Incubation

The egg sponge, held externally beneath the female's abdomen, is afforded no physical protection from the environment by the abdomen and is therefore susceptible to inundation by fresh or salt water and exposure to desiccating conditions.

Inundation by fresh or salt water. Developing eggs are enclosed by membranes which insulate the egg from short-term changes in the external levels of inorganic ions and water resulting from exposure of the egg to fresh or salt water. As eggs near maturity the protective membranes begin to break down, rendering the egg susceptible to osmotic and ionic stress if exposed to fresh water. In mature eggs the majority of the membranes have broken down and the eggs act as osmometers and eclose immediately on contact with fresh or salt water.

Hence it is only when eggs reach maturity that ovigerous females need protect their egg mass from short-term exposure to fresh or salt water. Females with mature eggs encountering water pools or 'wet' areas characteristically lift the abdomen and egg mass as high as possible off the ground while at the same time raising the rear of the body by straightening the rear ambulatory legs. This way the female can cross shallow pools without wetting her eggs. Exposure of mature eggs to rain results in eclosion and washing away of the zoea larvae.

Exposure to desiccating conditions. Ovigerous females in dry conditions experience rapid dehydration of their egg mass. The female's modified fifth pair of pereiopods, used in grooming of the egg mass, have been observed passing repeatedly from both the branchial chamber and the mouth to the egg mass, presumably utilising branchial water reserves and body fluids respectively to maintain egg hydration. The fifth pair of pereiopods appears to play a vital role in grooming and hydration of the egg mass.

The presence of an egg mass susceptible to 'rapid' desiccation in low-humidity conditions appears to influence markedly the temporal activity pattern and the habitat requirements of the ovigerous female.

Temporal patterns of activity in ovigerous females. While males and non-ovigerous females are frequently observed moving about during the day on Christmas Island, ovigerous females, particularly those with well-developed eggs, are most active during dusk and early evening. The onset of activity occurs earlier in the afternoon when the day is humid (e.g. after rain) or overcast. Protracted dry periods followed by rain elicit intense activity among ovigerous coconut crabs. Greenaway (pers. comm.) observed that activity of land crabs on Christmas Island was reduced during windy conditions. Similarly, anecdotal data from Niue indicate that ovigerous females are less active during windy conditions. It is possible that the presence of an egg mass imposes on

the female an 'obligate nocturnality' aimed at reducing the possibility of eggs being exposed to dehydrating conditions. Night activity of ovigerous females may, in addition, be limited to periods of low wind velocity.

Habitat requirements of ovigerous females. Vitellogenesis and incubation of extruded eggs requires access to water and inorganic ions (see below). Terrestrial Crustacea, such as *B. latro* and *Gecarcoidea natalis*, with no accessible salt water in their normal habitat, must migrate to coastal areas to access salt water prior to extruding their eggs. These crabs remain in the coastal area during egg incubation and hence must find suitable areas to inhabit. To minimise dehydration of the egg mass, ovigerous females require shelter with high humidity, minimal exposure to drying winds and limited direct sunlight. This contrasts with the land crab *Cardisoma guanhumi*, which migrates to the coast only to release its eggs, returning immediately inland (Gifford 1962). Water required during vitellogenesis and egg incubation is readily available from the crab's 'normal' habitat, avoiding the necessity of individuals having to locate and construct temporary shelter in a 'foreign' coastal environment.

The habitat requirements of gravid and ovigerous *Birgus* females are typified by a coastal freshwater cave complex on Christmas Island. The complex contains a large network of holes and crevices in a humid environment, has ready access to fresh water, and is only 200 m from the ocean. During reproductive periods the complex is used by large numbers of females to extrude and then incubate their eggs. The density of ovigerous females was often so great that crabs were observed climbing over each other or that crevices and holes were occupied by more than one crab. Aggressive interactions in such circumstances were rare. This is in contrast to the findings by Helfman (1977a) that coconut crabs are not gregarious, maintaining individual distances of approximately 1 m through agonistic display. At least during times of reproductive activity, the coconut crab is more gregarious than has been reported previously.

It is suggested that the water requirements of egg production and incubation necessitate that female coconut crabs leave their 'normal' habitat and migrate to the coast, there locating shelter suited to the requirements of a developing egg mass. Near-shore habitat types characterised by a constant and high humidity, ready access to fresh and salt water, an abundance of holes and crevices, and protection from drying winds and direct sunlight are utilised by gravid females to extrude their eggs. The need for specific shelter requirements may result in high local densities of ovigerous females.

Incubation period. Literature on development time of coconut crab eggs is scant and imprecise. Reese (1987) reported that *Birgus* females carry their eggs for about three weeks prior to hatching/larval release in the ocean. Accurate determination of the embryonic development time of coconut crabs is difficult. *Birgus* females with freshly extruded eggs placed in enclosures for the purpose of monitoring egg development

rates have, without exception, aborted their eggs. The only alternative therefore is monitoring individual crabs in their natural environment. Two techniques were used in this study—radio-tracking and mark-recapture.

Radio-tracking technique. Small transmitters were attached to female crabs carrying freshly extruded eggs enabling them to be relocated using a radio receiver. Repeated visits over several weeks allowed the development of eggs on the tagged crab to be monitored visually. As mentioned earlier radio tags were fitted to two crabs with fresh eggs. Both crabs exhibited general site fidelity, remaining in the same area along the coastal habitat. The crabs were rarely active day or night and were sighted only three times during the monitoring period. An important constraint to the effectiveness of radio tracking is the thick rainforest and limestone crevices and pinnacles that constitute the coconut crab's natural habitat. Such conditions are not conducive to long-range reception of radio signals, with the result that tags placed on crabs in crevices in the jungle may have an effective receiving range of only 5–10 m. None the less, radio-tracking has great potential to provide information on many aspects of female coconut crab reproductive activity and behaviour.

Mark-recapture technique. Female crabs carrying eggs, or with large expanded abdomens, were marked using both a felt pen and a carapace-etching tool. Marked crabs encountered during repeat visits were examined and development of the egg mass recorded. Obviously this technique incorporates a sizeable 'chance' factor in that it relies on the observer and marked crabs 'crossing paths'. In addition, data from Vanuatu and Christmas Island indicate that crabs with relatively immature eggs are less active than those with more mature eggs and so are less likely to be encountered by an observer, resulting in 'gaps' in the information on egg development.

Data on coconut crab egg development times, collected using both radio-tracking and mark-recapture techniques, are presented in Table 1. Egg development was divided into six categories using morphological criteria determined through years of observation (Table 2). Egg maturation, the period from extrusion to eclosion, required from 25 to 45 days, with the majority of eggs maturing 27–29 days after extrusion. The eggs requiring 45, 38, and 37 days to develop eclosed synchronously with eggs having a development time of only 27–28 days. It is not yet possible to ascertain whether all development stages of slow-maturing eggs are prolonged or just particular stages, with normal rates of development during the remainder of the maturation period. Crabs arriving on the coast and extruding eggs at different times may have different rates of egg maturation directed at synchronising egg maturation and hence eclosion.

Osmolality and volume of developing eggs

The osmolality of egg contents was measured using the following procedure. Eggs from the endopodite of the first pleopod were removed

Table 1. Development time (from extrusion to eclosion) of coconut crab eggs and the technique used in monitoring egg maturation.

Location	Month/year	Development time (days)	Assessment method
Vanuatu	March 1987	27	R-T
Vanuatu	April 1987	28	R-T
Christmas Island	December 1987	28	M-R
Christmas Island	December 1987	28	M-R
Christmas Island	November 1988	28	M-R
Christmas Island	November 1988	45	M-R
Christmas Island	December 1988	37	M-R
Christmas Island	December 1988	38	M-R
Christmas Island	December 1988	28	M-R
Christmas Island	December 1988	29	M-R
Christmas Island	December 1988	27	M-R
Christmas Island	December 1988	25	M-R

(r-t: radio-tracking; m-r: mark-recapture)

and ground to a paste using a mortar and pestle. The paste was squeezed through fine (180μ) nylon mesh to remove egg membrane debris. The resulting fluid was collected in a petri dish. A fluid sample was taken immediately and placed in a Wescor 5100C vapour pressure osmometer. If the resultant fluid was too thick for accurate dispensing direct to the osmometer, an 800μL sample was diluted with 800μL of triple deionised water prior to measurement in the osmometer.

Freshly extruded eggs had a mean osmolality of approximately 800 milliOsmoles per kilogram of water (mOsm/kg H_2O), which lies within the range of haemolymph osmolality recorded for adult *B. latro* (Henry & Cameron 1981, this study). *Birgus* produces eggs that in all probability have an inorganic ion composition similar to that of its own haemolymph.

During the course of embryonic development crustacean eggs typically increase in volume (Davis 1964). Freshly extruded eggs of *Birgus* approximate a prolate spheroid in shape (i.e. an ellipse rotated about its long axis) and become increasingly elliptic in longitudinal section as they mature. On Christmas Island, newly extruded (Stage 1) eggs averaged 0.78 by 0.73 mm (mean volume of 0.22 cu mm, n=190). With increasing maturation the eggs enlarged, near-mature (Stage 5) eggs averaging 1.05 by 0.82 mm (mean volume of 0.37 cu mm) (Table 3). As eggs became fully mature (Stage 6) the egg membranes broke up and their shape became irregular, hence no measurements of length or volume were possible. The calculated increases in cross-sectional area (51%) and volume (75%) of mature eggs compared to freshly extruded

Table 2. Stages used to classify embryonic development of *B. latro*.

Egg stage	Description

1 Freshly extruded eggs completely filled with yellow/orange yolk; cellular cleavage not advanced and egg round to ellipsoid in shape; egg contents bright orange in colour and 'granular' in appearance; egg mass resilient when squeezed.

2 Early stage of cellular differentiation up to and including the formation of a small non-pigmented (non-yolky) region; eggs ellipsoid in shape and eyespots present as two red or brown lateral slits; eggs (and egg mass) now deep orange in colour and resilient when squeezed.

3 Eyespots well developed and black in colour, well-formed embryo with limbs present; non-pigmented region comprises approximately 50% of egg; eggs dark orange (less mature and on outside of egg mass) to grey/brown (more mature and on inside of egg mass) in colour; egg mass less resilient when squeezed.

4 Eyespots prominent, embryo almost fully formed and little yolk remaining; eggs (and egg mass) light brown/grey in colour; some deformation of egg mass when squeezed.

5 Near maturity; embryo fully formed with discernible heartbeat; egg sponge dark grey in colour, eggs easily deformed by slight pressure but readily regain original shape. Osmotically inactive on exposure to fresh or salt water. Transition to next stage may be rapid (e.g. 20 minutes).

6 Mature; egg sponge dark grey/brown in colour, outer egg membranes have broken down and sponge is moist ('slushy') to the touch and readily deformed with no regaining of original shape. Exposure to fresh or salt water elicits rapid eclosion.

Table 3. Morphometric and osmolality data for each stage of development in maturing eggs of the coconut crab. The shape of the eggs approximated a prolate spheroid and the following formulae were used: Dimension = $a \times b$; Surface area = $\pi \times ab$; Volume = $(4/3) \pi \times abc$ where a = semimajor axis, b = semiminor axis and $c=b$.

Egg Stage	No.	Morphometrics Dimensions (mm)	Surface Area (mm^2)	Volume (mm^3)	Osmolality No	Osmolality (mOsm kg/H$_2$O)
1	19	0.78±0.03×0.73±0.02	1.79±0.10	0.22±0.02	27	807±28
2	8	0.88±0.05×0.76±0.03	2.10±0.18	0.27±0.03	11	860±25
3	5	0.97±0.03×0.79±.02	2.41±0.11	0.32±0.02	13	916±27
4	1	1.04×0.80	2.62	0.35	11	965±23
5	9	1.05±0.02×0.82±0.03	2.70±0.14	0.37±0.03	15	1054±30
6	2	n.a.	n.a.	n.a.	11	1126±35

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eggs of *B. latro* are similar to those recorded for many other families of Crustacea (Panadian 1970).

The increase in volume of maturing eggs is the result of both water uptake and embryonic growth, which in itself requires water. Only a small percentage of the observed increase in egg volume can be attributed to production of water within the egg itself via normal metabolic processes. Panadian (1970) calculated that only about 10% of the water required for the volume increase in mature eggs of *Homarus americanus* could be obtained via metabolic water production. Egg maturation is also associated with an increase in egg fluid osmolality. On Christmas Island the calculated increase was approximately 40%, mature eggs having a mean osmolality of 1118 mOsm/kg H_2O; hence mature eggs of *Birgus* are hyperosmotic to seawater (Table 3). The increase in osmolality is most probably the result of the accumulation of inorganic ions in ratios similar to that found in seawater (if eggs were of a different ionic make-up to that of seawater, larvae released into the ocean would be exposed to harmful osmotic and ionic gradients). Increasing osmolality of egg contents would most likely be effected by exposure of eggs to water hypertonic to the brooding crab's haemolymph.

Birgus females obtain the inorganic ions and water required during vitellogenesis and egg incubation by drinking from brackish coastal pools. Drinking is effected using the chelipeds, held flat, or points of the second or third pereiopods to transfer water to the third pair of maxillipeds. The maxillipeds either transfer the water to the mouth or to the tips of the fifth pair of pereiopods which in turn transfer the water to the branchial chamber.

Hatching and Release Cycle

While the reproductive season of the coconut crab, as discussed elsewhere, is well chronicled, the timing of egg hatching/larval release by female crabs within that reproductive period is little understood. In Palau Reese and Kinzie (1968) observed *Birgus* females releasing zoea larvae five days after a full moon and two days after the last quarter of the moon. On the basis of this and anecdotal evidence collected in Palau, Helfman (1973) suggested that hatching/larval release in coconut crabs was associated with lunar and tidal rhythms. Attempts by Amesbury (1980) to quantify the influence of lunar and tidal patterns on the release of eggs by *Birgus* on Guam failed.

One of the major objectives of the ACIAR coconut crab project in Vanuatu was to determine the main factors influencing timing of egg hatching/larval release in the coconut crab. To this effect, from November 1985 to June 1987, a narrow 400m strip of coastline in the north-east of the island of Espiritu Santo was monitored regularly for the occurrence of larvae-releasing female coconut crabs. The findings from data collected during this period follow.

During the reproductive season female coconut crabs bearing mature, or near-mature, eggs (Table 2) make their way to suitable coastlines (see

next chapter) for the purpose of releasing their larvae, arriving just on dusk. While it is possible to observe coconut crabs releasing their larvae over the entire reproductive period in Vanuatu, egg hatching in *Birgus* is, for the most part, synchronous, occurring in a semi-lunar rhythm. During the reproductive months of both 1985–86 and 1986–87 (i.e. November to April) release of larvae into the ocean was concentrated around the periods of first and last quarter phases of the moon (see Figs 1 & 2). However on several occasions maximum egg-hatching activity was associated with periods of syzygy (new moon) and full moon. On such occasions egg-hatching activity associated with syzygy was greater than that associated with the full moon.
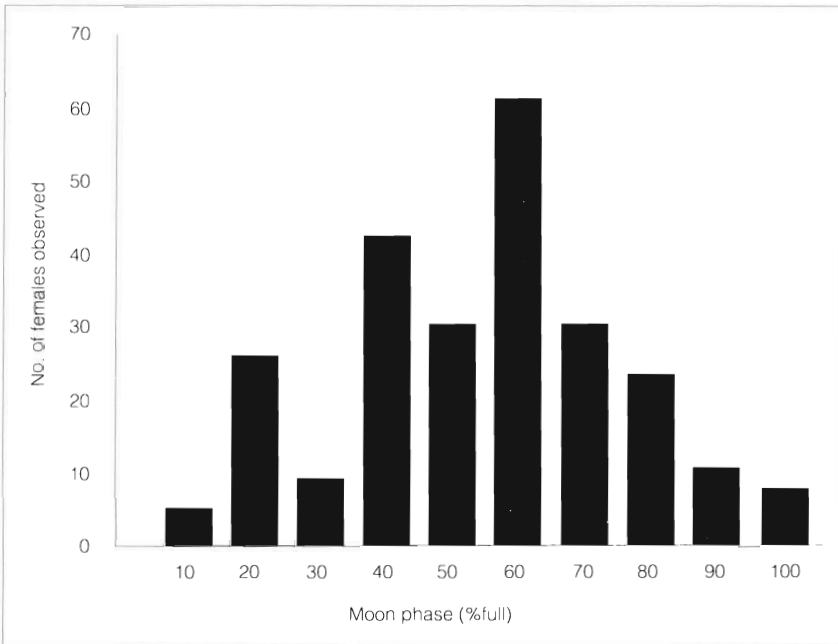

Figure 1. Number of female *Birgus latro* bearing mature eggs observed at different phases of the moon at the Espiritu Santo study area in Vanuatu (November 1985 to April 1987).

Periods of egg hatching and release of larvae persist for 4–7 days. During the first few days there is a rapid increase in activity, culminating in 1 - 2 nights of intense egg hatching activity. Following this 'peak', activity levels decline dramatically, falling close to zero within 2–3 days (Fig. 3).

Tidal data for Espiritu Santo revealed that 'peaks' of larval release activity occurred on or around the night of a dusk high tide. It is suggested that egg hatching and larval release by *Birgus* females in Vanuatu is linked to the period of a dusk high tide, with peak activity occurring on, or in close proximity to, the night of a dusk high tide. On Espiritu Santo, dusk high tides tend to occur 4–5 days after a new or full
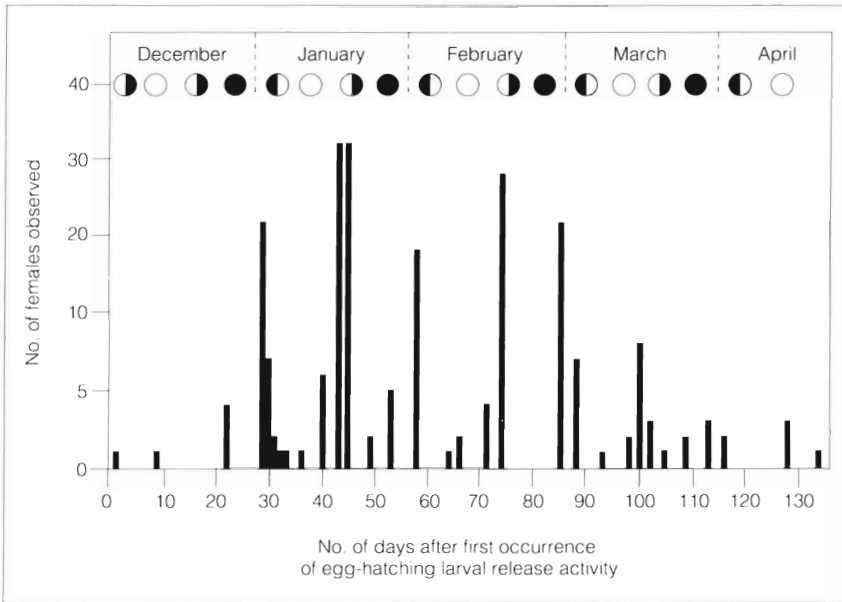
Figure 2. Number of female *Birgus latro* observed releasing larvae during the 1986-87 reproductive period at the Espiritu Santo Study area in Vanuatu. The X-axis indicates the number of days since the first recorded release of larvae on 17/12/86. Lunar phases are indicated with the solid circle representing new moon.
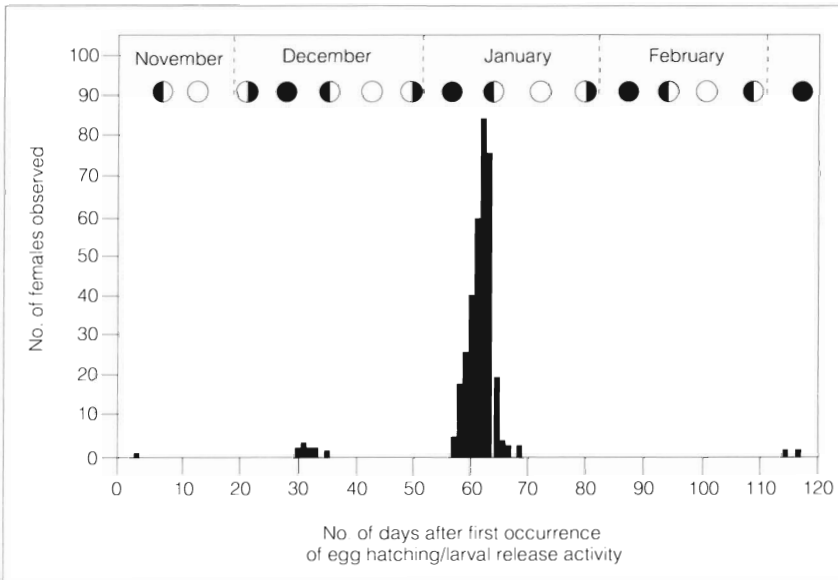

Figure 3. Number of female *Birgus latro* observed releasing larvae during the 1988-89 reproductive period on Christmas Island. The X-axis indicates the number of days since the first recorded release of larvae on 12/11/88. Lunar phases are indicated with the solid circle representing new moon.

moon and so may coincide with the first and last quarter phases of the moon. In Vanuatu it appears that the tidal rhythm, and not moon phase, acts as the main zeitgeber (timing mechanism) of the semi-lunar egg-hatching rhythm. Egg hatching and larval release was also influenced by the lunar cycle with a full moon having an inhibitory effect; however, demonstrating the relationship between lunar and tidal patterns in controlling the egg hatching/larval release rhythm in coconut crabs is not possible using existing data from Vanuatu.

During periods of egg hatching and larval release, activity was greatest in Vanuatu soon after 'last light', with 75% of larvae-releasing females observed within 90 minutes of last light (Fig. 4). A t-test indicated that this was significantly different (p < 0.05) from the temporal pattern observed for non-ovigerous females and males, both of which tended to appear later in the evening. Preliminary data analysis indicates that during periods of egg hatching/larval release on Christmas Island, egg-hatching activity was concentrated near last light on the days leading up to and including the occurrence of a dusk high tide. Maximum activity on nights subsequent to the dusk high tide occurred later in the evening. Patterns of egg hatching and larval release activity similar to that observed on Christmas Island have been recorded for the supralittoral crabs *Cardisoma guanhumi* (Henning 1975) and *Sesarma haematocheir* (Saigusa & Hidaka 1978).
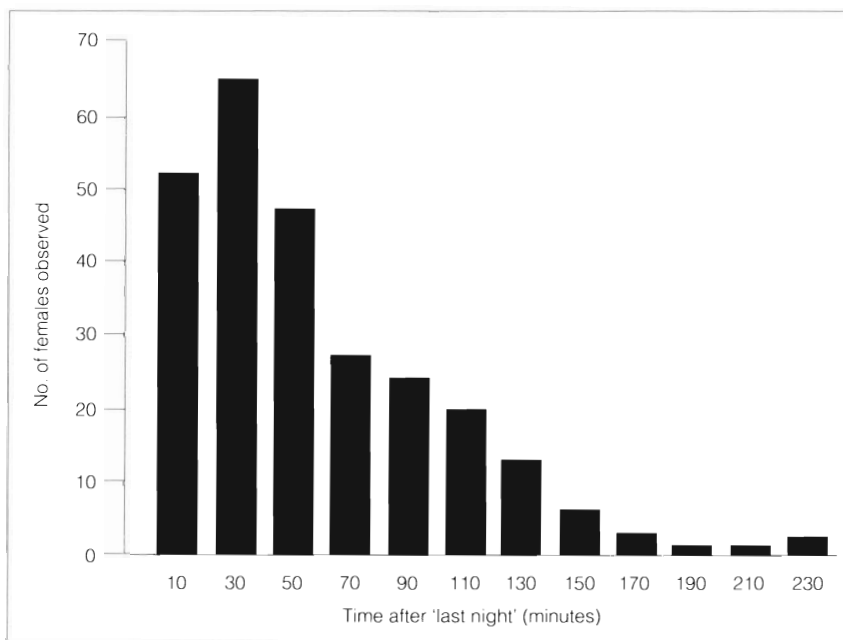

Figure 4. Number of female *Birgus latro* observed releasing larvae during the evening as a function of time (minutes) after last light.

Because of difficulty in visiting the Espiritu Santo study area in Vanuatu with sufficient frequency to sample during all combinations of tide, moon and time of night, it is possible that the Vanuatu data are

biased towards early evening observations. Hence the earlier suggestions that in Vanuatu coconut crab egg-hatching and larval release occur in a semi-lunar rhythm with 75% of hatching/larval release activity occurring within 90 minutes of 'last light' may be specious. It will be necessary to obtain more data from Vanuatu to fully clarify the situation.

Egg-hatching and larval release by coconut crabs on Christmas Island follows a lunar rhythm (Fig. 3), with only one monthly 'peak' of activity, around the period of syzygy. Unlike Vanuatu, dusk high tides on Christmas Island occur within 1–2 days of the full and new moon.

Through amalgamation of Vanuatu and Christmas Island data, a predictive model of coconut crab egg-hatching and larval release activity has been developed. Release of larvae by females bearing mature eggs is synchronous and rhythmic, with lunar, tidal and diel cycles acting as zeitgebers. Each zeitgeber influences the timing of the rhythm at a different level, with the lunar cycle (i.e. occurrence of syzygy) broadly defining the timing of egg hatching within each month, the tidal cycle (i.e. occurrence of dusk high tides) more precisely defining the actual days of egg hatching/larval release, and the diel rhythm defining the time at which egg hatching/larval release commences. Increasing temporal separation between syzygy and occurrence of a dusk high tide is associated with a concomitant decrease in the influence of the lunar cycle on the timing and intensity of the egg-hatching activity. As the lunar influence decreases, there is a shift from a lunar to a semi-lunar rhythm of egg-hatching activity. The intensity of activity in each egg-hatching/larval release period of a semi-lunar rhythm is dependent upon the temporal proximity of the period of activity to full moon or syzygy. Increasing temporal separation from syzygy decreases the intensity of egg-hatching/larval release activity, while increasing temporal separation from the full moon increases the magnitude of the activity. Daily egg hatching/larval release during the active period is generally associated with the time of dusk/night high tide. On days prior to 'peak' activity on a dusk high tide, tides are high during the late afternoon and egg hatching/larval release activity commences at dusk. In the days following the dusk high tide, as high tides occur progressively later in the evening, the onset of egg hatching/larval release is synchronised with the time of high tide.

The diel rhythm component of the proposed model is not yet fully developed. At present the extent to which egg hatching/larval release activity remains synchronised with the time of high tide, as the tides occur later each night, is unknown. Paula (1989) suggests that egg-hatching activity is only synchronised with high tides that occur between sunset and about midnight. It is anticipated that the inclusion of additional data from Christmas Island will permit the relationship between time of egg hatching/larval release and time of night high tide to be quantified, the result being a more accurate predictive model.

According to the model, egg-hatching activity in *Birgus* has a lunar rhythm when dusk high tides coincide with periods of syzygy. This is precisely the situation observed on Christmas Island. For a region such

as Vanuatu, with dusk high tides approximately equally spaced between full moon and syzygy, the model predicts that egg-hatching/larval-release activity will have a semi-lunar rhythm, the timing of each active period being dependent upon the occurrence of dusk high tides. Because the dusk high tides occur between full moon and syzygy and so experience a similar 'moon influence', the two periods of egg-hatching/larval-release activity each month would be of similar magnitude.

The egg-hatching/larval-release model has reached a stage of development suited to confident predictions, for a given coconut crab population, of the periodicity (lunar or semi-lunar) of egg-hatching/larval-release rhythms, the general timing of egg-hatching/larval-release rhythms, the relative magnitude of the two activity peaks in a semi-lunar rhythm of egg hatching/larval release, and (less confidently at present) the time of day during active periods that egg-hatching/larval-release activity will commence.

The generality of the predictive model of egg-hatching/larval-release activity in the coconut crab has been partially validated through correctly predicting the type and time of the egg-hatching/larval-release period for the month of March 1988 on the island of Niue.

Methods of Egg Hatching/Larval Release

Published data on where and how coconut crabs release their eggs are sparse. Reese and Kinzie (1968) observed several *Birgus* releasing their eggs on a rocky shore at Eniwetok and Hicks et al. (1984) observed coconut crabs releasing on a 'sandy' beach on Christmas Island. Helfman (1973) makes reference to freshly spent coconut crabs being observed near a beach at Eniwetok but gives no details while Amesbury (1980) failed to observe any egg-releasing coconut crabs during a two-year study. Research conducted in Vanuatu, Niue and Christmas Island between 1985 and 1989 resulted in hundreds of observations of coconut crab egg hatching/larval release. Four different techniques of egg hatching/larval releases were identified and each was associated with a particular coastline type. The four methods, together with associated coastline types, are:

1. Associated with cliff coastlines having a narrow or non-existent intertidal shelf. A crab bearing mature eggs approaches the edge of a cliff, climbs forward over the cliff edge and reorientates, turning around until it is facing up the cliff. The crab slowly reverses down the cliff until a wet section, or wave splash, is encountered. At this point the crab stops and flexes its abdomen away from the cliff face, letting the egg-bearing pleopods dangle loosely, thus exposing its entire egg mass. If, after a few minutes, it is not splashed by a wave, the female will move further down the cliff and then pause again. In this manner the crab slowly descends the cliff until it is washed over by a wave which results in rapid hatching of the mature eggs and washing away of the newly eclosed zoea larvae. Usually one or two waves are sufficient to 'hatch and wash away' the egg mass. Immediately after egg hatching/larval release the crab rapidly climbs the cliff and usually departs the shore area.

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Cliff-type coastlines with little or no intertidal shelf often experience severe wave action. Large waves breaking heavily on cliff faces on Christmas Island have been observed to wash away coconut crabs attempting to hatch their eggs. It would be to the crab's benefit to have egg hatching/larval release occur as high as possible on the cliff face to ameliorate the dislodging force of breaking waves. It is possibly for this reason that coconut crabs with mature eggs descending a cliff to effect egg hatching/larval release can take 30–60 minutes to traverse only a metre or so. A hasty descent during the periods of calm often associated with wave 'sets' could see the crab suddenly overwhelmed by large waves and washed into the ocean.

2. Associated with coastlines having an intertidal shelf. A crab bearing mature eggs walks rapidly across the intertidal shelf until it encounters a saltwater pool. The crab uses its second pair of pereiopods to test the water depth and if not too deep will cautiously enter the pool, uncurling and raising its abdomen to keep the egg mass clear of the water. The crab orientates itself such that it is near the edge of the pool, facing towards the shore with its eggs held clear of the water. In the absence of waves or wave-induced water currents in the pool, the crab usually will not attempt to hatch her eggs and ventures further out across the intertidal shelf, either by exiting the pool and walking around it, or, if the water is shallow, by walking across the pool. A wave inundating the crab while it is positioned in a pool or walking across the intertidal shelf elicits egg-hatching/larval-release behaviour in which the crab lowers its egg mass into the water and rapidly flexes its abdomen backwards and forwards in small rapid jerking movements. Abdominal flexion or 'pumping' facilitates rapid eclosion of the eggs with most larvae released within 3–4 seconds of the egg mass being submerged. During periods of frequent wave action on the shelf, the crab remains above the reach of the waves until it is ready to move. As the water from a wave recedes the crab quickly moves down onto the shelf and positions itself in readiness for the next wave, usually in close proximity to 'high ground'.

During periods of infrequent wave action, the method employed to effect egg hatching/larval release is similar to that described above, in that the crab will slowly venture out across the shelf until it is swamped by a wave.

3. Associated with coastlines having an intertidal shelf. A crab bearing mature eggs walks out across the shelf and upon encountering a saltwater 'stream' draining the shelf, or flowing from pool to pool, enters the flowing water, orientates so that it faces upstream and lowers its egg mass into the water—abdominal flexing as described above may occur. This method of egg hatching and larval release has been observed infrequently and was usually associated with 'terraced' intertidal shelves across which pools occur at different levels. Inundation of the shelf by waves produces a cascading effect with water flowing from high to low level pools.

4. Associated with coastlines having a sand or coral rubble beach. This method is similar to that described in method 2; in that a crab

bearing mature eggs walks slowly, often diagonally, down the beach towards the ocean. Upon contact with wet sand or water the crab reorientates until it is facing up the beach slope away from the water and raises its abdomen/egg mass into the air. If, after a few minutes, the crab is not washed over by a wave it moves further down the beach and again reorientates. This process is repeated until the crab is inundated by a wave, whereupon the female instigates rapid abdominal flexion resulting in egg eclosion and release of larvae. As with the other methods only one or two waves are required to 'hatch and wash away' the egg mass (Rumpff pers. comm.). This method of egg release is not common and was observed by Rumpff on Christmas Island during the peak egg hatching/larval releasing period. It is possible that high densities of crabs attempting to release their larvae on adjacent rocky cliffs resulted in an overflow of crabs onto the beach. In two years of observation in Vanuatu no coconut crabs were observed releasing their larvae from the extensive sandy beach adjacent to the Hog Harbour study site.

In each method, egg hatching/larval release is invoked by exposure of the eggs to moving water, usually via inundation by waves. The hatching of eggs into still intertidal pools runs the risk of larvae being trapped in the pool until the next high tide. Larvae released into landlocked intertidal pools in Vanuatu were preyed upon by fish and by the crab *Grapsus tenuicrustatus*. Egg hatching/larval release in moving water decreases the possibility of larvae being trapped in tidal pools on the shelf and reduces larval mortality through predation.

In Vanuatu and Niue the varied coastal topography often resulted in egg-release methods 1–3 occurring in close proximity to each other. From limited comparative observational data, it appears that when the ocean is relatively calm, egg hatching/larval release on the intertidal shelf is preferred over egg hatching/larval release from a cliff face. In rough sea conditions, egg hatching/larval release from a cliff face appears the preferred method.

Larval Recruitment

The continuation and proliferation of populations of terrestrial animals producing planktonic larvae relies on the successful recruitment of individuals into that population. This requires that sufficiently large numbers of larvae/juveniles survive as plankton and are able to return to replenish the parental stock (Sandifer 1975). The geographic isolation of the majority of insular (i.e. island) coconut crab populations, combined with the short duration of the planktonic larval phase, suggests that glaucothoe/juveniles recruited into an island population are sourced exclusively from zoea larvae released from that island.

Prior to the ACIAR coconut crab project in Vanuatu there was little published data pertaining to coconut crab recruitment. Such information was considered crucial given that effective management of coconut crab populations is reliant upon a comprehensive understanding of all aspects of the crab's reproductive biology and behaviour.

Despite extensive searches over a two-year period in a wide range of littoral and supralittoral habitats on various islands in the Vanuatu archipelago (e.g. Espiritu Santo, Mavea, Banks group, Torres group), no glaucothoe or juveniles in gastropod shells were found. Similar problems have been encountered by other researchers, with a dearth of small coconut crabs (thoracic length <10 mm) and even fewer glaucothoe being recorded in the literature (Fletcher 1988). Reese (1987) proposed that the fossorial nature of coconut crab glaucothoe and juveniles makes them extremely difficult to find.

Given the difficulty of directly investigating the glaucothoe it was necessary to use size-frequency data to ascertain an estimate of rates of recruitment in coconut crab populations in Vanuatu. On this basis Fletcher (1988) calculated that satisfactory recruitment of glaucothoe and juveniles into Vanuatu coconut crab populations occurred every 5–10 years and could be considered both infrequent and unpredictable. Sporadic recruitment is not restricted to the coconut crab, having been demonstrated in several other crustacean species (e.g. *Gecarcoidea natalis*, Gray 1981).

Larvae released as plankton into the ocean are at the 'mercy' of oceanic and wind-induced surface currents which may transport the larvae substantial distances from the parental stock. Recruitment of larvae back to the parental population is dependent on the vagaries of ocean currents and hence incorporates a large element of chance.

The relative importance of oceanic and surface currents in transporting planktonic larvae will depend on the normal distribution of larvae with depth. The depth at which larvae occur is determined by a complex interaction of phototactic, geotactic and bathymetric responses by the larvae. No such taxis information was available for the larvae of the coconut crab. Consequently a series of light and pressure experiments was conducted on the four zoea larval stages and the post-larval glaucothoe. A preliminary analysis of results suggests the following.

1. First-stage zoea larvae exhibit pronounced positive phototaxis and, in the absence of light, negative geotaxis influenced by a bathymetric pressure response. In dark conditions, first stage zoea larvae will slowly swim towards the surface. Larvae exposed to a pressure increase of 5 kpa (eqivalent to larvae being at a depth of approximately 1.5 m) demonstrated an increased negative geotaxis and rapidly swam upwards towards the surface. The net result is that first stage zoea larvae remain in surface waters (to a depth of 1.5 m) both day and night and so become part of the neuston (surface-dwelling plankton).

2. Second-stage zoea larvae exhibit phototactic, geotactic and bathymetric responses similar to those described for first-stage zoea larvae.

3. Third-stage zoea larvae exhibit phototactic, geotactic and bathymetric responses similar to that described for first-stage zoea larvae although in the absence of light there is a waning of the negative geotactic response, and an increase in the threshold of the bathymetric

response to 10 kpa (equivalent to a depth of approximately 3 m). These changes suggest that third-stage zoea larvae may occur deeper at night and rise into the neuston layer during the day.

4. Fourth-stage zoea larvae exhibit a reduced positive phototaxis, a weak negative geotaxis and an increase in the threshold of the bathymetric response to 20–30 kpa (equivalent to a depth of approximately 7–10 m). These changes suggest that fourth-stage zoea larvae may occur as nekton (mid-water plankton) by night and as neuston by day.

5. Post-larval glaucothoe are epi-benthic (on or near the bottom) and exhibit weak positive phototaxis and slight negative geotaxis. Of the glaucothoe tested, only 40–50% exhibited a pronounced negative geotaxis when exposed to a bathymetric pressure of 100 kpa.

From these results it appears that larvae of the coconut crab occur predominantly as neuston, venturing to greater depths only as fourth-stage zoea larvae or as post-larval glaucothoe. The glaucothoe adopts an epi-benthic lifestyle, although this may be reliant upon the availability of bottom substrate at depths less than approximately 30 m. From this it is concluded that coconut crab larvae are dispersed primarily by wind-generated surface currents, and not by oceanic currents. Hence recruitment of larvae/juveniles into coconut crab populations is probably dependent upon wind conditions prevalent during the larval phase. Put simply, if, after egg hatching/larval release, zoea larvae experience a similar number of days of 'landward' as days of 'seaward' prevailing winds, then net seaward transport of larvae will be minimal and recruitment of glaucothoe/juveniles back into the parental population is possible.

Successful recruitment may be dependent also on the availability of coastal areas suitable for emergence (from the ocean) of recruits onto land (Fletcher 1988). Two aspects of coastal areas may be important.

1. The presence of 'shallow' water near the coastline. Fletcher (1988) suggests that the presence of a steep bathymetric depression close to shore may result in the epi-benthic glaucothoe being 'lost' to the depths.

2. Rugged coastline topography swept by non-depository ocean currents provide little opportunity for safe emergence of the glaucothoe. It is logical to assume that planktonic larvae would be more likely to occur on depository (i.e. sand or coral rubble beach) rather than erosion type coastlines. Coconut crab zoea larvae identified from plankton samples taken from coastal waters around Espiritu Santo in Vanuatu were present only in samples taken from areas with depositional currents.

Given the importance of recruitment in maintaining individual island populations of coconut crabs, particularly in light of the rapid decline occurring in many of these populations, it is essential that every effort is made to locate the habitat of juvenile coconut crabs in order that accurate estimates of rates of natural recruitment may be obtained.

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3 Moulting and Growth Characteristics

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THE rate at which individuals grow is one of the most important aspects of a species' biology. Differences in the speed at which individuals increase from egg to harvestable size and then to asymptotic size have significant implications for the types of policies required for effective management.

Determination of growth rates in crabs (as in other crustaceans) is difficult because the exoskeleton, together with any attached mark or tag, is lost when the animal moults. This makes it very difficult to identify an individual which was marked before its most recent moult. If individuals are maintained in captivity, growth measurements can be made without the need for tagging, but because the species' natural environmental conditions rarely can be duplicated in the laboratory, growth rates calculated from such experiments frequently bear little relationship to those in the wild. Anchor tags are retained by some crustaceans through the moulting process, and have been used effectively in mark-release-recapture experiments on lobsters and crabs (see Aiken 1980 and Hartnoll 1982 for reviews). Unfortunately, anchor tags cannot be used on coconut crabs because the species lacks a suitable consolidated muscle block to hold the tag (Amesbury 1980). Alternative techniques of freeze and heat branding were therefore developed to mark individuals through a moulting cycle (see Fletcher et al. 1989 for details).

Crustacean growth has two components—the increment of growth at each moult, and the time interval between each moult episode. As both factors are subject to sex and size-related variation, animals of both sexes covering a range of sizes need to be examined to determine the age–length key for the species. The only documented growth studies on coconut crabs have been done under laboratory conditions using small individuals (Held 1963; Reese 1968). From the results of the growth of one small male kept in captivity for 18 months, Held (1963) suggested that it would take five years for a coconut crab to reach a large (approximately 1 kg) size. However, on the basis of results of earlier studies on juveniles, Reese (1987) predicted a much slower growth rate, with individuals living for perhaps 30 or 40 years.

Several attempts have been made to estimate the growth rate of large crabs, and most have involved studies on captive animals in some form of enclosure (Helfman 1973; Horstmann 1976; Amesbury 1980). None, however, yielded any useful information, either because the animals failed to increase in size after moulting (Amesbury 1980) or because the project was terminated before data were gathered (Horstmann 1976).

In our study we anticipated that the use of freeze and heat-branding techniques in the field would minimise our dependence on enclosure studies and improve the reliability of growth estimates accordingly. Enclosure studies on captive crabs were done nevertheless, but primarily to provide information on aspects of moult behaviour that would have been impossible to obtain in the field. Moulting frequency was investigated through repeated field observations on marked and recaptured crabs, and regular population censuses were carried out to provide information on moulting chronology. The result of much of this work appear in Fletcher et al. 1989 and 1990.

Methods

Enclosures

Various types of enclosures were constructed to house a large size range of coconut crabs for the determination of moult frequency and to observe their behaviour. The largest (to house the largest crabs) were of chain-link mesh construction, about 1 m wide by 2 m long by 1 m high, sunk into the ground to a depth of 0.7 m. The base of the mesh was covered with concrete, and hinged lids were made from timber-framed mesh or plywood to allow access. Crabs of intermediate size were housed in concrete pipes 1 m diameter by 1 m high, sunk vertically into the ground to a depth of 0.5 to 0.8 m. The bases of the pipes were concreted into place, and they were covered with plywood lids. Other enclosures of a similar size were made from 200-litre steel drums which had been cut in half and capped with plywood lids. The smallest coconut crabs were maintained in 10 to 50-litre plastic bins.

Soil, vegetation and stones were placed in all enclosures, along with containers of fresh and salt water. Crabs in the enclosures were checked three times a week, and fed chicken pellets, fresh vegetables and coconut. The pellets were eaten by smaller crabs, but were generally ignored by animals heavier than 1 kg. At each observation time the activity of the crabs in each enclosure was noted, and a record made of whether the crab had burrowed or was at the surface, and whether or not it had eaten.

Freeze-branding

A detailed account of this method of marking coconut crabs is given by Fletcher et al. (1989). Liquid freon was decanted into a small jar containing various branding tools made from 5 mm foam plastic cut into a variety of shapes (bar, dot, cross, etc.). Excess coolant was then shaken from the brand, which was immediately pressed onto an abdominal tergal plate in one of nine possible positions for about 10 seconds. The procedure was then repeated to ensure a clear mark. This operation appeared to induce little more discomfort in the crabs than resulted from general handling. The mark showed initially on the tergal plate because of atmospheric condensation, but after this surface moisture evaporated no visible sign of the brand remained. Therefore, to allow the identification of crabs prior to their next moult, a unique number was scratched on the carapace with a sharp metal scribe.

Heat-branding

Heat brands were fashioned from 2 mm diameter wire bent to various shapes and welded to the ends of metal rods. The brands were heated until red-hot, then touched against the crabs' tergal plates for three seconds, resulting in the normally blue surface of the carapace turning red at the point of contact. Heat-branding caused a greater immediate reaction from the crabs than did freeze-branding, but no mortality occurred among heat-branded crabs kept in enclosures for periods of several weeks.

Introduction of crabs to Bier Island

Because of the low numbers of marked crabs recaptured from the larger islands (see Fletcher et al. 1990a for details), we established a major sampling and marking program on Bier Island, a small uninhabited islet off the southern Santo coast. All crabs that could be found on this island were marked and released, and another 160 branded crabs collected from other areas in Santo were introduced, bringing the number of marked crabs on the 1.1 ha island to 200. This strategy greatly increased the probability of recapturing marked crabs, and consequently improved our estimates of growth rates.

Purchases of crabs

To increase further the likelihood of obtaining information on the moult increment of naturally-moulting crabs, we ran a series of advertisements on local radio offering a reward of 1000 vatu (approximately $A10) for the return of any crab which had moulted in an underground burrow and which was accompanied by at least part of its exuvium or moult shell. These broadcasts resulted in 20 immediate post-moult crabs, with accompanying exuvium fragments, being brought in to the project team.

Abdomen expansion

The observation of Amesbury (1980) that the coconut crab's abdomen swells significantly prior to moulting was confirmed in this study. In crabs which had recently moulted or had a long period to wait before their next moult, the abdomen were flaccid and the tergal plates were close together. Abdominal swelling results in the hard tergal plates being forced apart in animals accumulating fluid and nutrient stores prior to moulting. We hypothesised that the degree of expansion of the crab's abdomen could be used to estimate the time interval to the next moult, and used, as a simple but effective index of expansion, the linear distance in millimetres between tergite plates divided by the thoracic length. Because the reproductive organs are located in the abdomen in this species of crab, ovarian development prior to ovulation also contributes to abdominal swelling, and it was therefore necessary to analyse abdominal expansion data separately for each sex. Figure 1 shows the standard length measurements made.

Shell condition

Shell age or condition is an alternative method of determining moult stage in crabs, and was recorded for all crabs caught during the
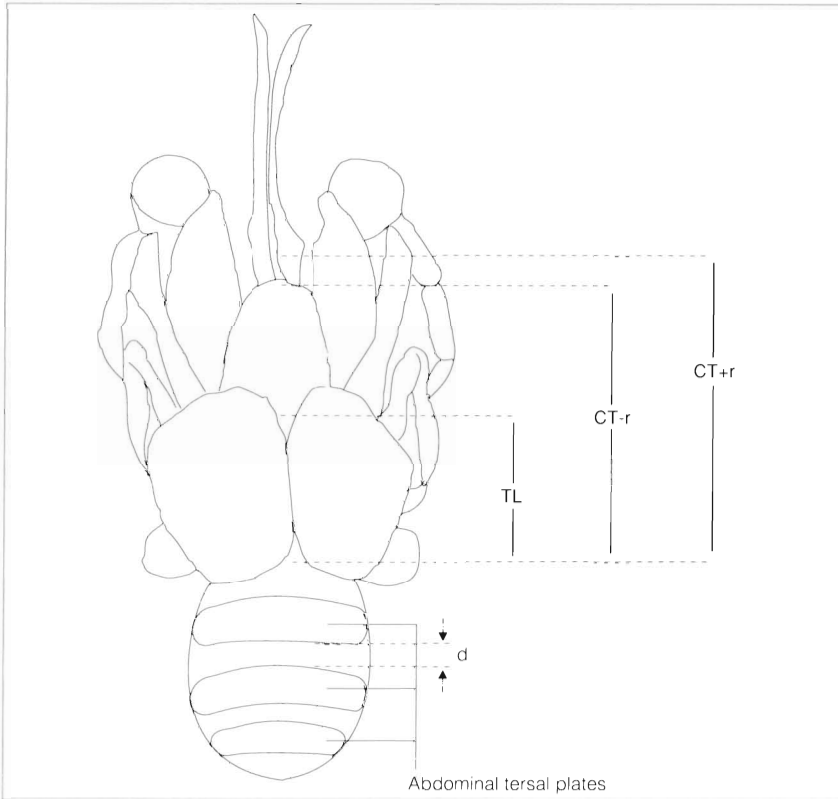
Figure 1. Dorsal (top) view of a coconut crab showing the standard size measurements taken. TL = thoracic length, used in the calculation of abdominal expansion index. CT refers to cephalothoracic length, including (+r) or excluding (-r) the rostrum. d is the distance (mm) between the first and second tergal plates. Note that the crab's abdomen is not normally extended but is depicted that way for clarity

population censuses after mid-1986. This index was a subjective scale which could be rated instantly on the basis of the 'newness' of the carapace. The scale ranged from 1.0, which applied to an immediate post-moult shell, to 4.0 which indicated that the animal had probably not moulted for a period of 10–12 months. The criteria used to assess the condition of the shell were the general appearance of the carapace (its colour and softness, and evidence of abrasion and scratches) and the legs, particularly the dactyls or terminal segments. The dactyls of newly moulted crabs are covered with many fine hairs, and end in a needle-sharp point, but with time the tips become blunt and the hairs are worn off. Although the rate at which this occurs varies between locations, depending upon the terrain, it was easy to distinguish early post-moult from inter-moult crabs, and the most reliable between-site comparisons were thus on the basis of the proportion of newly moulted individuals in the population. Analyses were done both by site and by pooling all individuals and treating size groups separately. Similar types of visual

assessment of moult stage have been used for many crustacean species (e.g. Brown and Bennett 1978.)

Market surveys

Additional information on moulting seasonality was obtained from monthly measurements of abdominal expansion and shell condition of crabs on sale at the open-air market. Samples from this source tended to be limited to the larger males, but sample sizes were frequently much greater than those obtained from the field program.

Buried crab searches

Regular searches of a part of Elephant Island (offshore from Hog Harbour, Fig. 2), were made over an 18-month period to collect moulting coconut crabs. This island was frequented by collectors specifically looking for crabs in a soft-shell condition. Crabs which had recently moulted provided additional data on the moult increment and its relationship to pre-moult body size, as well as on the seasonal cycle of moulting activity.

Results

Moulting behaviour

The use of subterranean burrows is evidently a special adaptation to facilitate the moulting process of coconut crabs in a terrestrial environment. Data from our enclosure studies enabled us to estimate the length of time the crabs spend underground while they are moulting, and also the time required for the new shell to harden. During the course of this study 24 crabs moulted in the enclosures and were buried for periods ranging from three to 16 weeks. The time taken to moult was related to body size, with smaller animals generally being buried for less time than larger individuals (Fig. 3). In three instances moulting was achieved without the individuals being buried, and this provided an opportunity to observe the method of shedding the old exoskeleton. Field observations provided information on the structure of the burrows.

Prior to moulting the crab generally makes a burrow by digging a hole and tunnelling underground in a sandy area some distance from its normal rocky habitat. As the crab begins to dig, it scoops out the soil using its large chelae and leaves a tell-tale fan of disturbed earth around the entrance. As tunnelling continues, the soil is replaced behind the crab, blocking off the entrance. These tunnels are often complicated, doubling back on themselves and passing beneath rocks and trees, and making them difficult to follow by probing from the surface. The average distance from the entry point to the terminal moult chamber was about 1 m (Fig. 4) and there did not appear to be any relationship between the size of the crab and the length of its tunnel. The end chambers were typically about 50 cm below the soil surface, although smaller crabs tended not to dig as deeply as large individuals (Fig. 5). The volume of the moulting chamber was directly related, however, to the size of the crab (Fig. 6) and was about twice the volume of the animal, presumably
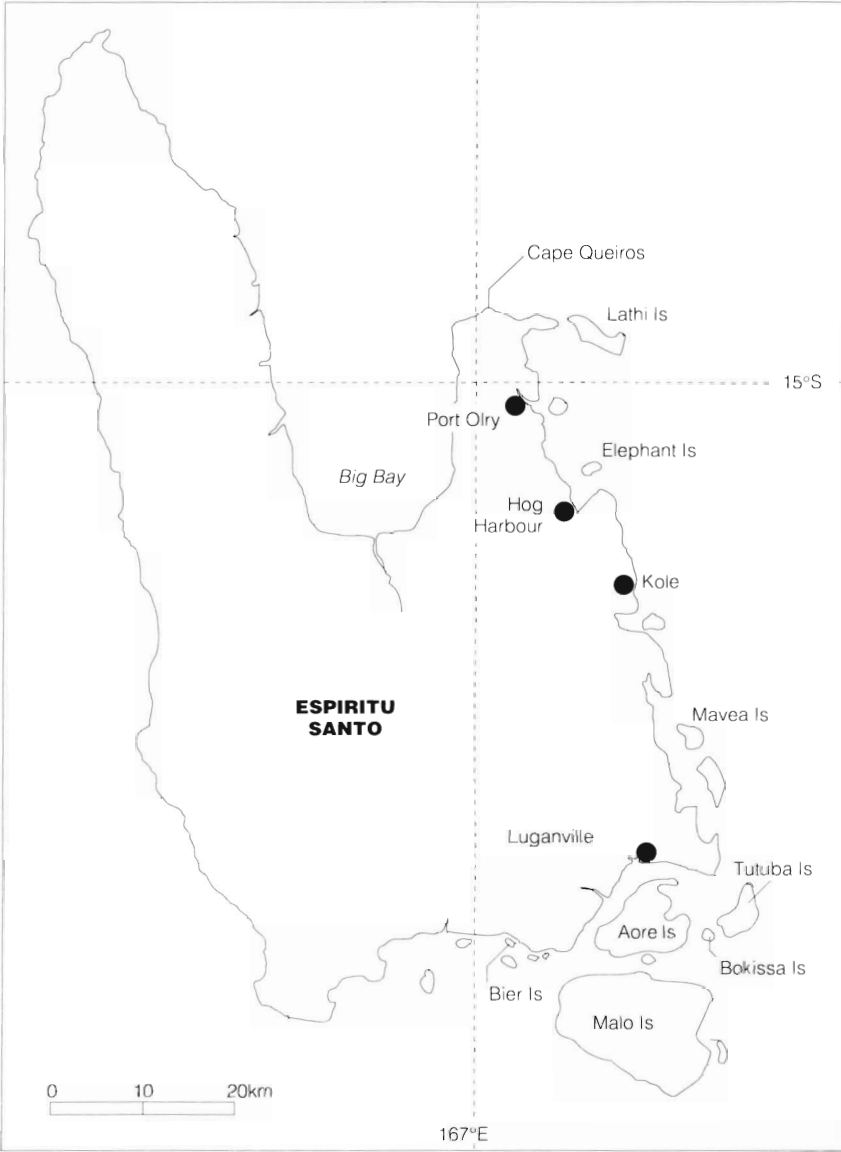
Figure 2. Espiritu Santo (Vanuatu) showing the sampling sites at Hog Harbour and Elephant Island.

to allow it sufficient space to turn round. The walls of the chamber were well compacted, preventing the friable surrounding earth from caving in. It is interesting that these chambers were excavated in dry sandy soil, and no free water was present in any examined.

After completing the tunnel the crab begins to resorb minerals from the old exoskeleton which becomes brittle, and the crab beginsto lose
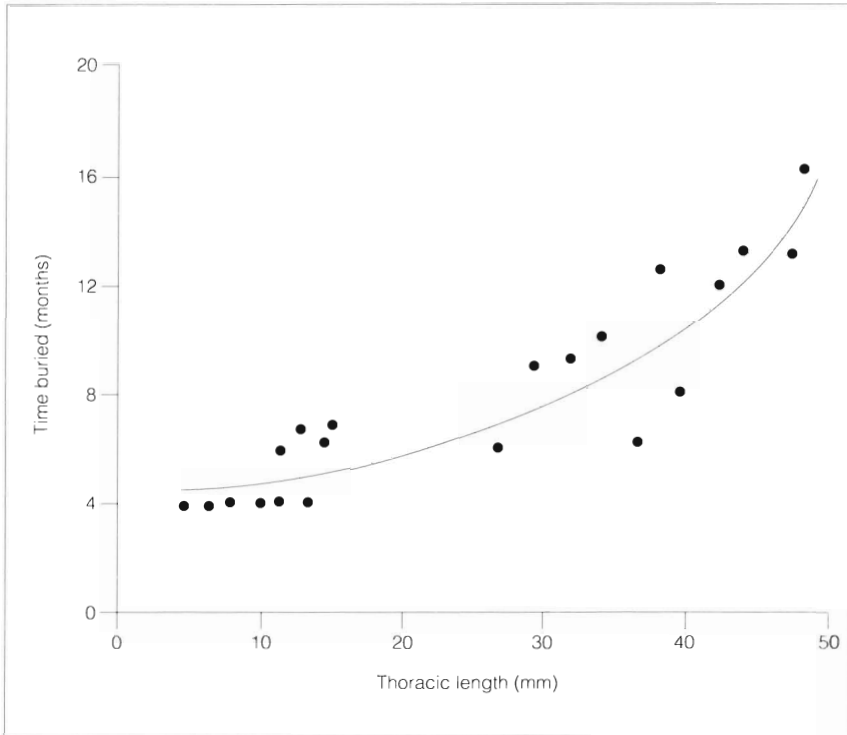
Figure 3. Relationship between the size of the crab and the length of time it remains underground to moult.

mobility. Immediately before moulting it can barely move at all, and the exoskeleton is so brittle that it can be broken with mild pressure. We were also able to use this characteristic to estimate how close a crab was to moulting. At this stage the crab's abdomen is still greatly distended, and considerable care is needed to avoid damaging the animal during handling.

The old exoskeleton separates where the thorax and abdomen join, and the crab then pulls back very slowly, over a period of one to two hours, drawing out the new limbs. The new exoskeleton has a soft leathery feel and is pale bluish-white in colour, particularly at the ends of the legs. It appears at this stage to have little capacity for further expansion. After withdrawing from the exuvium the crab remains immobile for one to two days, during which time the abdomen is reduced to about half its previous volume. At this point the crab would be very susceptible to dehydration if it were not in a burrow or enclosed space with high humidity. Crabs in this condition placed in large enclosures rapidly lost moisture, their osmolality (an inverse measure of the amount of water in their body fluids) increasing from 700 to more than 1000 units during a period of only a few days, and most subsequently died.
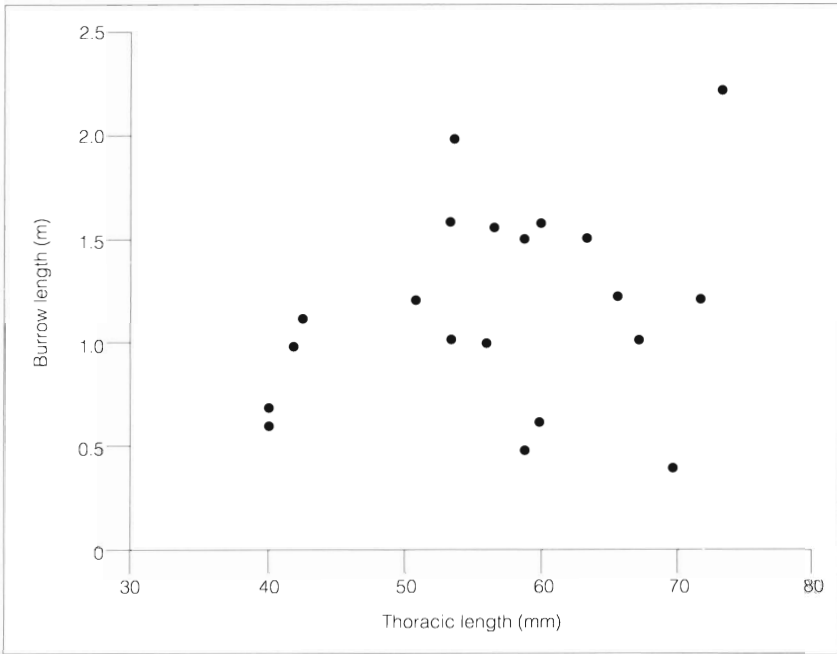
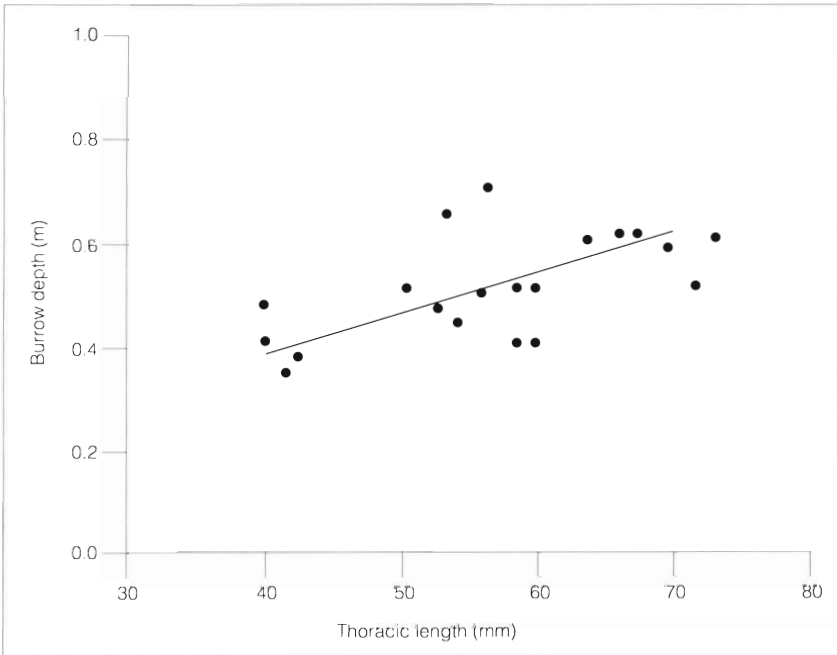**Figure 4.** Relationship between crab size and the length of the moulting burrow.

Figure 5. Relationship between crab size and the depth of the moulting burrow.
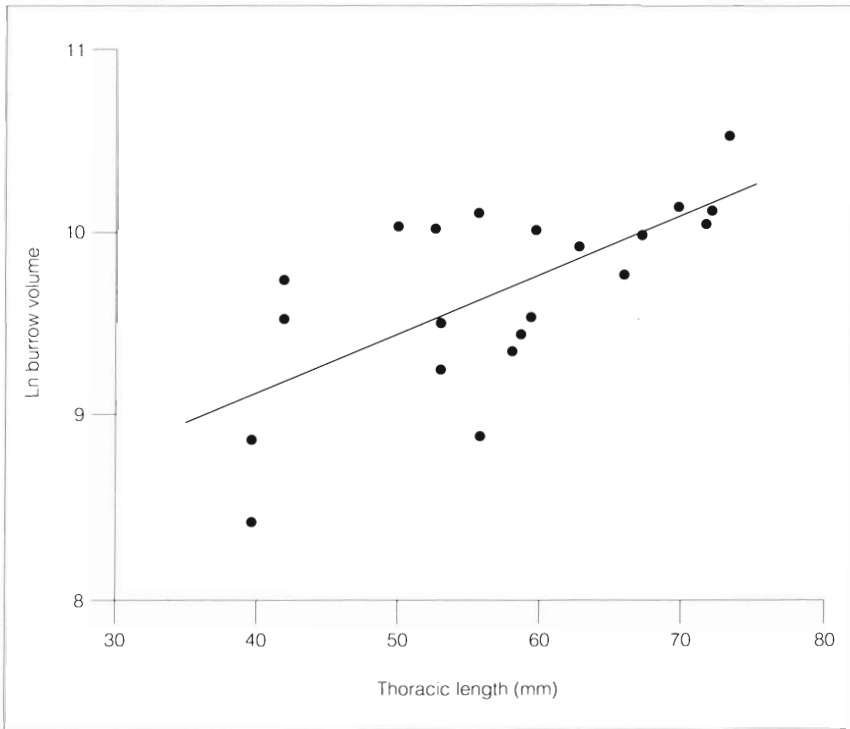
Figure 6. Relationship between crab size and the natural logarithm of the moulting burrow volume.

A few days after moulting, the crab begins to consume the exuvium, and the new shell begins to harden. If the crab is deprived of its exuvium, the new shell does not attain the same degree of hardness. Generally the first parts to be eaten are the thinner thoracic parts of the shell; the heavy claws are almost always the last to be consumed. Only small fragments of the old shell remain when the crab finally emerges from its burrow. It takes from three to four weeks for the carapace of a large crab to harden to the extent that the animal can emerge from its burrow, and by this stage the abdomen is nearly always flaccid, its fluid and nutrient store having been exhausted. On the basis of these observations it seems that large crabs may remain underground for at least six weeks during the moulting process.

Growth increment estimation

Moulting wild crabs. Crab burrows were located by probing the soil with a thin steel rod. Measurements on 14 crabs excavated from their moulting burrows provided the most reliable information on the pre- to post-moult size increase. Since most excavated crabs which had moulted had done so more than a day previously, the recovered exoskeletons were rarely intact, and it was often impossible to take the standard

thoracic length measurement on the exuvium. To overcome this problem we measured various parts (leg segments, claws, etc.) of a few recently-shed exuvia, and were able to estimate the premoult thoracic length (and hence the moult increment) from changes in the size of other skeletal structures. There was considerable variation in the proportional increase in the size of various structures, particularly the chelae, which ranged from 1.2% in a 60.5 mm TL male to 7% in a 53.5 mm male (Table 1). There was also evidence of variation in moult increment between individual crabs of the same size (Table 1).

Table 1. Variation in proportional growth increment in different parts of the exoskeleton of four male coconut crabs.

Thoracic length (mm)	Appendage	Pre-moult length (mm)	Post moult length (mm)	Percentage change
53.5	Left chela	72.0	77.1	7.0
	Right chela	56.0	60.5	7.0
	Pereiopod	65.5	70.5	7.6
60.5	Left chela	96.8	98.0	1.2
	Pereiopod	76.1	78.5	3.1
	Pereiopod	53.0	55.0	3.7
58.3	Left chela (part)	27.3	29.5	8.0
	Pereiopod (part)	35.6	37.9	6.0
53.0	Left chela	85.5	88.2	3.2
	Right chela	64.6	66.8	3.4
	Pereiopod	73.1	75.7	3.5

Mark–recapture experiments. A total of 28 post-moult crabs with brands was recovered, all but two being from Bier Island. In two cases the brands were indistinct, making it impossible to identify the crabs with certainty, and measurements from these crabs were excluded from the analysis.

Enclosure experiments. Apart from a group of small crabs which were kept in the plastic bins, captive crabs failed to provide any useful information on moult increments. In only one instance was there an appreciable increase in size (3.9 mm), and in five cases a negative growth increment was recorded (Table 2). There appeared to be a weak relationship between time in captivity and the size of the moult increment, suggesting that the longer the crabs were kept in captivity, the less they grew. Even crabs which moulted within a day of being put in the enclosures grew markedly less than those that moulted naturally in the field (Table 2). Clearly the environment in the large enclosures was having an adverse effect on the moulting process, so no data from these crabs were included in the analysis.

Table 2. Data on the growth of crabs that moulted in the large enclosures.

Enclosure number	Inter-moult period in enclosure (months)	Growth increment (mm)
A1	4.0	0.5
A2	9.0	-0.5
1.2	7.0	2.0
2.1	6.0	1.0
2.2	1.0	-2.9
3.1	4.0	1.1
3.2	3.0	0.5
5.2	4.0	3.6
6.1	3.0	0.1
7.1	5.0	-0.9
7.2	0.5	2.0
5.3	10.0	0.0
4.2	6.0	0.0
4.3	8.0	-0.5
5.3	2.0	0.3
8.1	11.0	-2.0
3.6	5.0	0.1
6.2	6.0	0.0
6.3	0.5	2.0
5.4	0.5	0.0
11.1	6.0	0.0
10.1	0.5	1.0

Data from only the first moults of the group of small crabs were used in the analysis, as subsequent moults also appeared to be influenced adversely by conditions within the enclosures.

Using the combined data from the three methods described above, we determined that the proportional size increment over a moult cycle in coconut crabs is quite small (Fig. 7). The largest observed increment was 16% for a very small (TL 6 mm) male which moulted in an enclosure, while the largest field observation was 12% in a TL 28 mm male (Fig. 7a). The increment, expressed as a proportion of pre-moult size, declined steadily with increasing body size. Most adult male crabs grew less than 10% per moult; those larger than about 50 mm TL increased by 3 or 4%, and the largest crabs grew by less than about 2% per moult. The relationship between size and growth increment for male coconut crabs is described by the equation

$Y = 13.44 - 0.176 \times X$

where Y is the percentage increment and X the pre-moult thoracic length in millimetres. Given this type of relationship, the absolute

increase in length at each moult would be expected to conform to a quadratic function, with small increments at small body sizes, large increments at intermediate sizes and small increments again at large sizes. This appeared to be the case, as is shown by the dome-shaped curve in Fig. 8a.
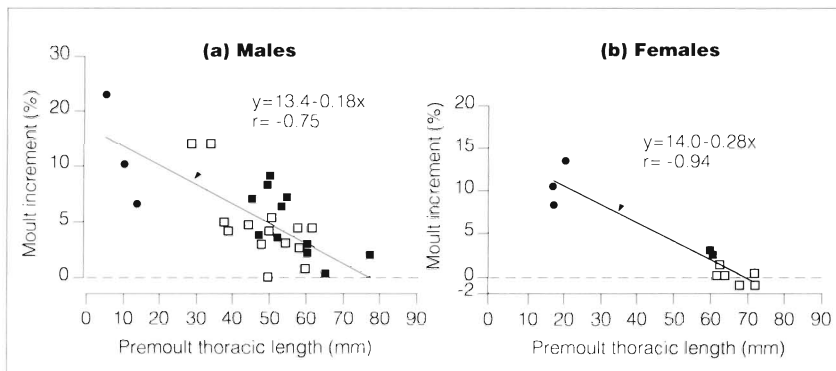
Figure 7. Changes in the magnitude of the moult increment (as a proportion of pre-moult body size) and increasing thoracic length in male and female coconut crabs. Data from enclosure experiments are represented by solid circles, from measurements on excavated crabs by solid squares, and from mark – recapture experiments by open squares.
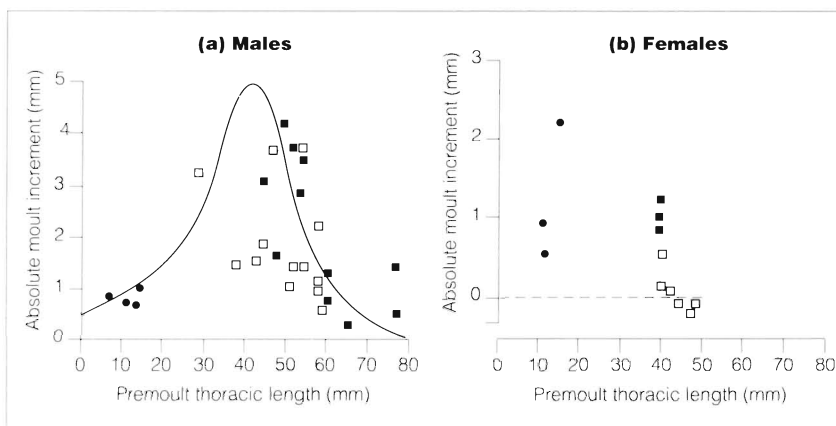
Figure 8. Changes in absolute moult increment with increasing body size in male and female coconut crabs. The curve in (a) was fitted by eye. See Fig. 7 for explanation of symbols.

The same effect was apparent in a Walford-Hiatt graph (Fig. 9), which plots the size (length) at time t against the corresponding size at time t-1. For the juvenile phase of the animal's life history the slope of the regression was 1.1 (the fact that it was greater than unity indicates increasing absolute growth increments with increasing body size). For adults the slope was 0.91 (signifying decreasing increments), and the

point of intersection of the two lines was around 28 mm, which corresponds approximately to the size at sexual maturity. The regression line for adult crabs intersected the diagonal at 84 mm, giving an estimate of the asymptotic length L_∞. The slope of the regression line for females was much steeper than for males (Figs 7b and 8b), as is indicated by the equation

$$Y = 14.0 - 0.28 \times X$$

This line intersects the x-axis at a TL = 50 mm, which approximates the maximum observed size for females. The maximum increment, however, was similar to that of males, suggesting that at smaller sizes they grow at similar rates. Although the data are insufficient to demonstrate it, the main change in the rate of growth for females probably occurs at the onset of sexual maturity, around 25 mm TL. The relationship between proportional growth increment and size in females would therefore be better represented by two separate lines, one before and one after the attainment of sexual maturity.
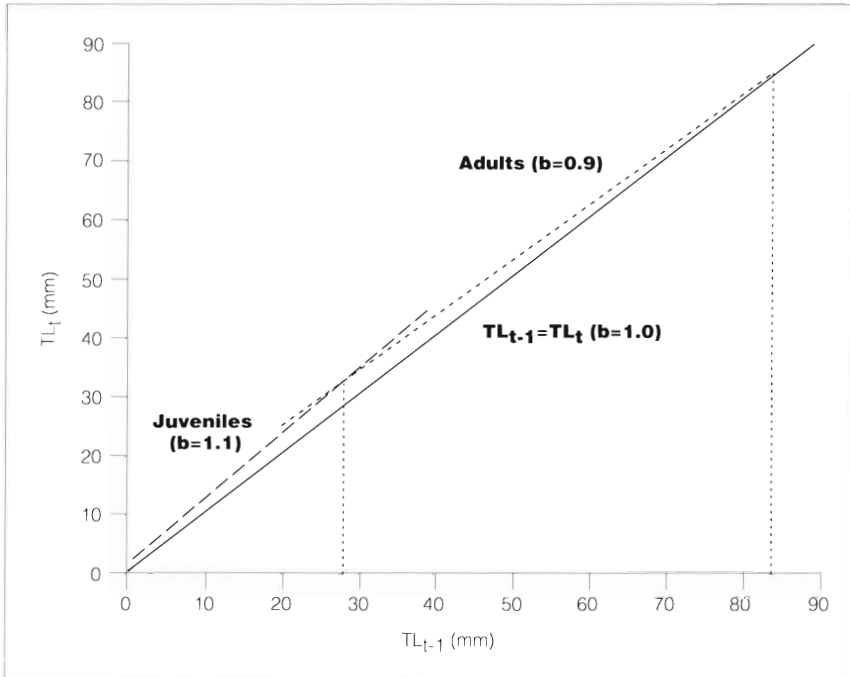
Figure 9. Walford plot of size at time t against size at time t-1. Note differences in slope between juvenile and adult stages, and that the regression lines intersect at approximately 28 mm TL.

Abdomen Expansion

Seasonal changes in the abdominal expansion index of male and female coconut crabs at the various sampling sites are shown in Fig. 10.

Similar plots of the proportion of the sampled crabs which showed no evidence of abdomen swelling are presented in Fig. 11. Clear indications of seasonal cycles in abdominal expansion were evident in populations at Hog Harbour sites A and B (Fig. 10a) and the Mavea Cliff site (Fig. 10e). Abdomen expansion (indicating the onset of moulting activity) in male crabs in these populations peaked in the dry seasons (from about March to July) in both 1986 and 1987. At other sampling sites (e.g. Kole Coast, Fig. 10c) a peak occurred in 1986 but not in the following year, while at the Hog Harbour (ocean) and Kole Cliff (Figs 10b and d respectively) sites the reverse occurred, with a dry-season peak in 1987 but not 1986. The situation for female crabs (dashed lines in Fig. 10) was less conclusive, presumably because of the additional effect of gonad development on the volume of the abdomen. At times when the expansion index peaked in males there tended to be a corresponding peak in the data for females, but fluctuations at other times of the year make it difficult to interpret the cycle with any degree of certainty.

It would be expected that at times when the average index of expansion is high the percentage of crabs with no swelling tends to be low, and vice versa. This in fact is shown in virtually all the site data subsets in Fig. 11, with the greatest proportion of male crabs lacking any appreciable abdominal expansion occurring in the wet season (from about September to February). Again, the situation for female crabs was unclear, for the reasons described above, and although there was a general correspondence in the seasonal pattern between the sexes (e.g. at Hog Harbour (ocean), Kole and Mavea cliff sites and Hiu Island), intermediate peaks and troughs and other inconsistencies were apparent.

Pooling the entire data set (Fig. 12a) gave a clear indication of the moult cycle in male crabs, with peaks in the proportion of non-expanded abdomens evident during the wet seasons in 1985-86, 1986-87 and towards the end of 1987. As expected from previous results, the pooled data for females showed no interpretable pattern. When the data for only very small crabs (<30 mm TL) were plotted (Fig. 12b), there was a significant increase in the number of annual peaks for males, suggesting that coconut crabs of this size moult more frequently than once per year. There was also a much closer correspondence between the sexes in the seasonal pattern, possibly because most of the female crabs would have been below the size at which they become sexually mature, and hence the confounding effects of gonad maturation would have been absent, or at least greatly reduced.

The recapture of marked individuals provided a way to test the value of the abdominal expansion index. There was a significant positive relationship ($r=0.8$, $p<0.01$) between the change in abdominal expansion index and the time interval between measurements. On average, an increase of 1 mm was observed every month, so for larger crabs a greatly distended abdomen occurs every 10 to 12 months, while smaller animals achieve an equivalent degree of expansion in considerably less time.
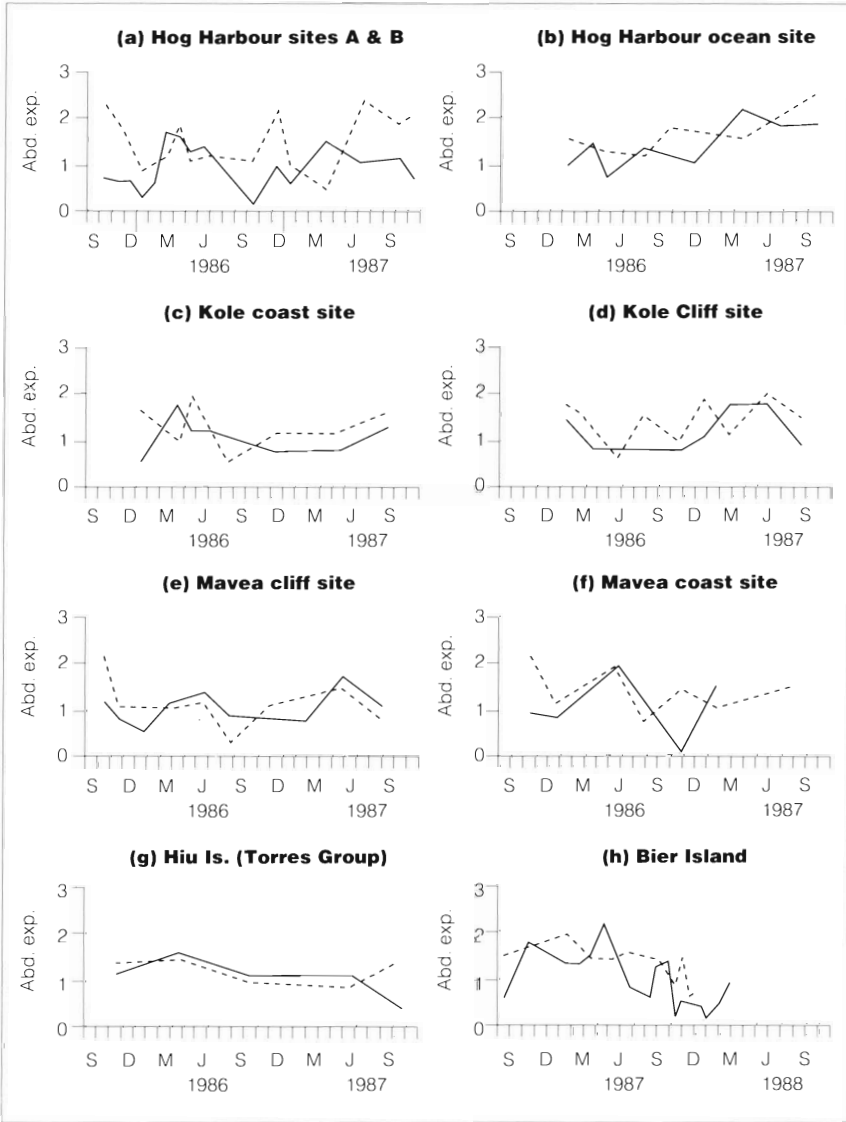
Figure 10. Seasonal changes in abdominal expansion index of male and female coconut crabs (males: solid line; females: dotted line) at the major sampling sites in northern Vauatu.

Shell condition

Another assessment of seasonality in the moulting activity of coconut crab populations was based on visual analysis of plots of the proportion of crabs which had recently moulted (as estimated from the shell index) against time. Shell indices of 1.5 or less were considered to be indicative of recent moulting.

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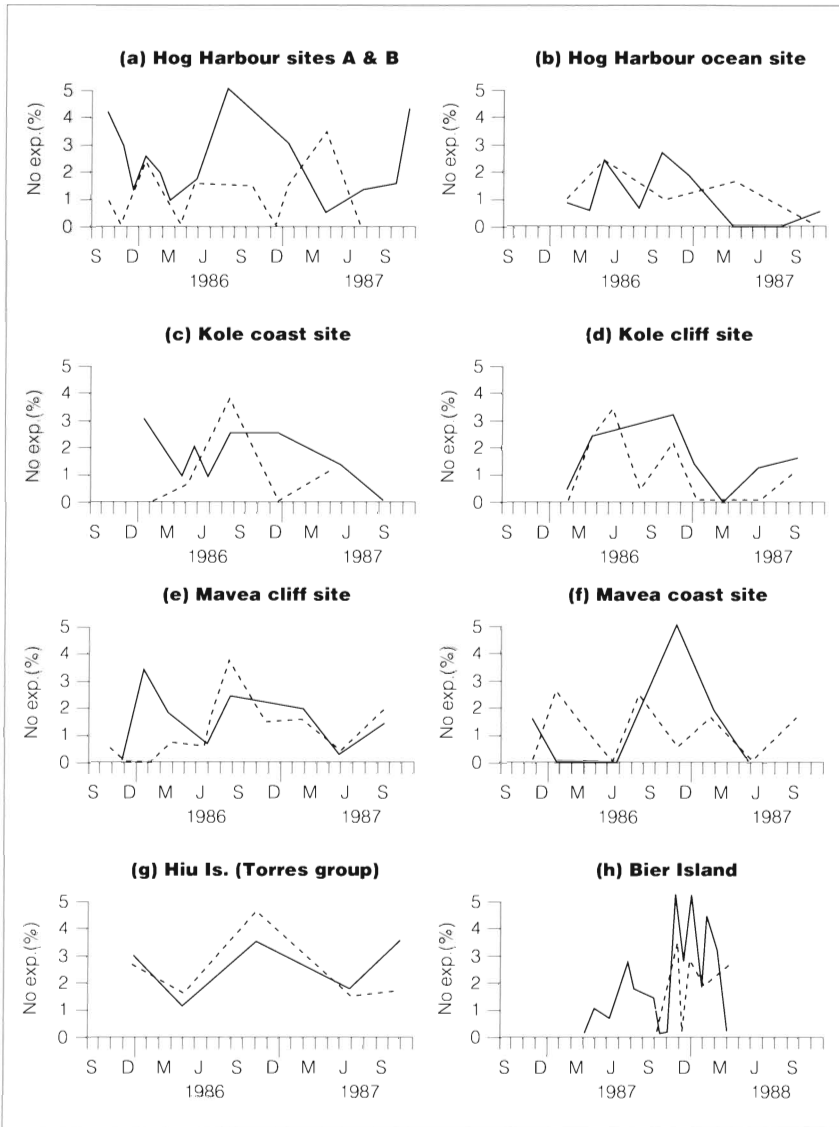
Figure 11. Seasonal changes in the proportion of sampled coconut crabs at the major sampling sites showing no abdominal expansion (males: solid line; females: dotted line).

At all sampling sites the proportion of newly moulted crabs (with a shell index of 1.5 or less) was lowest in the dry season, particularly during the months June to September (Fig. 13a-h). This corresponds well with the results of analyses of abdominal expansion. Peaks in the frequency of new-shelled animals, however, were somewhat variable between sites and from year to year. At Hog Harbour sites A and B and
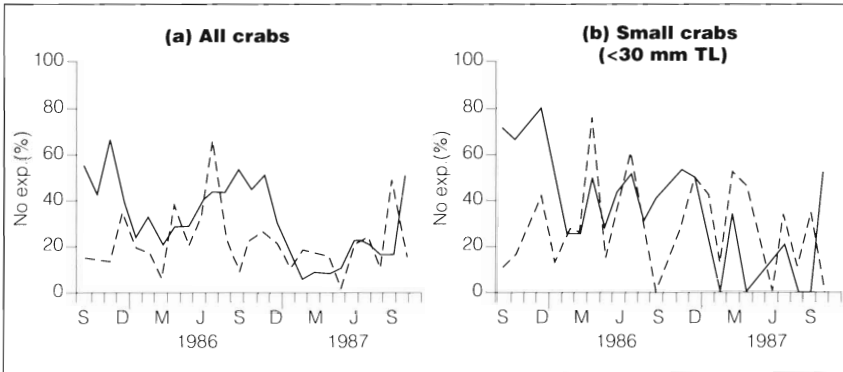
Figure 12. Seasonal changes in the proportion of crabs (at all sites pooled) showing no abdominal expansion (males: solid line; females: dotted line).

the Mavea cliff site (Fig. 13 a and g respectively), males appeared to be moulting at maximum frequency between about July and October, while at the Hog Harbour ocean site (Fig. 13b), Kole Cliff (Fig. 13d), and Bier Island (Fig. 13h) the peak was rather later, between October and February. Identification of the moulting peaks in the Torres islands of Tegua (Fig. 13e) and Hiu (Fig. 13f) was difficult because of the infrequency of sampling, but the tendency was for recently moulted crabs to be more abundant around October in both years.

Female moult patterns based on the shell condition index closely followed those of male crabs at Kole Cliff (Fig. 13d), Hiu Is. (Fig. 13f) and to a lesser extent Mavea Cliff (Fig. 13g) and Bier Island (Fig. 13h). However at the Hog Harbour sites (Fig. 13a and b) and at the Kole Coastal site (Fig. 13c) the seasonal pattern of female recent moults appeared to be out of synchrony with the males.

Examination of recaptured tagged crabs from the Bier Island population allowed an assessment of the method's validity for estimating moult condition. Twenty-seven crabs which had not moulted between observations were recaptured, and in all but three of these the shell index was scored higher than it had been on the previous recapture date. There was a significant positive relationship ($r=0.78$, $p<0.01$) between the increase in shell index and the time interval between measurements (Fig. 14). The index increased by 1.0 unit every three months. Thus the duration of the period between newly moulted (shell index = 1.0) and old (shell index = 3–4) would, therefore, be about 10 months, which is consistent with the hypothesis that crabs moult once per year.

The seasonal pattern in the frequency of moulting crabs found on the Elephant Island transects were at variance, however, with the hypothesis of one moult during the winter (Fig. 15). This figure shows the number of burrow sites which were searched and in which a moulting crab was located and the number of sites at which the crabs could not be located. During 1986 large numbers of burrowed moulting crabs were found in

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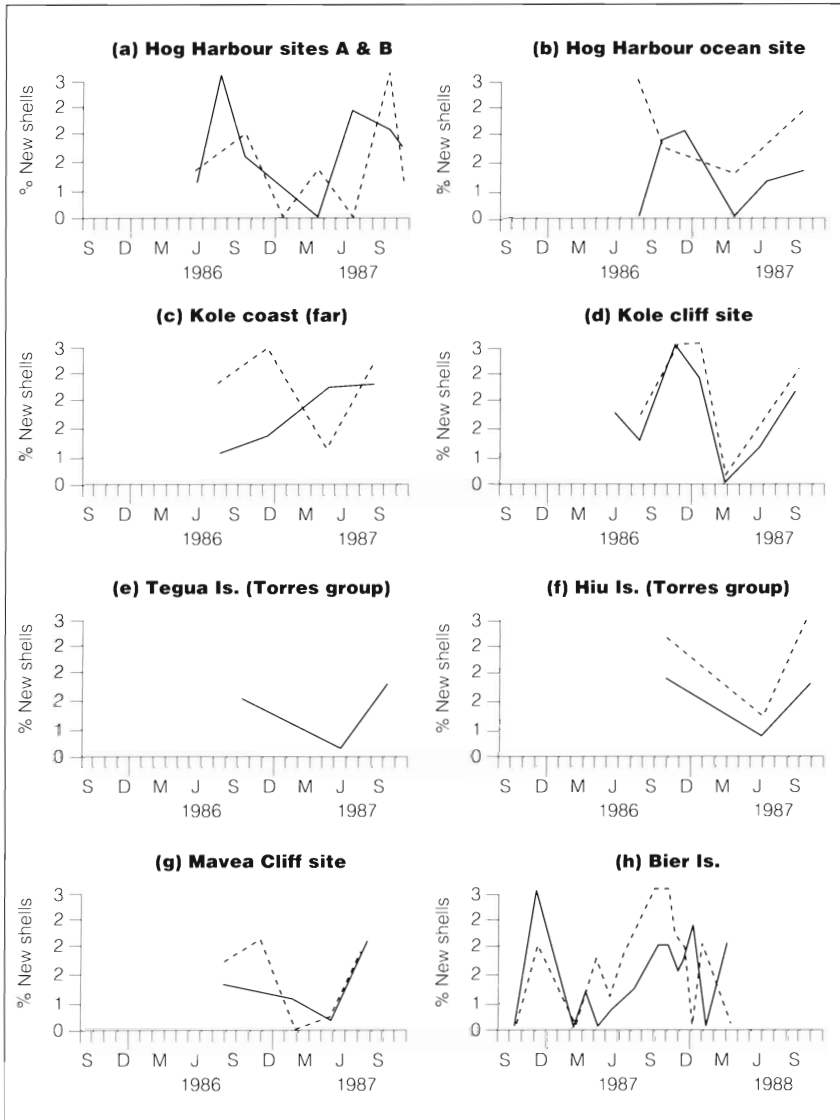
Figure 13. Seasonal changes in the proportion of coconut crabs with 'new' shells (i.e. with a shell index of 1.5 or less) at the major sampling sites (males: solid line; females: dotted line).

June and July but few in November, but in 1987 the pattern was less easy to interpret, as only one moulting crab was located in June. In the second year of sampling the largest numbers of moulting crabs were found in March-April, and there was a second subsidiary peak in early September. The fact that on many occasions (despite evidence of fresh burrow workings) no crab could be found indicates that the probing
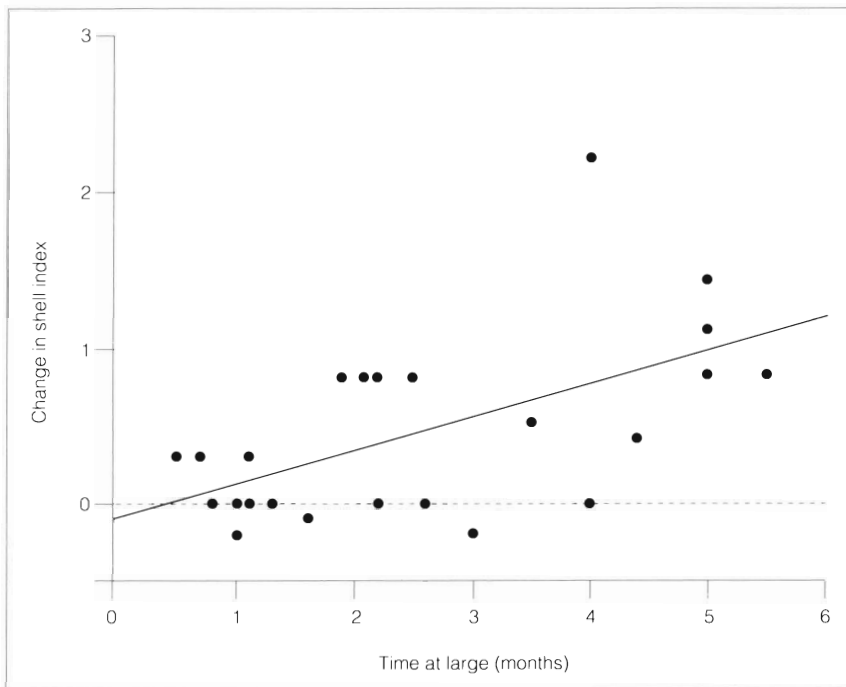
Figure 14. Relationship between change in shell index and the time at large (i.e. interval between time of release and time at recapture).
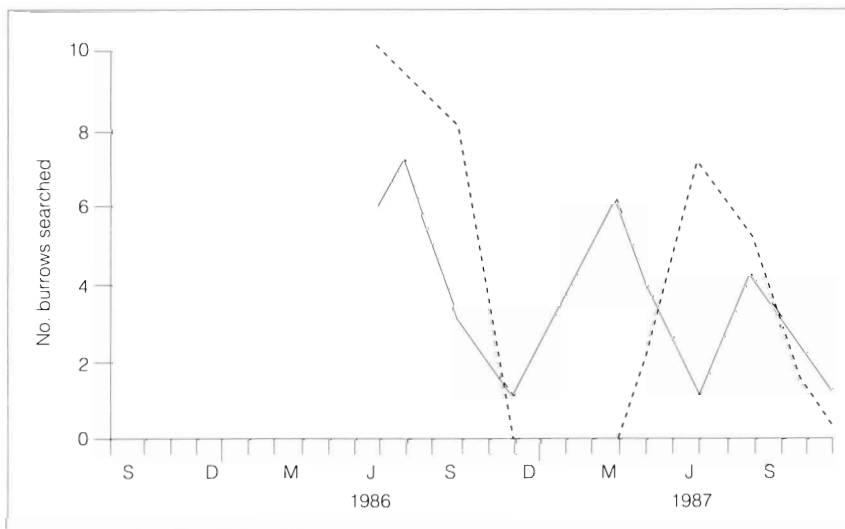
Figure 15. Seasonal changes in the number of searched moulting burrows in which crabs were found (solid line) and in which no crabs were located (dotted line).

technique is not always successful. Thus the total number of burrows located (regardless of whether an occupant was found) may be a better indication of moulting activity. This pattern supports the previous moulting season interpretation, with periods of high burrowing activity during the dry season (June-September both years), and little activity during the wet (November-February).

Growth rates

The length-at-age key or growth curve for male coconut crabs was derived simply by summing over t years the product of the size-specific average growth increment and yearly frequency of moults for each of i time-periods such that

$$L_t = \sum_{i=1}^{t} I_i F_i$$

where L_t is the size (thoracic length) at time t, the I_i are size-specific growth increments, and the F_i are the size-specific moult frequencies. A smoothed curve resulting from plotting this growth model (Fig. 16) shows that the age at which legal size is attained is approximately 13 years, and the asymptotic size (L_∞) is approximately 80.0 mm, which is consistent with the size of the largest crabs found in Vanuatu. The growth curve shown in Fig. 16 is representative of population growth rather than individual growth, which would take the form of a discontinuous growth 'staircase'. Since the smoothed curve is of a decaying exponential form, notional von Bertalanffy growth parameters were estimated from a series of curve coordinates using least-squares procedures. As would be expected in such a long-lived species ($T_{max} \approx$ 50 years), the growth coefficient k is very small, about 0.06. On the basis of an estimated mean environmental temperature of 28°, the empirical formula of Pauly (1980):

Log M = - 0.0066 - 0.279 log(L_∞) + 0.6543 log(k) + 0.4634 log(T)

produces an estimate of natural mortality (M) of around 0.2 for the Santo population of coconut crabs, which (in the absence of exploitation) would correspond to a survival rate of approximately 80% per year.

Discussion

Burrowing for protection is common among crustaceans (Farmer 1973; Chapman and Rice, 1971). Coconut crabs burrow prior to moulting presumably for protection against predation during this vulnerable time, and to minimise the risk of dehydration. It also seems likely that some crabs, instead of burrowing underground, may moult in small crevices which potentially provide a similar refuge. It is not clear what proportion of the population utilises burrows as distinct from crevices nor whether there is any consistent difference on the basis of the size of the animal. The burrows clearly do not protect the crabs from being located by man, and pigs are able to locate moulting crabs in burrows by smell and dig them up.
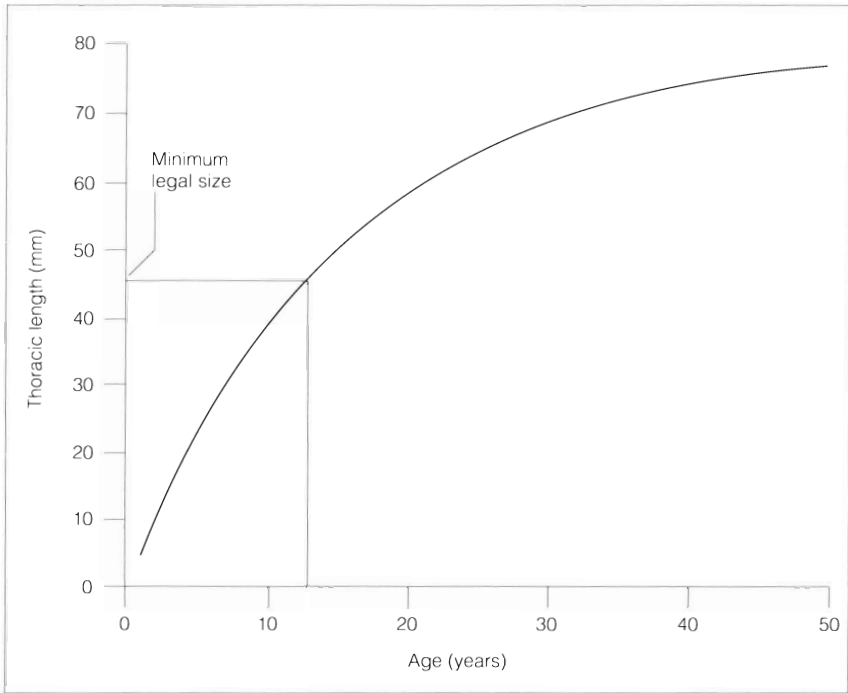
Figure 16. Von Bertalanffy growth curve for the coconut crab *Birgus latro* showing approximate age at the current minimum legal size in Vanuatu.

The method of moulting in *Birgus* is similar to that described by Fielder (1964) for the lobster *Jasus lalandei*, but the time required to complete the process is evidently very different between the species. Fielder (1964) estimated that ecdysis in *J. lalandei* was completed in 15 minutes, while our research indicates that coconut crabs can take from one to two hours. This difference could be due to the structure of the carapace in *Birgus* being more complicated than that of a lobster, or perhaps the mechanical constraints of shedding a massive exoskeleton in the absence of a dense supporting medium may slow the process down.

The time taken between moulting and emergence from the burrow is much longer in larger animals. Small crabs were able to complete moulting in less than one month, but it took up to three months for large individuals. Much of this difference is presumably due to the time taken for the new shell to harden. Held (1963) found that it took only six days for a very small crab (TL=10 mm) to consume the exuvium and emerge, yet the larger crabs in our enclosures required three weeks to complete the task.

The swelling of the abdomen in *Birgus* prior to moulting has been noted previously (Keating 1835; Reyne 1939; Held 1963; Amesbury 1980). Unlike most crustaceans, coconut crabs do not have access to free water at the time of ecdysis, and the distended abdomen is believed to

contain water and a store of nutrients within the enlarged hepatopancreas (Amesbury 1980). Many of the crabs which were observed drinking seawater at the shore had distended abdomens. There seemed to be a general increase in the numbers of crabs found near the seashore, but not involved in any spawning activity, prior to and during the moulting season. The blood osmolality of the crabs at this stage (800 mmol/kg) was not very much higher than normal (700 mmol/kg), so if a large amount of seawater is consumed, the crabs either excrete the salt (Greenaway et al. 1990) or drink a sufficient quantity of fresh water to compensate (Gross 1955).

The consumption of the exuvium by the crab allows for the recycling of minerals which would otherwise be difficult for the crab to procure from its terrestrial habitats. The exoskeleton of coconut crabs is quite thick (more than 1 mm in larger individuals) and represents a substantial metabolic investment. The difficulty of replacing such a large quantity of minerals while the crab is in a subterranean burrow, except through the ingestion of the old shell, was confirmed by a reduction in the hardness of the carapaces of crabs which for one reason or another had been unable to consume their exoskeleton.

Lack of water at the site of ecdysis may partly account for the fact that the observed growth increments in *Birgus* are very much less than the average (23%) for crustaceans (Rice 1968). Moulting on land may constrain the amount of increase possible, particularly as body size increases. A certain threshold level of rigidity must be maintained by the new exoskeleton to avoid distortion due to the force of gravity, and from our observations it appears that the new exoskeleton does not increase significantly after the old exuvium is shed, but rather, through an initial swelling, forces off the old carapace.

The very poor growth performance of captive coconut crabs maintained in enclosures appears to be a common problem. Amesbury (1980) found that, even when the crabs moulted, they did not grow when maintained in enclosures, and similar results have been reported in other unpublished studies (e.g. Horstmann 1976). This effect could be due to either a dietary deficiency or an adverse behavioural response to conditions in captivity, or both, as there was a demonstrable relationship between time in captivity and reduction in moult increment. Crabs did not adapt well to the enclosure environment, and most spent a considerable amount of time and energy attempting to escape. Even crabs which moulted within a few days of being brought to the enclosures failed to increase in length, suggesting that it was not necessarily entirely a nutritional problem. These factors must be considered when evaluating any proposal to farm coconut crabs intensively.

The maximum growth increment observed in this study was 16% of the pre-moult thoracic length, in a small (6 mm TL) male crab. Held (1963) recorded increments of between 9 and 11% for a small male (10 mm TL) kept in captivity, but most of the increments recorded in our study were less than this. The pattern of a declining percentage increment with increasing size is similar to that found in most other

decapods (see review by Hartnoll 1982). Furthermore, the observed difference in growth increment between the sexes is also a common feature of crustaceans, and helps explain the smaller mean and maximum sizes recorded for female coconut crabs. This difference is likely to be a result of the different metabolic investments in reproduction which occur in most crustaceans (Hartnoll 1982). Mature female coconut crabs appear to spawn one clutch of eggs per year, accounting for as much as 30% of their body weight (Helfman 1973). It is not surprising, therefore, that they are not able to invest as much energy in growth as do the males, particularly as the latter may not mate at all in some years.

Data on growth of females is limited, especially for animals in the middle size range. It is possible that there may be two growth curves, one describing the period prior to the attainment of sexual maturity (which would have a similar slope to the males), and one after maturity (which occurs at about 25 mm TL). This has been found to be the case in a number of other decapods, including crabs (Cleaver 1949; Kurata 1962). In contrast to the conclusions of Hiatt (1948), male coconut crabs also showed evidence of a change in the slope of the Walford plot at the size of sexual maturity.

Variability in the magnitude of growth increments for individuals of the same size may be due to dietary conditions prior to moulting or a particular local environmental characteristic (Breitler 1970). The growth increments in crabs on Bier Island were significantly lower than those in crabs from mainland Santo. The vegetation on Bier Island during the monitoring period was poor; the island was dry, and much of the vegetation was consumed by cattle and large resident populations of rats and flying foxes. This may have left little high-quality food for the coconut crabs to eat. A confounding factor to this hypothesis, however, is that all data on growth from Bier Island were obtained from branded crabs, while almost all the data from the mainland were obtained from crabs excavated from burrows. There is no way of determining whether the effect was due to site conditions or the method of measurement.

Our data suggest that adult coconut crabs moult once per year, during the winter months. This evidence was derived from the pattern of abdominal expansion and shell indices of crabs both caught during field trips and measured at the local market. The times at which marked crabs were at large without undergoing a moult provides additional evidence supporting the hypothesis of a single moult per year.

A yearly cycle with moulting occurring in winter was also suggested by Keating (1835) for coconut crabs on Christmas Island; he stated that in June-July 'they all had a large bag full of yellow fat ready to retire and cast their skins. Upon reappearance they look wretchedly lean and their bag is quite empty'. Similarly, both Andrews (1900) and Seurat (1905) stated that there was a single moulting season per year for coconut crabs. Such a pattern has been found in a number of other decapods (Haefner and van Engel 1975; Pollock and Roscoe 1977; Campbell 1983; Newman and Pollock 1974).

At sizes smaller than 30 mm TL, which is close to the size of sexual maturity, this clear pattern was no longer evident. This situation could arise if the smaller animals moult more frequently, or if they do not have a specific moulting season. The high percentages of small crabs with new shells occurring throughout the year suggests that it is unlikely that they moult only once. The small individuals we kept in enclosures certainly moulted twice during the year, and one female (8 mm TL) moulted three times in just over a year. The small crab kept in captivity by Held (1963) moulted four times in 15 months. Larger crabs, however, moulted only once, usually between May and October.

Seasonal patterns in moult condition as determined by the shell index also indicated that smaller-sized crabs moult twice a year. The change in frequency (from 2 moults to 1 per year) may be associated with the onset of sexual maturity, as has been found in other studies (Hartnoll 1982). It seems highly unlikely that female coconut crabs, in particular, could moult more than once and spawn in the one year, and in fact some species are known to spawn and moult in alternate years (Campbell 1983). The pattern for small individuals may have been clearer if only individuals less than 25 mm TL had been included in the analysis, thus effectively excluding mature crabs, but the numbers in the smallest size-group in most monthly samples were too small to allow meaningful analysis.

Some local people believe that the largest crabs do not moult every year, but we have no data to confirm or dispute this. It seems unlikely that the interval between moults could be much more than one year, because the shells quickly become worn and the tips of the legs need to be replaced to enable the crabs to climb efficiently.

No significant differences were observed in moult frequency between males and female coconut crabs. There was a tendency for females to moult slightly later than males, which conceivably is due to the influence of spawning on the time taken for the animal to accumulate sufficient nutrients to undergo a moult. Females may need to moult each year to renew their pleopods, which are important structures involved in anchoring the egg-mass to the abdomen. Because of abrasion and general wear-and-tear, pleopods more than 12 months old may not be adequate for the successful attachment of eggs.

Given the relatively small moult increments and the infrequency of moulting, coconut crabs have a very slow rate of growth (k = 0.06). As a result of the variability in growth increment among individuals, a given size-class contains a broad spread of ages, and individuals from a particular cohort may, after a number of years, attain very different sizes. This precludes the use of length-based frequency analyses as a means of assessing the age structure of coconut crab populations. The estimated longevity, which is very much greater than for most crustaceans (Mauchline 1977; Smith 1980) ranges from 40 to 60 years, with a mean of about 50. This corresponds closely to the estimate of Reese (1987), which was based solely on extrapolation of the growth of juveniles.

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4 Structure and Dynamics of Populations

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and A. Obed

UNDERSTANDING the effect of exploitation on the dynamics of a population requires the estimation of the density and size or age-structure of the population. In populations which cannot be completely censused, and particularly where the animals are caught using bait or traps, an index of the relative population size or density based on catch per unit of effort (CPUE) is frequently used. It is usually assumed that this index varies in proportion to changes in population density or individual catchability (Miller 1979). Determining the size structure of populations is necessary for the assessment of patterns of recruitment and mortality, and can be particularly valuable if samples can be taken before exploitation commences. However, as Miller warns, biased sampling methods can lead to large errors in the parameter estimates.

In this part of the study we looked at the relative density of coconut crabs at a number of different sites that had substantial historical differences in exploitation levels. It was thought that by monitoring a large number of sites, emerging patterns would provide a better understanding of the factors which affect the density of the population. Each area was sampled regularly to determine whether the crabs' abundance varied temporally as a result of exploitation or recruitment. Seasonal variation was also analysed to determine whether coconut crabs exhibit similar changes in catchability or movement patterns that are known to occur in other species of crab (e.g. Carroll 1982) and lobsters (Cooper et al. 1975).

Apart from Helfman (1973), who estimated the size of coconut crab populations on two islands in Palau, there are no data available on either absolute or relative densities of wild stocks of this species. Most researchers have only made subjective assessments of the abundance of crabs in their study areas (e.g. Amesbury 1980), and no monitoring programs have been undertaken to follow changes which may have resulted from exploitation.

Previous studies of coconut crabs have found differences in size structure between the sexes, with males growing to a much larger size than females (Helfman 1973; Amesbury 1980). Observed differences in the average size of individuals between areas have been attributed to variations in environmental conditions (Helfman 1973) and harvesting patterns (Amesbury 1980). All studies involving an analysis of size structure have reported a surprising lack of small individuals in the samples. Reese (1987) believed this was due to sampling bias, but Hartnoll (1982) showed that for long-lived, slow-growing species, relatively few juveniles would be expected, even if the population were maintaining a stable age-structure.

Methods

Study areas

Two main study sites were used in this project: Santo and Torres Islands. The island of Santo (Fig. 1) is the largest in the Vanuatu Archipelago, with an area of 3800 km^2 and a coastline length of 320 km. Its climate is typical of tropical areas, with temperatures generally above 25° C throughout the year, and an annual rainfall exceeding 4000 mm.
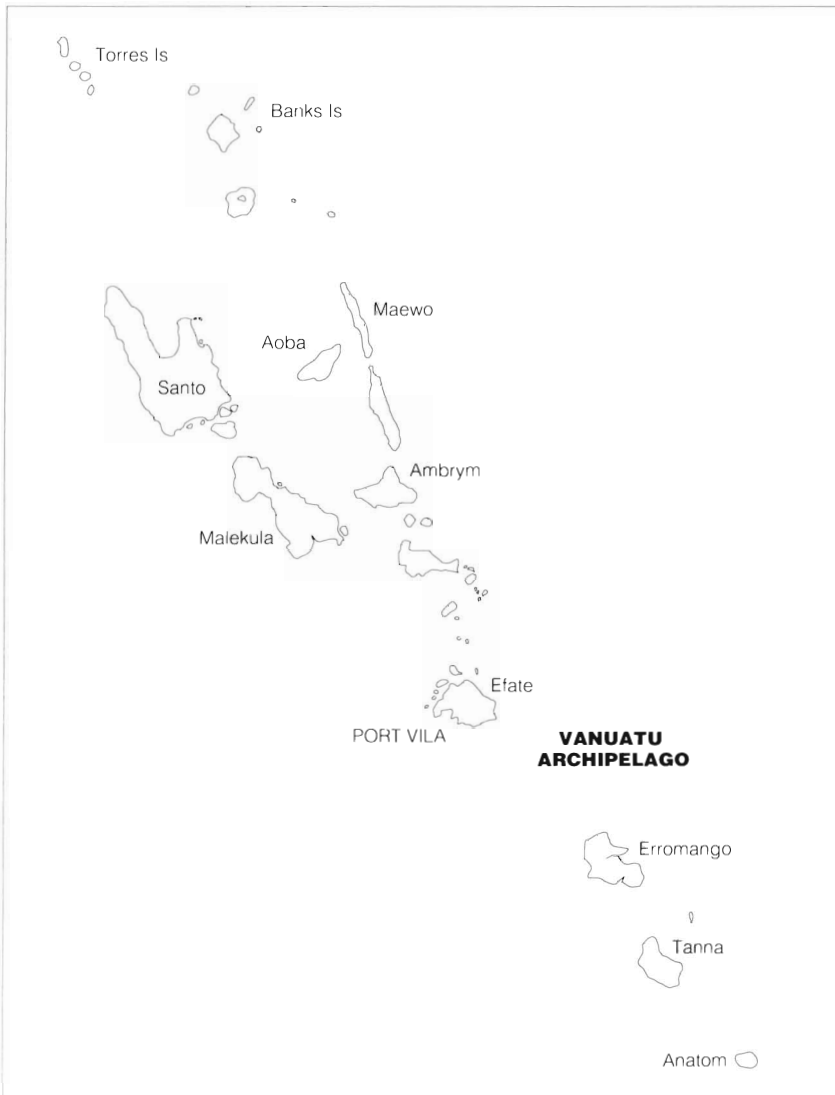
Figure 1. The Vanuatu Archipelago, showing the main study areas.

Most of the study was carried out in north-east Santo (Fig. 2), in the vicinity of Kole, Hog Harbour and Port Olry/Cape Queiros. The region is heavily forested mainly with milktree (*Antiaris toxicoraic*) and whitewood (*Endospermum medullosum*). The dense understorey, comprising many species including nail palm and wild rattan, has not formed a mature canopy because of the disruptive influence of cyclonic winds. The geology of this area is composed of an uplifted limestone reef complex (Robinson 1969), and the study sites were mostly located on a large band of cliffs about 100 m high, the result of an episode of geological uplifting.
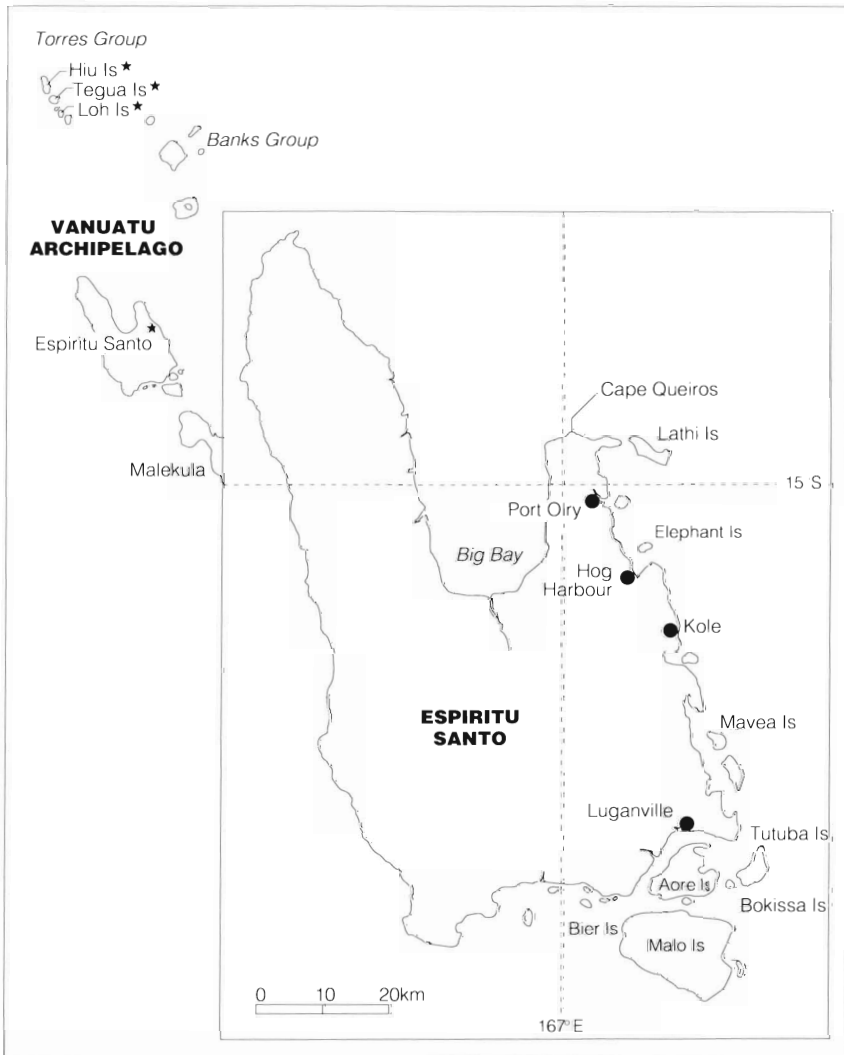
Figure 2. Primary study sites on Santo and in the Torres Group.

Hog Harbour sites A and B were located on the corner of the main cliff, ranging from 30 to 250 m from the ocean. The area was typical of this region with the cliffs providing a series of caves and crevices interspersed with patches of soil supporting a dense vegetation which covered about 70% of the area. This was a very steep site, rising to a height of 30 m above sea level.

The Hog Harbour ocean site was located on the seaward side of a cliff approximately 200 m from sites A and B. This area had less soil than the previous sites and consisted mainly of large uplifted coral boulders. Patches of dense bush were also present, but they constituted less than 50% of the area. Sampling could only be done between 20 and 80 m from the coast because the cliffs were too steep to climb beyond this point.

The sampling site referred to as Hog Harbour Point was situated at the tip of this promontory. There was a series of crevices encircling the point about 5 m above sea level, corresponding to the most recent uplift. Between the sea and these crevices there was little soil but some vegetation (mostly vines) managed to flourish. Behind the crevices the jungle was more dense and the amount of soil was greater.

The village of Kole is about 12 km south of Hog Harbour. Samples in this district were obtained from three sites. The Kole Coast site was similar to the Hog Harbour ocean site, which is not surprising as it is part of the same geological formation. Boulders, caves and ledges were abundant in this area, which extended further inland, to about 150 m from the coast. The cliff formation was somewhat less precipitous, allowing us to sample to a greater vertical height (40 m). The very steep Kole Cliff site was within one km of the coast, but its elevation (approximately 150 m) was much greater than that of the coastal site, and it consisted essentially of a long series of crevices at the top of the cliff. Surrounding these areas were thick bush on soil and above the cliff was a plateau which continued inland.

Mavea Island is a substantial island about 4 km off the south-eastern coastline of Santo (Fig. 2). Sampling was carried out at sites to the north-east and north, where there was a cliff which circled the island approximately 100 — 300 m inland from the shoreline, forming a continuous series of crevices. The area adjacent to the cliff site was thick bush, but much of the land at the base of the hill was under cultivation (primarily with coconuts). The coastal site on the northern perimeter consisted of an undisturbed 50 m band of bush covering a raised limestone platform which was heavily eroded on the exposed ocean side, forming a 'makatea' zone (Wiens, 1962). This provided numerous habitats for the crabs to hide.

Bier Island, a very small island off the southern coast of Santo, consists primarily of limestone with a very thin layer of topsoil. Vegetation on this island is consequently more sparse than in the other areas, and of different composition.

Bokissa is another small island, situated midway between the much larger islands of Aore and Tutuba off the south-eastern corner of Santo

(Fig. 2). It is a mainly sand island with very little vertical elevation or substrates with boulders or crevices. Half the island was an old plantation littered with germinating coconuts, while the remainder was a mixture of pandanus stands (close to the ocean) and typical coastal forest.

The Torres Islands lie in the northern-most part of the Vanuatu Archipelago, some 200 km from Santo (Fig. 1). While different in many ways from Santo and its adjacent islands, raised limestone reefs in a stepped series of terraces are similarly the dominant geological formation (Greenbaum et al. 1975). Overlying the limestone are clay soils of increasing thickness at higher levels. Volcanic outcrops are major features on some of the islands.

Hiu Island is the most northerly of the Torres Group, with an area of 50 km^2. There are two villages, both on the east coast, with a combined population of 80 people. Three main sites were examined on this island. Site 1 consisted of a mixture of raised reefs and areas covered by sand and gravel. The latter had abundant vegetation, mostly hardwoods (*Intsia bijuga*) which formed a dense canopy, but the understorey generally allowed walking through without much difficulty. Site 2, a cliff formation, was similar to that at Hog Harbour, but the foreshore was an unvegetated rock platform that extended for about 30 m. Site 3 (Picot Bay foreshore) was mostly 'makatea' which extended back to just above high-water mark. Behind this was coastal limestone covered with semi-consolidated surface soil supporting dense forest (Greenbaum et al. 1975). The only boulders in this area were close to the cliff.

Tegua (Fig. 2) is the second-largest of the Torres group of islands. It is more circular than Hiu and has two reasonable boat anchorages in the bays on the south and west coasts, where the population of only 20 people lives. Two sites were examined. Site 9 (the main site) was at the head of Latua Bay close to the only village on the island, and was a flat region of sandy soil with few boulders. The vegetation was characterised by a dense canopy with very little understorey. Site 10, on the southern edge of Hayter Bay, was also an area of sandy soil with abundant vegetation, which changed to the south into a series of poorly-vegetated cliffs and crevices.

Catch per unit effort

Our methods of assessing the population density, size and sex structure of the coconut crab population made use of the techniques employed by indigenous crab collectors throughout Vanuatu. This involved cutting a trail through the rainforest in a direction either chosen randomly, or following a trail previously frequented by local collectors. Along these trails we staked out a number of opened coconuts adjacent to habitat considered capable of supporting coconut crabs.

The coconuts were left unhusked, but split into three. They were secured by strands of the fibrous husk tied onto vines, saplings or sticks which had been driven into the ground, or sometimes simply skewered on sharp stakes. The baits were normally set at least two hours before dusk to minimise the possibility of disturbing crabs which may have

been emerging to forage. Between 30 and 50 baits were generally deployed at a sampling site, distributed among 2 to 4 trails or transects. It was originally envisaged that these transects could be analysed separately as replicates, but in most cases the number of crabs caught was too small to allow this. Therefore in most analyses the data from all transects were pooled.

The baits on the trails were generally revisited immediately after dusk, and any crabs encountered either at the bait or on the trail were measured and marked. The following information was recorded: length in mm (cephalothorax including rostrum [CT+], cephalothorax excluding rostrum [CT-], thoracic [TL], and left chela [CLW]), weight, abdominal expansion index, shell age (condition) index, and details of time and locality. More comprehensive descriptions of these measurements may be found elsewhere in this volume, and in the paper by Fletcher et al. (1990a).

Initially the data obtained on the numbers of crabs in an area were to be analysed using mark-recapture techniques. Unfortunately, the very low recapture rate precluded the estimation of population densities using this technique. We therefore used catch rate or catch-per-unit-effort (CPUE) as an estimate of relative density, defined as the number of crabs caught and/or seen on a transect as a proportion of the number of baits set. This index was calculated separately for all crabs caught, for legal-sized crabs (CTL > 90 mm) and for undersized crabs.

Relating these indices to measures of population density is based on the assumptions (i) that the crabs behave similarly in different areas, both in foraging frequency and the range over which they are attracted to a bait; (ii) that CPUE is linearly related to density (i.e. as density increases, CPUE increases proportionately); and (iii) that the size distribution of crabs found at the baits or on the transect are representative of the size distribution of the local population. The first two assumptions were examined directly by experimental addition and removal of known numbers of crabs to and from the population, and indirectly by monitoring areas in which it was possible to estimate the numbers of crabs removed by harvesting. It was hoped that these techniques might allow the estimation of absolute population density.

Estimation of abundance

The relationship between catch per unit effort (CPUE) and absolute population density was determined by a series of modified 'depletion' or Leslie-deLury experiments in conjunction with a Petersen tag release—recapture procedure. These experiments produced an estimate of the catchability (which relates CPUE to abundance), and the results may be found in the paper by Fletcher et al. (1990b).

Activity levels

Another method of assessing the potential yield of crabs at a site was the measurement of activity level, viz. the proportion of baits that had been eaten by coconut crabs at some stage during the evening prior to

our visit. This differs from the CPUE in that it takes into account crabs which have fed but left the bait before the transect was sampled. It is therefore probably a more realistic measure of the number of crabs foraging on a given night.

For this index to be of value we needed to tell with some degree of certainty whether the bait had been eaten by rats, hermit crabs, or coconut crabs. It took about a year's sampling experience to be able to discriminate correctly between the three. Coconut crabs generally make a large incision in the flesh of the coconut and leave chunks of flesh lying on the ground, while rats make a small neat incision in the shell and leave little debris about.

The activity index was only used as a supplement to CPUE in assessing geographical differences in abundance because of the disadvantage of its having a maximum score (100%). This could be overcome only by increasing the number of baits to such an extent that even in the densest population there would always be some baits that remained untouched. It is therefore more appropriate as a relative measure of activity between samples at the one site than as a means of comparing different sites.

Results

Analysis of catch per unit effort (CPUE)

Hog Harbour — Site A. Catch rates of both legal and undersize crabs at this site during the 27 months of sampling were relatively small (Fig. 3a), varying from 0.29 (nearly three crabs per ten baits) to 0.13 (about one crab per ten baits). The largest catch rates were recorded during the early part of the year (January – March), and the smallest during the later months (August – December). Added to this there was a general decline in the overall CPUE over the period of monitoring, from a maximum of 0.29 in 1985 to 0.17 in early 1987 and 0.15 later the same year. This decrease appeared to be due mainly to a reduction in the number of legal-sized crabs in the area. During most field trips in 1985-86 some legal-sized crabs were caught (mean CPUE = 0.05), but by late 1986-87 many samples included no legal crabs at all, and the mean value had declined to 0.015. However, there was little change in the pattern of catch rates for undersize crabs; these varied from zero to 0.15 in the three years of sampling (Fig. 3a).

Hog Harbour — Site B. The temporal catch-rate pattern at this site (Fig. 3b) was similar to that at Site A (Fig. 3a). Maxima of 0.8 during the 1985-86 wet season and 0.5 in the 1986-87 wet season contrasted with the relatively small values of 0.1 and 0.15 in the two intervening dry seasons. There was also a more marked decline in the apparent abundance of crabs during the two years of study. The rate of capture of legal-sized crabs fell from 0.2 in 1985 to about 0.14 in 1986-87, and to less than 0.1 by late 1987 (Fig. 3b). The apparent abundance of undersize crabs also declined, from 0.6 in 1985 to only 0.11 at the end of the field study.

Hog Harbour — ocean site. A similar cyclic pattern in CPUE was evident at this sampling site (Fig. 3c). Highest catch rates (0.45 and 0.78) were experienced in early and late 1986 respectively, but by late 1987 CPUEs had declined to a maximum value of only 0.4. There was a gradual decline in the catch rate of legal-sized crabs, especially in 1986, from about 0.15 to almost zero by the end of the study, but undersize crabs showed no decline in apparent abundance during the period.

Hog Harbour — point site. The catch rate at Hog Harbour Point fell markedly from 0.5 in late 1986 to 0.2 at the end of sampling (Fig. 3d). All size classes of crabs showed reductions in numbers with the CPUE legal-sized crabs falling from 0.25 to 0.05 and undersize crabs from 0.25 to 0.15.

Kole — cliff site. The catch rate at this site (mean CPUE = 0.4, maximum = 0.7) remained generally high throughout the year (Fig. 3e). A nearby site sampled in 1987 yielded results very similar to those from the main site, suggesting that the method was consistent and capable of giving repeatable results. The catch rate of legal-size crabs was small but variable, ranging from 0.15 at the commencement of sampling in 1986 to zero in September 1987. The density of undersize crabs caught during this period did not decline appreciably.

Kole — coast, close site. CPUEs at this site were considerably lower than at the cliff site throughout the entire study, with a mean of only 0.14 crabs per bait (Fig. 3f). Even so, there was a significant decline in the mean annual catch rate of legal-sized crabs from 0.075 in 1986 to just 0.015 in 1987. In contrast, there was a marked upward trend in CPUE for undersized crabs, from 0.06 in January 1986 to 0.23 in September 1987.

Kole — coast, distant site. There was a dramatic decline in the apparent abundance of coconut crabs at this site (Fig. 3g). Legal-sized crabs were caught at a rate of 0.2 crabs per bait in April 1986, but by the end of the study in September 1987 their catch rate had dropped to zero. A similarly marked decline was also recorded for undersized crabs, the catch rate for which fell from 0.8 to 0.2.

Mavea – cliff site. There was no obvious long-term trend in the overall catch rate of crabs at this locality (Fig. 3h); CPUEs remained high throughout the study (overall mean = 0.45), with annual maxima of 0.5 in May 1986 and 0.7 in June 1987. The capture rates of legal-sized crabs were greatest (>0.2) during the wet season in both years, and the seasonal cycle in apparent abundance of undersize crabs followed a similar pattern.

Mavea — coast site. The numbers of crabs found in this area changed far more dramatically through the year than at the cliff site (Fig. 3i). Catch rates were highest at the end of the dry season and early in the wet (October — November), a pattern which resembled that at the cliff site but which was several months out of phase. The mean CPUEs both for legal-sized and undersize crabs were around 0.2 during the monitoring period, and neither size group exhibited any appreciable decline in density at this location.

Torres Islands — Hiu. Sampling on Hiu Island involved the use of both baited trails and random walks through the bush without baits. There was a seasonal CPUE cycle (Table 1), with a wet season peak and a dry season trough, similar to that found for the non-baited transects. Over the three consecutive wet seasons the daytime catch rates declined (Table 2). For example, in December 1985 the observation rate (i.e. number of sightings per hour) was about 14 during the day and at night. In later trips daytime sightings dropped to less than one crab per hour, although the night-time observation rates remained high.

Baits were not set during the first trip to this region, but judging from the numbers of crabs observed while walking and from the numbers attracted to coconuts which had been opened during the day it is estimated that the catch rate would have been in the vicinity of 4 or 5. The catch rates for the next two summers indicate a fall in the rate of capture to 3.6 in 1986 and to only 2.4 in 1987 (Table 1). This site also exhibited the usual cycle of a reduced catch during winter with rates of only 1.2 and 1.0 during the two trips made in April 1986 and June 1987.

Torres Islands — Tegua. Sampling on Tegua provided dramatic evidence of over-exploitation of a coconut crab resource. The locality was sampled using baited transects in three consecutive wet seasons, and the catch rate fell dramatically between each trip. In 1985 the mean CPUE at Area 9, for example, was 4.1; this fell to 2.7 in 1986 and plummeted to 0.5 in 1987 (Table 3). The lack of sampling during the dry season precludes any analysis to confirm the usual pattern of reduced CPUEs during that period.

Table 1. Seasonal and inter-annual differences in baited sample catch rate (CPUE) of coconut crabs on the island of Hiu (Torres Group). W and D refer to the wet summer and dry winter seasons respectively, and the asterisk indicates that the 'CPUE' was estimated from the observed number of crabs present.

Site	1985		1986		1987
	W	D	W	D	W
1. North	5.*	1.1	3.6	1.6	2.4
4. Cliff	0.2				
7. Inland					0.5
3. Picot Bay					0.6
6. South-east					1.4
8. South-west					1.4

Pooled catch rates

As an alternative method to assess the observed cyclical pattern in CPUE variation throughout the year, we calculated an index that was pooled over all sites in the Santo region. For this the CPUE for each sampling date at each site was calculated as a percentage of the
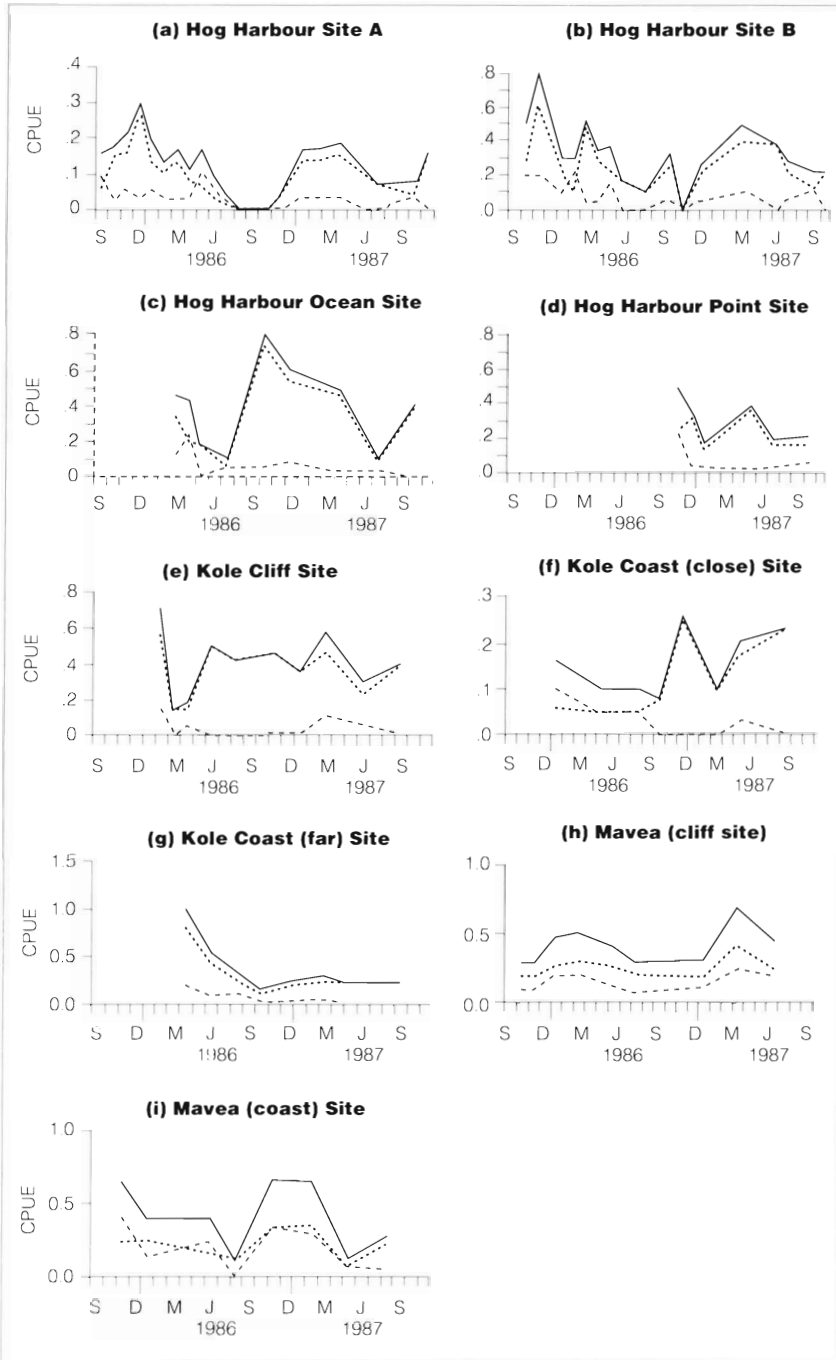
Figure 3. Seasonal changes in CPUE (catch per unit effort) at the primary study sites. The catch rate of legal-sized crabs is represented by a dashed line; that of undersize crabs by a dotted line, and that of the total by the solid line.

maximum CPUE for that site, thereby allowing us to pool all the data from all the sites (irrespective of absolute rates). A plot of the mean percentage for each month (Fig. 4) clearly shows the cyclical pattern in the CPUE levels during the year. When these data were statistically compared to a sine curve with a period of one year and an amplitude equal to the difference between maximum and minimum CPUEs, there was a highly significant correlation ($r=0.667$, $p<0.01$) indicating strong seasonality in the cycle of crab catches.

Table 2. Seasonal and day-night differences in the non-baited catch rate (CPUE) of coconut crabs on the island of Hiu (Torres Group). D and N refer to day and night respectively.

Site	12/85		4/86		10/86		6/87		10/87	
	D	N	D	N	D	N	D	N	D	N
1	14.5	14.5	1.5	6.0	0.5	15.0	0.0	8.0	1.0	15.0
2	6.0	15.0	0.0	0.0	0.0	16.0	0.0	4.8		

Table 3. Inter-annual and between-site differences in the baited sample catch rate (CPUE) of coconut crabs on the island of Tegua (Torres Group). Samples were taken only during summer (wet season) months. For other details see heading to Table 1.

Site	1985	1986	1987
Area 9	4.1	2.7	0.5
Area 10	5.0*	0.8	1.8
Area 11			1.4
Area 12			1.5
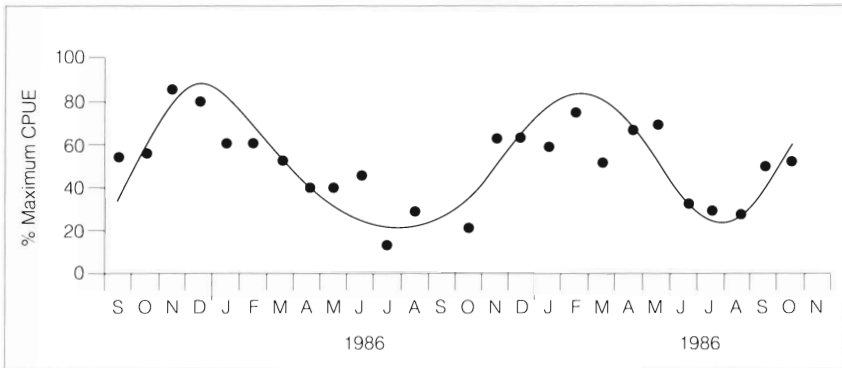
Figure 4. Seasonal changes in CPUE at all Santo sites pooled, expressed as a percentage of the maximum value recorded at any site.

Activity levels

Activity levels conformed to a more clearly discernible cyclic pattern throughout the year than did the CPUE values. This is probably due to variation in the numbers of crabs present but not detected by the sampling methods used in the calculation of CPUEs. Both the A and B sites at Hog Harbour exhibited very similar variations in activity throughout the monitoring period (Fig. 5a). Differences between the two abundance indices (activity and catch rate) were parallel; site B generally had higher levels than site A (43.5% and 26% respectively) which were approximately twice the respective CPUE values (0.29 and 0.13). The consistency of this pattern suggests that we only caught about 50% of the crabs foraging on the baited transect line at night.

At most sites (with the notable exception of Kole cliff and Bier Island) there were periods during the year — particularly in the dry season between June and August — when the crabs' activity levels declined markedly. The magnitude of the change in activity level varied. At some sites (e.g. Hog Harbour Site A in August 1986) there were periods when no activity was observed at all, while at others (e.g. the Kole Coast far site) the minimum value was never less than 30% (Figs 5a, 5b).

Although there was some evidence of an early decline in activity at the Kole cliff sites, activity levels were very high (>50%) during the 1986 dry season, and the cyclic pattern was variable and indistinct (Fig. 5b). At Bier Island there was also little observable pattern in activity (Fig. 5c), with the possible exception of a period of reduced activity between July and September 1987.

Hermit crab abundance

The overall abundance of the other species of Coenobitidae (hermit crabs or 'nakato') varied greatly among sites (Figs 6a-c). The site with the greatest number of hermit crabs was Bokissa Island, where the average number on a bait was about 10, and in many instances exceeded 30. At most sites, however, the numbers were much smaller. The next highest hermit crab density was recorded at Hog Harbour (Fig. 6a), where each bait yielded, on average, about one animal. Kole appeared to have a low hermit crab population density (Fig. 6b), but higher than Mavea (Fig. 6c) where the catch rate was particularly low (around 0.1 per bait). There was some evidence of an increase in the numbers of hermit crabs at Kole and Hog Harbour where the numbers of legal-sized coconut crabs had been reduced. Statistical tests indicated that hermit crab relative density (CPUE) was inversely related to that of legal-sized coconut crabs present at a site (r=0.57, n=12).

Hermit crab abundance also varied seasonally, although not to the same extent as *Birgus*. These variations may have been short-term responses to local weather conditions rather than long-term cycles, which may account for the lack of consistency between sites.

Size structure

The average size of coconut crabs varied widely between sites (Table 4). The mean thoracic length (TL) of males varied between 32 mm
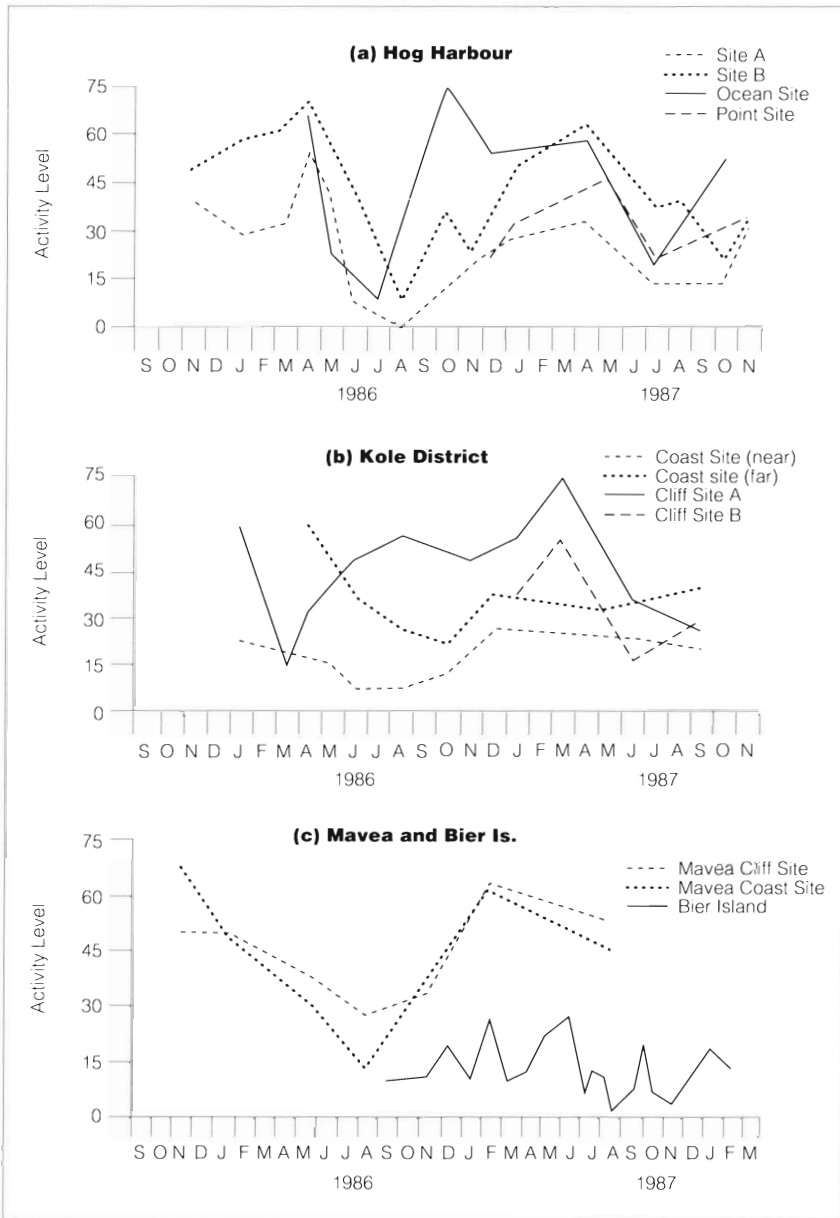
Figure 5. Seasonal changes in activity level index (estimated from the proportion of baits which had been eaten by coconut crabs) at the major sites.

(Bokissa Island) and 55 mm (Tegua Island), while that of females ranged from 29 mm (Bokissa Island) to 39 (Kole Coast). The maximum size of male crabs found at the various sites ranged from

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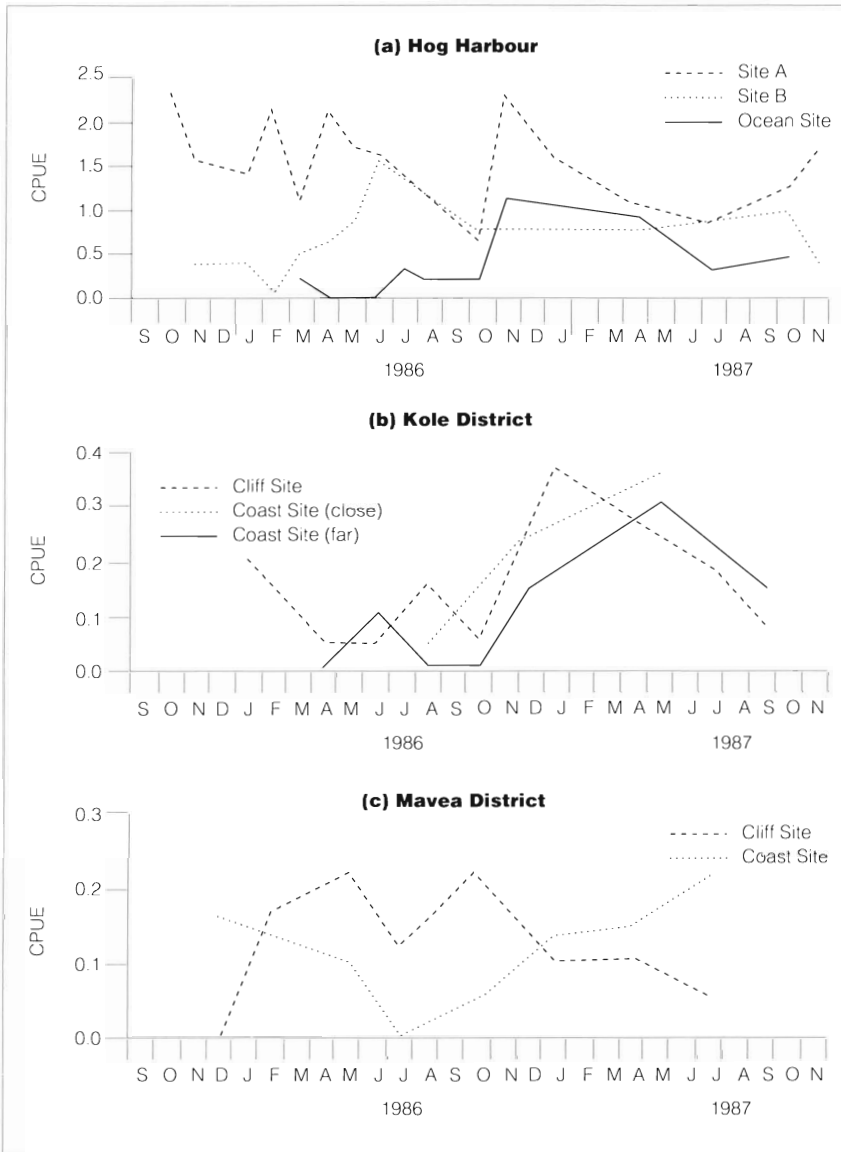
Figure 6. Seasonal change in relative abundance (CPUE) of coenobitid hermit crabs (nakato) at the major sampling sites.

55.0 mm (Kole cliff and Bokissa Island) to 80.0 mm (Hiu Island). There was a strong positive correlation between average size and CPUE (r=0.72, p<0.05), such that areas where catch rates were high had a greater proportion of large crabs in the population. The average size of

female crabs was typically about 20–25% less than that of males (Table 4, Fig. 7).

There was no trend at any sampling site in the average size of individuals during the period of monitoring (Fig. 7). As the number of individuals of either sex captured on any one trip was usually small (<10), the potential for variation was large, and most of the calculated standard deviations exceeded 10 mm. Differences between most sampling dates are therefore almost certainly non-significant. At neither Mavea (Fig. 7c) nor the main Hog Harbour (A and B) sites (Fig. 7a) was there any appreciable reduction in the mean size of crabs of either sex.

Table 4. Average size of crabs at each of the main sampling sites at the beginning of the program, and the estimated exploitation history of each of the sites.

Site	Mean CPUE	Mean size (mm)		Exploitation history
		Males	Females	
Hog Harbour A	0.25	38.7	29.8	heavy
Hog Harbour B	0.43	38.7	29.8	medium
Hog Harbour ocean	0.48	41.8	30.7	medium
Hog Harbour point	0.50	43.3	30.2	medium
Kole coast, close	0.13	37.0	32.0	very heavy
Kole coast, far	1.0	42.0	39.0	light
Kole cliff	0.4	35.6	30.0	medium
Mavea cliff	0.4	45.2	37.3	light
Mavea coast	0.5	47.8	36.0	light
Bokissa Island	0.3	32.0	28.9	heavy
Hiu Island	5.0	53.3	36.8	nil
Tegua Island	4.2	54.7	38.9	light

Given the evident high rate of exploitation of crabs in some of the other areas (e.g. the Hog Harbour point and ocean sites) and the observed decline in density of legal-sized crabs, it was surprising that only at the Kole coast site (Fig. 7b) was there an apparent decline in the mean size of male crabs, but even this was not statistically significant. Moreover, there was no reduction in the mean size of crabs on the Torres Islands (Fig. 7d), despite the drop in CPUE from 4 to less than 1 due to very intensive harvesting. As average size is evidently not a reliable indicator of changes in population size structure (over short time periods at least), size frequency distributions must be examined in detail.

Interesting differences were observed in the size frequency composition of the catches between the various sites at Hog Harbour. The populations at Sites A and B (Fig. 8a) were significantly different
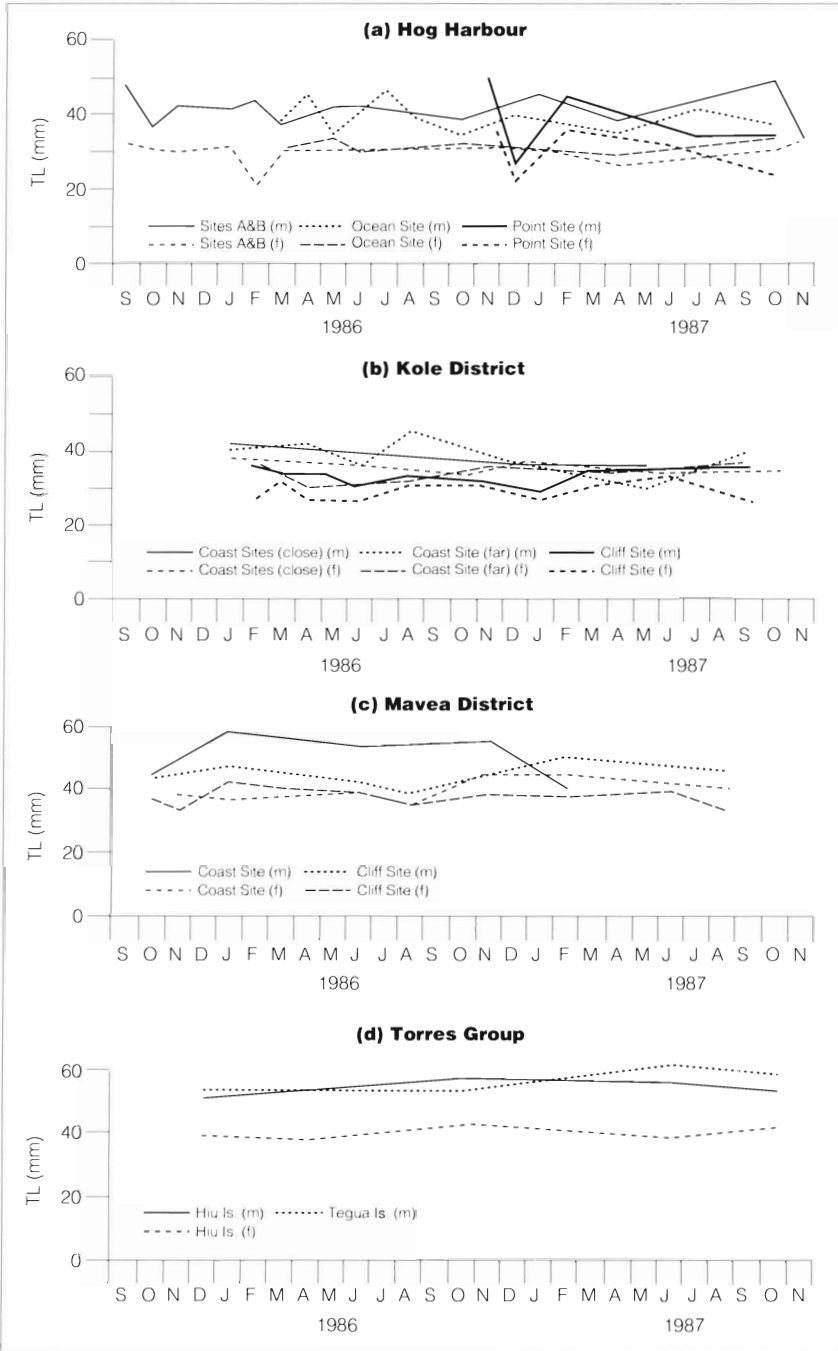
Figure 7. Seasonal changes in mean size (thoracic length) of male (m) and female (f) coconut crabs at each of the major sites on Santo, Hiu and Tegua during the project period.

from those at the Point site (Fig. 8b) (Kolmogorov-Smirnov D=0.3358, p<0.05) because of the abundance of larger individuals at the former. The Point site was one of the most productive for juveniles; seven individuals less than 20 mm were found there in one year, compared with only three at the main site over two years. Significantly, many spawning females had been observed near the Point site, and it was close to a small sandy beach populated by numerous coenobitid (hermit crab) glaucothoe. There was an apparent difference in population size structure between the Point site and the Ocean site (Fig. 8b), but according to the Kolmogorov-Smirnov test this was not significant (D=0.233, p=0.1). No difference at all was found between the main sites and the ocean site at Hog Harbour.

The Mavea population was characterised by the broadest size distribution of any site (Fig. 8d). Despite the large CPUE recorded at Mavea, a reasonable number of juvenile crabs was caught on most censuses, which resulted in a distribution that extended from 7 to 70 mm TL. The small number of coconut crabs captured on Bokissa Island (Fig. 8e) makes it difficult to draw any conclusions about the population at that site, except that it was rather restricted in its size range, and, somewhat unusually, the larger (>40 mm TL) crabs tended to be females rather than males.

Although there was no statistical difference in the population size distribution between the coast and cliff sites at Kole (D=0.23, p=0.08), six individuals smaller than 20 mm TL were captured at the cliff site, while the coastal site yielded no crabs of this size (Fig. 8f, g).

Only in the Torres Islands were enough crabs measured to enable yearly differences in size structure to be analysed (Fig. 9). Figure 10 indicates a substantial difference in the size distributions of crabs between this region (about 30 - 75 mm TL) and Santo (20 - 65 mm TL). On Hiu Island (in the Torres Group) differences in size structure were apparent all three years of the sampling program. There was an apparent increase in modal size from between 52 and 56 mm in 1985 to around 56 mm in 1986, which may have been the result of the 50-52 mm size class growing to 54-56 mm. This is consistent with our understanding of the rate of growth in individuals of this size. Between 1986 and 1987, however, the difference appeared to be due to the loss of this large (56 mm) size-class, perhaps to the crab collectors, or merely because the survey in 1987 was more wide-ranging.

Only one juvenile crab (an 18 mm TL female) was caught at the Hiu Island site (Fig. 9a), and a mere four or five individuals smaller than 30 mm TL were caught during the entire study. This was so even in areas where crab density had been greatly reduced, and where presumably the possible adverse effect on CPUE of intraspecific competitive behaviour would likewise have been reduced.

There was no significant change between years in the size structure of the coconut crab population on the Torres group island of Tegua (Fig. 9d-f). The increase in the range of sizes captured after 1985 probably reflects an increasing number of sites sampled. Similarly to
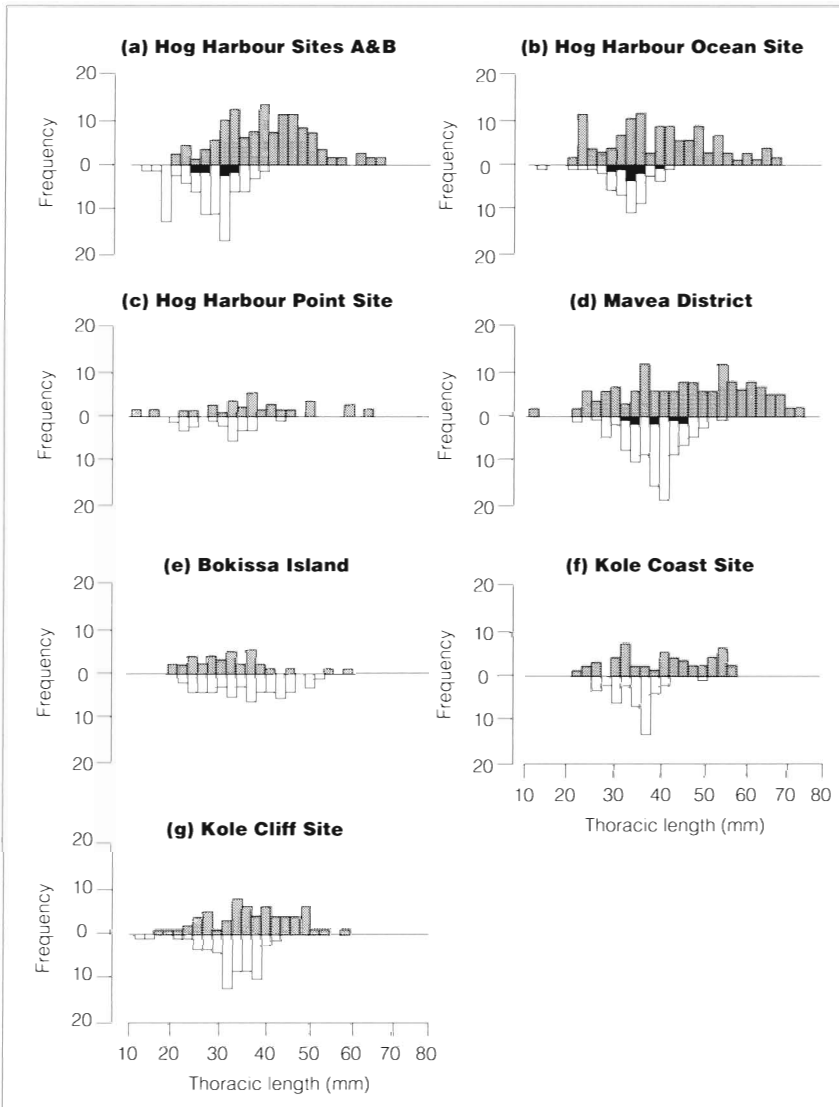
Figure 8. Pooled size—frequency distributions of coconut crabs at each of the major sampling sites. Males are represented by stippled bars, females by open bars, and ovigerous (egg-bearing) females by solid bars.

Hiu Island, very few small crabs were found, and none was less than 30 mm TL. This was still the case even after a significant reduction in population density.

Discussion

There were large differences in CPUE and activity level indices among sites. CPUEs varied from 0.13 (about 1 crab per 10 baits) at Hog
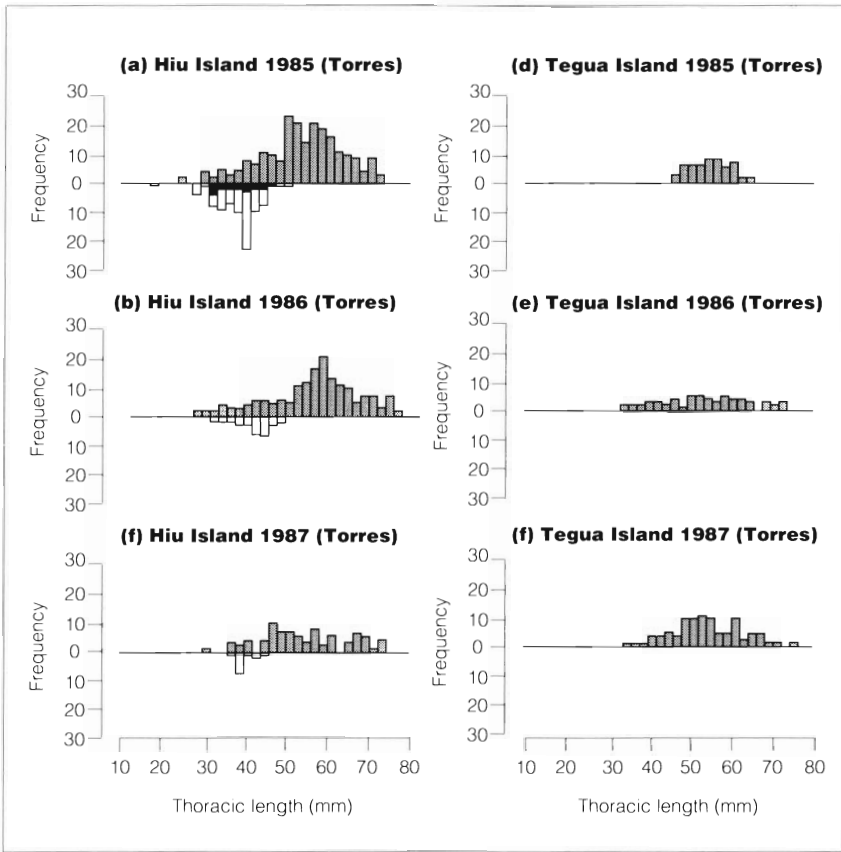
Figure. 9. Pooled annual size-frequency distributions of coconut crabs at sites on Hiu Island (a-c) and Tegua Island (d-f) in the Torres Group. Males are represented by stippled bars, females by open bars, and ovigerous (egg-bearing) females by solid bars.

Harbour to 4.2 (42 crabs per 10 baits) at one site on Tegua Island in the Torres group. The changes in catch rate over the project period were related to the sites' previous exploitation history (Table 5), determined by discussions with local people and confirmed by counting the remains of old coconut baits left in the area. The latter provided a good guide, as the broken shells and husks of coconuts used for catching crabs can last for several years before disintegrating. The coconut crab population on Santo has been depleted as a result of a long history of exploitation, but on the Torres Islands exploitation on a commercial scale began quite recently, with the advent of a regular air service.

It is difficult to compare the capture rates recorded in this study with those from other areas, but from Helfman's (1973) data it is possible to determine a comparable CPUE index. Helfman placed 40 baits
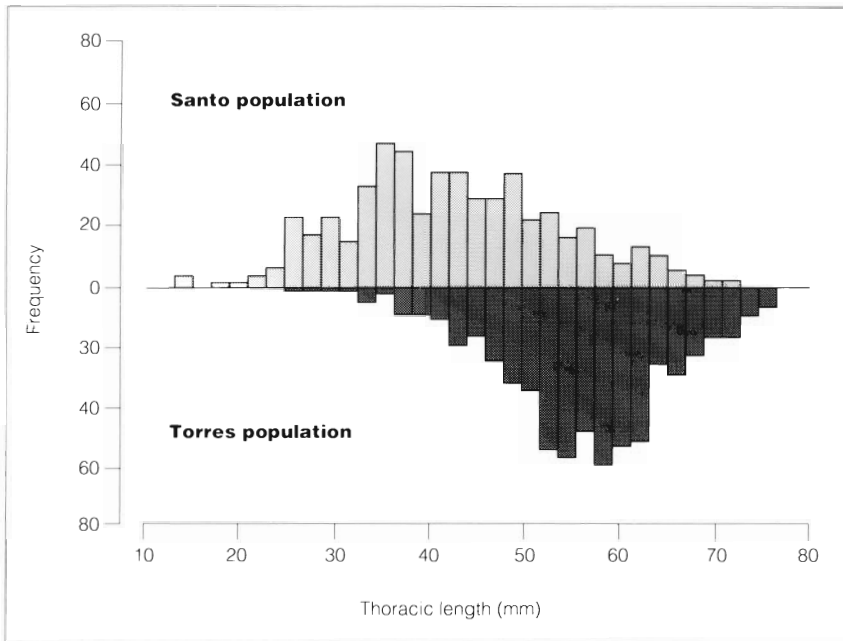
Figure 10. Geographical differences in the pooled size–frequency distributions of coconut crabs between the Santo and Torres populations.

randomly around Ngerkersiul Islet (Palau) on a number of occasions, and caught an average of 84 crabs each time, which corresponds to a CPUE of about 2.1. The author considered this site to have a high density of crabs and not to have been heavily exploited. A CPUE of 2.0 is relatively high on our scale and his estimate may have been greater had the baits not been placed randomly. At Igurin, the other site examined by Helfman (1973), no baits were used, so that a direct comparison is impossible. Gilchrist and Abele (1984) found twice as many hermit crabs by setting baits as they did simply when walking along an observation transect. There were some important differences in rates of foraging of crabs found here from those we observed. Helfman (1973) suggested, on the basis of a number of assumptions, that between 15 and 70% of individuals were out of their burrows on any one night. If our index is used (merely the number of recaptures/total marked), then the two estimates, between 2 and 8% on any given night, are comparable.

Both CPUE and activity level indices showed regular annual cycles at nearly all sites. A sinusoidal trend was also evident when data from all sites were pooled. Such a cycle in relative abundance for this species could have two possible causes. First, it could simply indicate a change in the foraging behaviour of the crabs due to seasonal variation in an environmental parameter such as temperature or rainfall. The period of

low catches, in fact, generally did coincide with the winter dry season, so either of these factors could have played some part in the observed pattern. We also observed that more crabs emerged after it had been raining, and high humidity has been associated with larger catches of crabs in Palau (Helfman 1973). Reese (1965) noticed that there were differences in the catch rates of coconut crabs at Eniwetok atoll between the wet and dry seasons and he ascribed this to variations in the crabs foraging behaviour due to humidity. Similarly, Reyne (1939) cites examples of collectors who state that the crabs were often seasonally rare or abundant, although the actual months were not reported. However, this simple environmental model does not completely fit the results of our studies, because winter catch rates were still small even if rain had fallen during the day of sampling.

Table 5. Estimated levels of exploitation and measured changes in catch rate (CPUE) at each of the main sites during the project period.

Site	Level of exploitation	Change in CPUE
Hog Harbour A	very light	0.07
Hog Harbour B	light	0.3
Hog Harbour ocean	moderate	0.3
Hog Harbour point	moderate	0.2
Kole coast, close	light	0.0
Kole coast, far	heavy	0.8
Kole cliff	light	0.0
Mavea cliff	nil	0.0
Mavea coast	very light	0.0
Bokissa Island	light	0.0
Hiu Island	heavy	2.0
Tegua Island	very heavy	3.5

Another explanation is that these reduced catches in the dry season were due to a large proportion of the population being unable to feed because they were in the process of moulting. Similar reductions in CPUE have been found in other species due to moulting behaviour (McKoy and Esterman 1981). It may well be, in fact, that both these factors play a part in determining the vulnerability of coconut crabs to capture on a baited transect.

At many sites there were downward trends in CPUE, suggesting a reduction in population density during the sampling period. Table 5 shows the relative harvesting intensity by crab collectors at each site subsequent to our initial visit. At all sites where some collections were known to have occurred there was a concomitant decline in the CPUE.

This drop was often not confined to the legal-sized crabs, which suggests that crabs were being collected illegally for sale at the market, or consumption by the collectors domestically or during their trip. Fragments of the carapaces of small crabs were often found on barbecue coals near the collectors' shelters. The most obvious decline was at Tegua Island, where thousands of kilograms of crabs were removed over this two-year period, and the CPUE dropped from 4 to 0.5.

This massive collection at Tegua contrasts with the situation on Mavea Island where, for religious reasons, virtually no crabs were harvested for sale, and there was consequently no decline in the CPUE of crabs either below or above the minimum legal size. This result is important because it demonstrates that the declines we witnessed at the other sites were not merely a result of our own activities driving the crabs away from the area.

Of equal importance was the fact that at Mavea and Hog Harbour site A there was no increase in CPUE, despite the absence of even moderate exploitation in those areas. No measurable increase in the density of the crab population had occurred during this period which, when the lack of change in the population size-structure is considered, suggests an absence of substantial recruitment. This situation has some important implications with respect to management of the coconut crab resource.

Competitive interaction between coconut crabs and other coenobitids, which were often present in very large numbers, may be a possible reason for this poor recruitment. On only three occasions were large coconut crabs and hermit crabs seen at the same bait, and all three coconut crabs were very small (less than 25 mm TL). When coconut crabs were at a bait, no coenobitids were generally present within a radius of about 1 m of the bait. On subsequent visits to a bait which had initially attracted a coconut crab, we frequently found hermit crabs but no coconut crabs. This suggests that there was some kind of aggressive interaction occurring between these species, the larger coconut crabs perhaps keeping the smaller coenobitids away from the bait.

The inverse relationship between hermit and coconut crab catch rates suggests that they may influence one another's recruitment or, more likely, that coconut crabs influence the other coenobitids' foraging behaviour and possibly prey upon them as well. Hermit crabs may affect the recruitment of juvenile coconut crabs because at small sizes, the former are far more numerous and much stronger, with larger claws, and have the added protection of a gastropod shell. Small coconut crabs may not compete well in encounters with hermit crabs at sizes less than 10 mm TL.

Hermit crabs also seem to thrive in areas into which the giant African snail has been introduced, since the molluscs provide strong, light shells in a wide range of sizes for the crabs to inhabit. Populations of hermit crabs may have increased quite substantially since the introduction of

the snails, a situation which Amesbury (1980) believes has occurred in Guam. Hermit crabs may also be prey to large coconut crabs when in high densities. On a number of occasions we witnessed coconut crabs consuming land crabs in the Torres Islands where there were very few large coenobitids, despite the abundance of juveniles on the foreshore. During the course of his study Helfman (1973) also recorded coconut crabs consuming hermit crabs.

The differences observed in the mean sizes and size structures among sites could be due either to inherent differences among the populations (e.g. recruitment histories and growth rates) or to different levels of prior exploitation, or to a combination of these factors.

Average body size is rarely a good indicator of the effect of exploitation on a population of animals, as it is so highly dependent on recruitment and growth rates and size selectivity of the harvesting process. In fact a stationary or increasing mean size may be associated with populations that are in greater danger of total collapse than those with a decreasing mean size. The former suggests either little or no recruitment and slow growth, or no recruitment and continued growth of the remaining stock. The latter may reflect a healthy level of recruitment of juveniles replenishing a population from which the accumulated stocks of older animals are being harvested progressively. Given that the growth rate of coconut crabs is particularly slow, there appears to be little evidence of significant recruitment to the coconut crab populations during the course of the investigation.

One uncertainty about this hypothesis relates to observed differences between sites in the average size of crabs. Such differences probably have arisen as a result of the pattern of collecting: when large numbers of crabs are available, usually only the legal-sized individuals are captured, but when crabs are scarce the smaller ones are taken as well. The very small crabs (<35mm TL), which are probably not harvested at all, contribute little to the mean size of animals in an unexploited or lightly exploited population. However, as the abundance of large crabs is driven down, the smaller animals obviously comprise an increasing proportion of the population. This may require a significant exploitation pressure in situations (such as in the Torres Islands) where the great majority of crabs in the population are old animals above the minimum legal size.

Very few small crabs were found in this study, and these included only two individuals smaller than 10 mm TL. This is not uncommon, as most major field studies have also reported an extreme paucity of juveniles (Held 1963; Amesbury 1980; Reese 1987). Reese (1987) believes that small juveniles are in fact present, but that they are very secretive and difficult to find. This does not, however, explain the fact that some of the larger size groups (e.g. 15-30 mm TL) were scarce at some sites but abundant at others. Such situations may be caused by intraspecific interactions: the larger size-classes were often most abundant in areas where small crabs were sparse, but this was not universally true. Helfman (1973) found a much younger population on

his Ngerkersiul study site (where many crabs were smaller than 25 mm TL) than at Igurin, and only on one island (Cocos) in Guam was Amesbury (1980) able to find small crabs.

Variation in the abundance of small coconut crabs may reflect different rates of recruitment between geographic localities. It appears as though the Torres Islands and Bier Island populations had not experienced any significant recruitment for some time (possibly for more than five years), while populations in other areas (such as Bokissa, Kole, Hog Harbour and Mavea) may have been boosted by a small recruitment during that period. Whatever the specific details, however, it appears that in Vanuatu, at least, recruitment of coconut crabs is sporadic and probably unpredictable.

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5 GENETIC CHARACTERISTICS

S. Lavery and D.R. Fielder

THE coconut crab (*Birgus latro*), the most highly terrestrial crab, has a wide distribution throughout the tropical regions of the Pacific and Indian Oceans, ranging from the Tuamotu Archipelago in the east to the coastal islands of East Africa in the west (Fig.1). Within this range the crabs are found only in isolated locations, particularly on relatively remote islands sparsely populated by humans.

On a number of Pacific islands coconut crabs provide an important food and economic resource but, in most parts of their range, *Birgus* populations have either been dramatically reduced in size or have disappeared altogether (Wells et al. 1983, and this study). There is an obvious need for management of this species to ensure its long-term survival. However, without some information regarding its population structure, there is little indication as to what scale of management should apply. The primary aim of the genetic research being undertaken on *Birgus* is therefore to describe the population structure of the species.
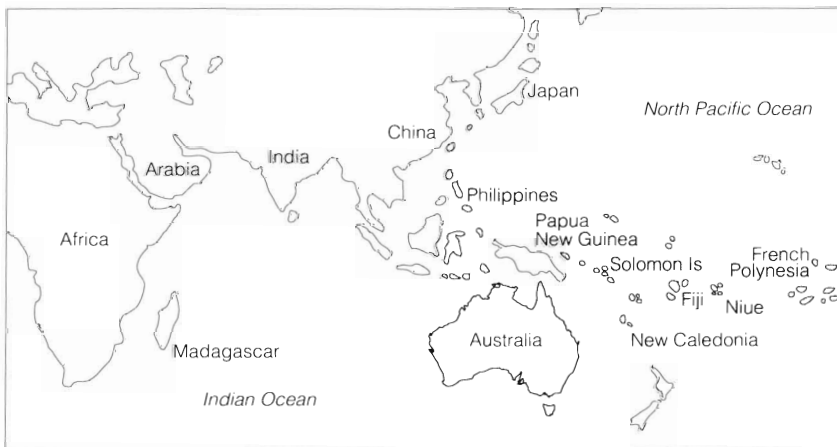
Figure. 1. Indo-Pacific distribution of the coconut crab.

The type of population structure which develops in a species depends largely on the type and degree of dispersal which takes place. An important feature of the biology of *Birgus latro* in this regard is that the larvae are released directly into the sea where they have a relatively short marine planktonic stage of two to four weeks (Reese and Kinzie 1968, and Schiller this study). This is the only phase permitting dispersal between islands.

There are two possible extreme alternatives in population structure. On the one hand, the crabs inhabiting each individual island or small group of islands may maintain their own distinct subpopulations in reproductive isolation from others surrounding them. This would occur if the planktonic larvae dispersed only short distances and were recruited back into the same population as their parents. These distinct stocks would be likely to develop slight genetic differences over generations. At the other extreme, the entire population of coconut crabs throughout their range may simply exist as one large homogeneous population. In this case there would be relatively free mixing of individuals or their offspring throughout the population, and it would not be possible for significant genetic differences to develop between groups of individuals.

The true population structure probably lies somewhere between these two extremes. Until now, however, there has been no information to indicate the true situation. Indeed, no comparative work had been undertaken to determine if there was more than one species represented in the coconut crab's large range. The geographic discontinuity of *Birgus* populations suggests that some degree of division into separate stocks is likely. However, other evidence suggests the contrary. As the marine larvae of this species may be pelagic for up to four weeks, it is possible that oceanic currents carry them a great distance. Offspring may therefore be dispersed over a very wide area, and genetic homogeneity may result. Furthermore, a number of other marine decapod crustaceans have been shown to exhibit very little, if any, population subdivision over large distances (e.g. spiny rock lobster *Panulirus ornatus*—Salini et al. 1986; prawns—Mulley and Latter 1981).

The type of population structure could have great implications for the effective management of *Birgus*. If distinct subpopulations exist, then each will be dependent on the successful recruitment of offspring from within that stock. This implies, therefore, that the level of recruitment may be determined by the size of the local spawning population. In this case it would be necessary to manage each stock on an individual basis to ensure that sufficient numbers of crabs survive on each island in each generation to produce adequate recruitment. If an individual stock is heavily depleted, then there can be no reliance on recruits from nearby stocks to rebuild the population. If, however, there exists one large homogeneous population, then a substantial degree of dispersal and mixing of larvae will occur, and each island will receive recruits from other locations. If, in fact, any island receives ocean currents consistently from the one direction during the spawning season of year, then it is quite possible that a large proportion of recruits will come from an adjacent island. This in turn means that if one population is decimated, recruitment on neighbouring islands may be drastically affected. Hence island stocks will be interdependent, with each ultimately dependent on the size and success of the entire population. In this case there is an obvious need for an overall co-ordinated management plan, to ensure that the total numbers of coconut crabs are kept at self-sustaining levels.

A useful method of examining population subdivision involves analysis of genetic differentiation between animals from different localities. The technique used in this study was allozyme electrophoresis, which has proved a very efficient and effective tool in studying genetic variation (Richardson et al. 1986). In this technique, the genetic variation is observed as different forms of any one enzyme. The different forms (allozymes) can be detected because they have slightly different electrical charges, reflecting differences in amino acid composition and hence differences in DNA sequences (alleles) in the gene encoding that enzyme. The allozymes are separated by placing tissue extracts in a gel subjected to an electric field for a period of time.

Using this technique, marine decapods (from which *Birgus* has been derived) generally have been found to possess relatively low levels of genetic variation between individuals (Hedgecock et al. 1982). This does not mean necessarily that population differentiation will not exist in marine crustaceans, but it may be more difficult to detect because of the limited variability among individuals. Furthermore, organisms which have a marine planktonic dispersal stage appear, in general, to have low levels of population differentiation, probably due to the lack of barriers to dispersal (Gyllensten 1985). The likelihood of population differentiation in *Birgus* may however be greater because of this species' brief larval life (2 to 4 weeks) compared to that of many other crustaceans such as lobsters, the larval stage of which can last for up to 12 months (Phillips and Sastry 1980).

Methods

As there was no initial indication of the distances over which population subdivision may occur, it was planned to collect samples in a hierarchical manner in order to make the following comparisons between groups of coconut crabs: (i) between adjacent islands, (ii) between islands in a group, (iii) between island groups, and (iv) between Pacific and Indian Oceans. Each of these comparisons differs approximately by an order of magnitude in distance, ranging from tens of kilometres in the first comparison, to tens of thousands of kilometres in the last.

Considerable effort was involved in organising the collection of samples from as wide a range of locations as possible. The primary sampling locations were in Vanuatu, the base for the ACIAR coconut crab project. In other parts of the Pacific, the results of a mail survey throughout the Indo-Pacific were used initially as a basis for likely sources of specimens. Countries targeted for approach were those which appeared to have a readily-available supply of coconut crabs, which had indicated they may be interested in coconut crab research, and which lay in a strategic position. For Indian Ocean samples, a variety of contacts was used, including personnel in the CSIRO Division of Fisheries Research, ACIAR, the University of Queensland and the University of New South Wales. In addition, other relevant contacts in Indian Ocean countries were canvassed. Personal contact was also made with

biologists from six locations (Seychelles, Maldives, Christmas Island, Papua New Guinea, Solomon Islands and Kiribati). Initial letters were sent to 15 locations requesting assistance, with further communication taking place with the five locations shown in Figure 2 giving a positive response (Vanuatu, Solomon Islands, Christmas Island, Cook Islands and Niue).

Figure 2. Indo-Pacific collection sites.

Eleven shipments of live or frozen crabs, comprising more than 300 specimens, were received from these locations. Details are shown in Table 1. As Vanuatu was the focus of attention of this research, specimens were obtained from four islands in the Vanuatu archipelago (Fig. 3). Espiritu Santo was the primary collection site, together with three of the Torres Islands (Hiu, Tegua and Loh), approximately 200 km to the north.

Once samples were received at the University of Queensland laboratories, they were frozen at -20°C until processed. Tissue extracts were prepared by dissection, homogenisation in buffer, centrifugation at 20 000 × g, and pipetting of the supernatant into individual plastic vials. Extracts were then stored at -70°C. Eleven tissues have been examined: skeletal muscle, abdominal muscle, heart, intestine, hepatopancreas, antennal gland, lung, gill, brain, gonad and haemolymph.

Tissue extracts were subjected to horizontal starch gel electrophoresis and enzymes were visualised using specific histochemical staining techniques (Harris and Hopkinson 1976). General proteins were also examined using horizontal, thin slab, polyacrylamide gel electrophoresis. Genotypes of each individual were recorded for each polymorphic enzyme to allow a genetic comparison of crabs from different areas. A diagrammatic summary of the electrophoretic procedure is given in Figure 4.
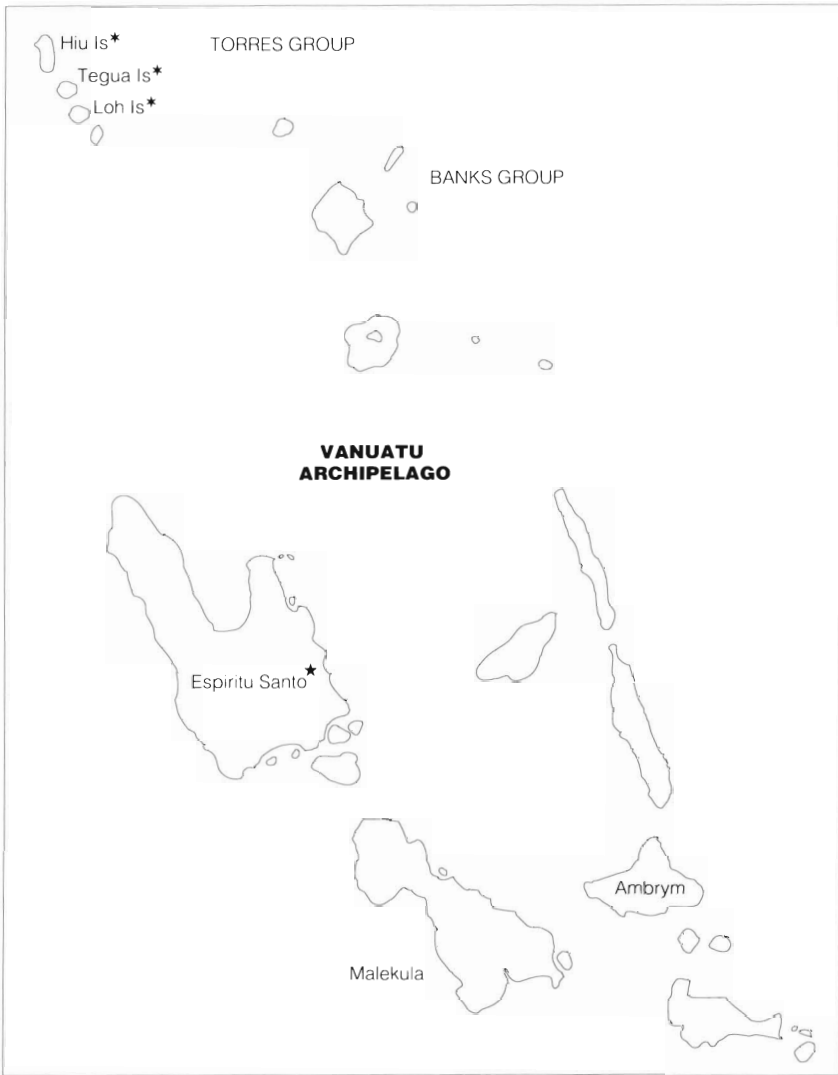
Figure 3. Vanuatu collection sites (∗).

Allele frequencies were calculated for crabs from each island. They were then compared between locations using contingency chi-square tables and F-statistics (Hartl 1980). FS_T measures the degree of genetic variance between locations compared to the total genetic variance between all individuals. Roger's genetic distance (modified by Wright 1978) was calculated between all pairs of locations and used to construct dendrograms (using UPGMA – unweighted pair-group method with arithmetic averaging) showing the genetic relationships between locations.

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Table 1. Coconut crab collection details

Location	Sample size	
Christmas Island		82
Solomon Islands		44
Vanuatu (total)		169
Santo	82	
Tegua	41	
Hiu	21	
Loh		25
Niue		18
Cook Islands		11
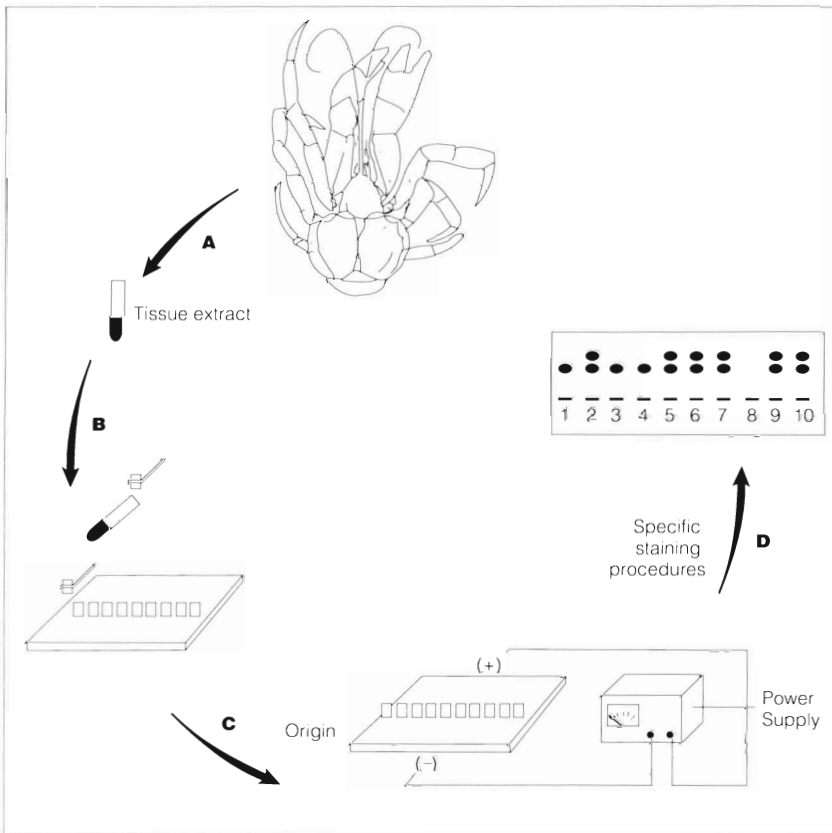
Figure. 4. Electrophoretic procedure. (Adapted from Utter et al. 1987. Used with permission.)

Results

Of the 76 enzyme systems initially screened, 83 different enzyme loci were detected in the range of tissues employed. Of these, 22 loci proved

to be uninterpretable and 54 loci were monomorphic, while only seven loci were polymorphic.

The seven polymorphic loci were analysed for allele frequency differences between locations using contingency chi-square tables and F-statistics. These analyses show that the collections from the Torres Islands in Vanuatu (Tegua, Hiu and Loh) appear to be genetically homogeneous, with no significant differences between collections at any loci. Similarly, there are no significant differences between the Torres collections and the Santo collection, 200 km to the south, nor between the entire pooled Vanuatu collection and Solomon Islands collection. There is, however, significant genetic heterogeneity (FS_T=0.045, p<0.001) between these collections and those from Niue and the Cook Islands. Finally, there exist highly significant genetic differences between the Pacific Ocean collections and the Christmas Island collection from the Indian Ocean.

The two most highly variable enzyme loci are Malate dehydrogenase-2 (Mdh-2) and Peptidase (Pep). In a contingency table comparison of the allele frequencies of these loci between Christmas Island and the pooled Pacific Ocean samples (see Figs 5 and 6), both loci exhibit a significant difference between areas (Mdh-2: G=6.40, p<0.05; Pep: G=28.66, p<0.001). In fact in the Pep locus, the 'slow' allele appears to be exclusively restricted to the Indian Ocean population while the 'fast' allele appears to be restricted to the Pacific Ocean population.

The level of genetic differences between *Birgus* populations from each of the eight locations can be summarised using a dendrogram of genetic distances between all sites (Fig. 7). This allows a good comparison of the relative degrees of genetic isolation of each *Birgus* population. Figure 7 emphasises that, firstly, the Vanuatu and Solomon Islands collections are relatively uniform. Secondly, it is apparent that while there are some differences between the Pacific Ocean collections, this heterogeneity is considerably less than that observed between the Pacific and Indian Oceans.
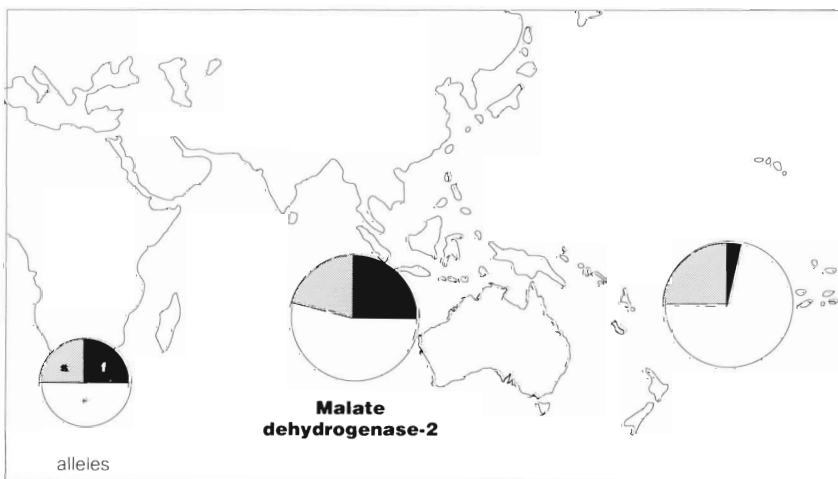
Figure 5. Mdh-2 allele frequency differences between Indian and Pacific Oceans.
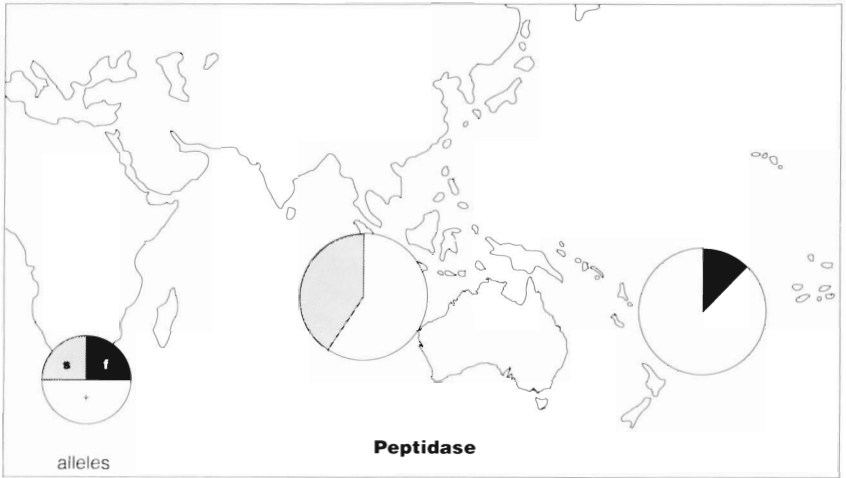
Figure 6. Pep allele frequency differences between Indian and Pacific Oceans.
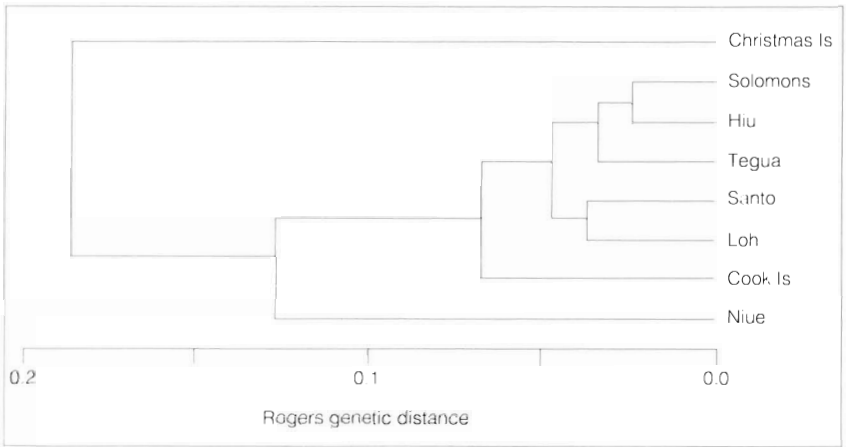
Figure 7. Dendrogram of genetic distances between sites.

Discussion

It appears from the genetic analyses that *Birgus* populations from the Vanuatu–Solomons group of islands are a relatively uniform group. The lack of statistically significant differences between these collections may be due to a number of factors. Firstly, it may be that this group is one large homogeneous population which experiences sufficient mixing of larvae between islands to maintain genetic uniformity. Alternatively, it may be that genetic differences do exist between the island populations, but that the differences have not been detected by examining these particular portions of the genome (i.e. these enzyme loci) of the organism. Real genetic differences may also go unobserved

if they are too small (and possibly too recent) to be detected with the sample sizes used.

In other words, the apparent genetic similarity of the Vanuatu and Solomon Islands collections must be treated with some caution. The nature of this type of genetic data is that only large differences can be detected using relatively small sample sizes, as is the case in this study. Of course it would have been preferable to have much larger sample sizes, however, the prohibitive costs and difficulties of acquisition of this already-endangered species made this impractical. Furthermore, the qualification which always exists in interpreting these genetic data is that differences between populations can be statistically proved, whereas the null hypothesis of genetic homogeneity can never be statistically proved.

These difficulties in interpretation of the results have been overcome somewhat by sampling very distant populations. This has been advantageous in that it provides information on the likely maximum levels of genetic heterogeneity between populations, with which all differences can then be compared. That is, we are able to say not only that genetic differences were not found between Vanuatu and Solomon Islands, but that the degree of differentiation was only a very small proportion (<10%) of that found between obviously distinct populations. This outcome gives us more confidence that *Birgus* from Vanuatu and Solomon Islands do indeed belong to only one homogeneous population.

It appears from the genetic analyses that distinct populations of *Birgus* occur in the eastern Pacific. This information must also be treated with some caution because of the very small sample sizes from these distant locations. One feature of the genetic data which strengthens the case for distinct populations in Niue and the Cook Islands is the presence of four low-frequency alleles which are unique to these populations (2 in Niue and 2 in the Cook Islands). If larger samples could be acquired from these locations it is quite likely that they would reinforce the evidence for population differentiation.

Delineating the boundaries of the proposed genetically-distinct populations would require more intense sampling from these and additional locations, and examining other genetic markers (e.g. mitochondrial DNA). It would then be possible to relate the pattern of population structure in *Birgus* to the pattern of oceanic currents in the Indian and Pacific Oceans. As these currents are likely to be extremely important to the dispersal of the planktonic larvae of many species in this region, the information could be used to make predictions about population structure in many other species too.

Conclusions

Population structure

Vanuatu and Solomon Islands appear to support one genetically uniform stock of *Birgus latro*. This means that the island populations in this region are inter-dependent and may therefore require an overall co-ordinated management plan for their continued harvesting and survival.

This may be good news in that depleted islands throughout this region may (in the absence of predators) be able to regenerate populations of *Birgus* over time with recruits from the larvae of other populated islands. Unfortunately, this may alternatively be bad news if the total population numbers in this region have already fallen below the critical number required to overcome normal larval and juvenile mortality and thus keep the region populated with *Birgus*. It may be the case that even well-populated islands rely on recruits from islands lying up-current. The evidence for a lack of recruits in recent years even on well-populated islands (e.g. Santo) may indicate that these are now isolated remnant populations which lose most of their larvae to the currents.

There is some indication, though not yet conclusive, that Niue and the Cook Islands have separate, independent populations which may therefore need managing as separate resources. In the case of Niue, at least, this may be very worrying as population numbers seem to have dropped so dramatically (Schiller, pers. comm.). This is not to say, of course, that other outposts of these populations do not exist on other nearby islands that have not been sampled.

This also suggests that a number of distinct populations may exist throughout the Pacific. By careful study of the morphology of these different populations, it may be possible to recognise different 'races' of *Birgus latro* throughout its distribution. Each population may even be adapted differently to its local environmental conditions.

Genetic implications for artificial culture

The presence of distinct populations of *Birgus* may have significant implications for artificial rearing and stocking in depleted areas—a proposal which has been contemplated on more than one occasion (Wells et al. 1983). If such a program is to be undertaken, there is a need to determine right from the beginning what the goals are to be, for different goals can have very different genetic implications for the species. For example, one goal may be to maintain all existing different stocks, while another may be simply to maintain representatives of the species on selected islands, leading to a process of homogenisation of the populations.

Although the latter goal may be worthwhile in itself, there are many possible risks involved in translocating individuals throughout the range (Utter et al. 1989). The process of artificial rearing, almost unavoidably, will result in a loss of genetic diversity, and perhaps survival traits, in the reared population compared to the source population (Sbordoni et al. 1986; Quattro and Vrijenhoek 1989). Also, the movement of reared animals from one population to another may swamp the existing gene pool with introduced alleles, resulting in an overall loss of genetic variation. Each population may be adapted to its own environmental conditions, and therefore the introduction of many individuals from another region may lower the overall fitness of the population. The consequences of this may be that we become tied to continual artificial

stocking of an area to ensure continued survival, or even that large amounts of money are spent producing animals that will not survive in different conditions from their parent region. A further problem is that if genetic variation is lost through artificial rearing and stocking, then this means a loss of the raw genetic material which could be used for future genetic improvement of stocks through breeding (e.g. faster growth rates).

At the same time, if the aim of a rearing program is simply to stock animals to ensure continuing numbers of *Birgus* on certain islands (e.g. to maintain the food supply and the economic resource), regardless of their long-term viability, then this may very well be the best choice of the indigenous peoples. It should at least ensure the survival of the species in more areas.

This is not to say that all, or any, of the possible genetic problems which have been outlined will eventuate. However, with such limited numbers of *Birgus* remaining in many parts of its range, it would be wise at least to be aware of the possible consequences when setting the aims of a rearing program. Furthermore, most of the potential problems could be overcome with a well-designed program. Such a program would emphasise: 1) the use of local brood stock for larval rearing or juvenile restocking, 2) the use of the maximum permissible number of brood stock in any one rearing operation, 3) genetic monitoring of larvae to ensure that genetic variation is being maintained, and 4) a quantitative genetic analysis of growth and survival traits for possible genetic improvement. Some of these precautions may prove to be unnecessary in the long term, but at least should be followed until more detailed genetic information on *Birgus* is available. At the very least, if there is a desire to cultivate this species artificially, there is a need to acquire a better knowledge of the range of genetic and morphological characters existing in *Birgus latro* throughout its distribution.

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6 Conclusions

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and W.J. Fletcher

THE biological and population characteristics of coconut crabs conspire to make the species particularly vulnerable to exploitation. They are terrestrial, relatively easy to catch, slow growing, and their recruitment success seems to be highly variable. With intensive harvesting a coconut crab population can be depleted very quickly, and the stock may only begin to recover many years after collecting has ceased. This appears to be the same pattern as in other areas where coconut crabs have been exploited. The results of this study have given biological credence to fears that the species is in danger of suffering increasing rates of local extinction.

The absence of significant evidence of successful juvenile recruitment to the terrestrial environment during the course of the Project may have been due to variability in the environmental processes which determine the direction and extent of larval dispersal. Other researchers also report an apparent dearth of very small crabs (less than 10 mm TL) in their study areas, so the phenomenon of irregular recruitment apparently is not restricted to Vanuatu. While many local people stated that they had never seen coconut crabs of a very small size (about 1 cm), it is impossible to state categorically that the apparent lack of small juveniles was not the result of inadequate or biased sampling. Most of the regular collectors said that on occasions they had seen some animals of that size.

The lack of juveniles seen cannot be due to our searching in the wrong habitat because in many cases we searched the entire island. They may be difficult to find because of their fossorial lifestyle: it is conceivable that small juvenile crabs rarely emerge from their burrows, and they may have a much lower rate of foraging than larger crabs. Results from our enclosure studies support this. However, this appears not to be the situation with larger juveniles (20–30 mm TL), because at some sites such as Bokissa and the Kole cliff they were common, but at others such as Torres and Bier Island they were rare. This tends to suggest that recruitment is variable in time, space and intensity. It seems that significant numbers of crabs may recruit only every five to ten years, perhaps when oceanographic conditions are favourable, causing larvae to become trapped close to shore. Because the crabs have a slow but variable rate of growth and a long life, the size distribution will still be large even if there is sporadic recruitment. When the possible size distribution of the crabs is simulated using variable recruitment this can be made to emulate the distribution found at some unexploited sites.

Because of the slow growth rates and probable low rates of natural mortality it would take monitoring of 10–20 years at the one location to reconcile these two hypotheses conclusively. In order to test the hypothesis that recruitment is dependent on environmental factors

which determine pelagic larval dispersion patterns, a long term program would be required to monitor oceanic current speeds and directions in the vicinity of the islands. Obviously this would have to be carried out in conjunction with a program to monitor the abundance of postlarval and juvenile crabs in a variety of terrestrial habitats.

It is likely that the continuing biochemical genetic investigations will provide some answers to the questions whether there are discrete sub-populations of coconut crabs, and if so, what their geographic limits are. If this work (which is now using the more sensitive mitochondrial DNA analysis technique) shows significant genetic differences between localities which are close together (e.g. between adjacent islands in the Vanuatu Archipelago), it will suggest that there is a close geographical link between parent stock and recruits. This implies either that the pelagic larval stages have evolved mechanisms which enable them to avoid being swept away from the land mass and out to sea where the probability of survival would be very small, or that there is significant larval entrapment by gyres and eddies on the down-current side of the islands.

Evidence of erratic recruitment suggests, however, that the scenario outlined above is unlikely to represent the true situation. If recruitment is a localised phenomenon, then it would be expected that juveniles would be found in at least a few sites after each spawning season. This was not the case, so it seems likely that few, if any, genetic differences will be detected between populations of coconut crabs within the geographic limits of a typical archipelago. In this scenario the population is well mixed in the genetic sense, suggesting that exchange of genetic material occurs regularly throughout the breeding stock, probably as a result of stochastic patterns of larval dispersal at least within (and possibly also between) island groups.

The second of these scenarios is the only one in which a protected 'replenishment' island would be of much significance to the maintenance of the resource. Such schemes, which involve the complete protection of a small, circumscribed spawning population (on an uninhabited island, for example) have been suggested by other workers. They have a certain attraction, but it is unlikely that they can be an effective substitute for very carefully controlled stock-wide harvesting effort. It may well be that a scattering of medium-density spawning groups is a better bet than one or two isolated populations of very high density.

The accumulation of older adults is the part of the stock most vulnerable to exploitation. In fisheries terms this group forms the non-renewable part—the part which, under continuous exploitation, will never return. Thus the initial CPUE figures and total catch will be far in excess of the actual level which could be expected to be exploited in a sustained way. This pattern has occurred in many fisheries and may be typical of stocks of long-lived, slow-growing animals. The danger with these types of stocks is that the rates of exploitation frequently increase too quickly because initial high catch rates raise the expectations of the fishermen to too great a level. Catch rates inevitably decline as the accumulated stock is progressively removed, and unless harvesting effort is constrained the stock may be wiped out.

There appear to be few options for the conservation of Vanuatu's remaining crab population. The area is too large (with more than 100 islands) and the people too divided for some plans to be effective. More than 60% of the island's crab production derives from the Port Olry area of Santo, where the inhabitants are often in open conflict with the government. They were not helpful to our project, as they refused us permission to sample in most places and ultimately would not allow project staff to work anywhere in the area.

Controlling the movement of consignments of crabs between Santo and Vila would be difficult because of the large number of inter-island vessels trading between these ports. There is, in any case, a local market in Santo which now provides an outlet for most of the local product.

Because the crabs are distributed over a wide area it is unlikely that they would ever become totally extinct (provided some reproductively viable stocks remain on nearby islands). Before this happened, crab collectors would cease to find it economically worthwhile (in terms of time and effort) to continue harvesting crabs. However, the possibility still exists that even though a residual population is left on the island, its density may be so low that effective mating may be impaired. This would constitute a stock-recruitment collapse, where the reproductive part of the stock is physically unable to contribute to subsequent recruitment, either locally or elsewhere.

In addition to the threat of continued excessive exploitation, there is also an ecological threat —that of deforestation. Obviously some of the more rugged parts of the crabs' range will continue more or less untouched, but this may have the effect of concentrating the crabs in small areas, increasing their vulnerability to capture. The main long term problem for Santo's crab stocks is that recruitment will be affected due to reduction of the spawning population.

It has been rather easier to develop a workable managment plan for the Torres Islands. This area is remote and sparsely populated, and a large proportion of the community's cash income is derived from the sale of coconut crabs. Until recently the marketing of crabs was poorly organised, with most sales either being handled by middlemen or being directed to hotels at a low price, usually less than 250 vatu (approximately $A 2.50) per kg. Often payments were not received. On occasions no records of the quantity shipped were kept, and the crabbers therefore did not know how much they were owed. In one case the agent was to have given them a power boat after the crabs (an unspecified number) had been delivered. This took about a year's worth of crabs, and when the boat finally arrived it lacked an engine, for which more crabs were required in payment. This situation was grossly unsatisfactory, as the crabbers were obviously not receiving a fair price for their product. Ultimately it resulted in the local government council's putting a temporary freeze on the sale of crabs between November 1987 and February 1988, during which time a more equitable arrangement could be negotiated.

This arrangement essentially involved a quota system, with collectors taking a maximum of 600 kg of crabs per month from each of the

islands Tegua and Hiu. Sales were permitted only to the government fish market, which would pay a standard price of 500 vatu per kg. Once the monthly quota had been reached, the airline would be instructed not to transport any more crabs. In any case the airline was requested not to carry crabs that were consigned anywhere but to the Fish Market. The village chiefs on each of the two islands would decide how the quota was to be divided up between collectors.

In the event that it appeared that the fish market was becoming over-supplied with coconut crabs, the surplus would be exported to Noumea (New Caledonia) where demand continuously exceeds supply. This would also overcome the potential problem of a black-ban by the restaurants on buying from the fish markets. This situation was seen as only temporary, however, because few places apart from the Torres Islands now have enough large crabs to satisfy the restaurants.

The other part of the management plan was to designate the small island of Metoma as a reserve area, where the collection of coconut crabs would be totally prohibited. Local folklore has it that this island is considered the source of all crabs in Vanuatu, so the concept of a reserve harmonises well with local custom.

The restriction of sales of coconut crabs to the two fish markets also may be generalised to include all sales of crabs. Through this the entire market could be controlled with quotas placed on collectors from different areas. This is probably the only feasible way of conserving the crabs in most areas. Its drawback is that it will be logistically difficult to keep track of the quotas of many collectors and also prevent the development of a 'black market' in crabs.

In general local knowledge about the plight of the coconut crab is now much better understood both by collectors and the general public. A number of radio broadcasts relating the life history of the crabs were made during the course of the study. As a result of the project's field orientation, many opportunities arose for staff to talk with villagers and (particularly) those who collect the crabs. This has resulted in a far better understanding on the part of the local people about the potential dangers faced by the crab stocks if no conservative measures are adopted.

Crab collectors in Vanuatu are no different from most people involved in the exploitation of renewable resources anywhere in the world. While catch rates remain reasonably high there is a general lack of concern about the state of the resource, even though effective effort may have increased considerably. It is only after the stock has declined dramatically, and catch rates are reduced to a point where there is an economic impact, that the problem receives due attention. Unless the true extent of the decline in coconut crab stocks in Vanuatu is recognised and continues to be an issue, then it is likely that within a very few years coconut crabs will no longer represent a commercially viable resource, even on a small scale.

7 Annotated Bibliography

I.W Brown and D.R. Fielder

THIS bibliography is of the non-taxonomic literature. Although annotations are restricted mainly to readily-accessible papers and articles (i.e. those published in English since the turn of the century), references to some works published earlier in European journals are included without annotation.

Following the bibliography is a section containing a listing of authors and dates (titles have been excluded for reasons of brevity) classified under the appropriate subject headings. Articles which were not seen are excluded from this compilation.

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ALEXANDER, H.G.L. 1979. A preliminary assessment of the role of the terrestrial decapod crustaceans in the Aldabran ecosystem. Phil. Trans. Roy. Soc. Lond. B, Biol. Sci., 286 (1011), 241–246.

Mean egg numbers of 90 730 carried by female *B. latro* are related to probable large larval mortality. Coconut crabs are basically herbivores and were seen feeding along beaches at night. The average weight of coconut crabs taken from coconut-dense areas was almost twice that from areas with no coconut trees. *B. latro* is probably an important predator on turtle hatchlings. The possibility of mosquitoes feeding on the fleshy abdomens of coconut crabs is discussed, as is the possibility of *B. latro* dispersing coconut trees outside of plantations.

ALTEVOGT, R. and DAVIS, T.A. 1975a. *Birgus latro*, India's monstrous crab: a study and an appeal. Bull. Dept. Mar. Sci. Univ. Cochin, 7, 11–24.

This paper (accompanied by 13 black-and-white plates) gives a well balanced if brief review of the literature on *Birgus*, and an account of observations on coconut crabs at South Sentinel (Andaman Islands) made in February 1973 and March 1974. Details of the crabs' habitat, activity patterns, feeding, agonistic and digging behaviour, locomotion and climbing ability, orientation and sensory behaviour are provided. Scanning electron micrographs show tactile and chemosensory structures within the antennular groove.

——1975b. The coconut crab and its need of conservation. Fish and Fishery, Special issue, 37–44.

——Locomotion on ground and tree in the robber crab, *Birgus latro*. Film to be published by IWF, Gottingen.

AMESBURY, S.S. 1980. Biological studies on the coconut crab (*Birgus latro*) in the Mariana Islands. Univ. Guam. Mar. Lab. Tech. Rept 66, 39 p.

A comprehensive account of studies carried out on coconut crabs primarily on the island of Guam during 1973 and 1974. Field surveys were also undertaken

on other islands in the Northern Marianas (Pagan, Asuncion, and Guguan), and Palau (Ngariungs Is., Kayangel Atoll). Features of the species' reproductive behaviour and development are reviewed, including the relationship between larval release and moon phase (and tide). Early life history is summarised (primarily from Reese and Kinzie 1968); amongst the numerous small shell-bearing coenobitids examined at Guam none was referable to *Birgus*. The pooled length-weight relationship is given, there being no significant difference in regression parameters between the sexes. Some captive crabs in small enclosures moulted, but no size-increase resulted. Crabs in a large enclosure failed to moult at all. Burrowing and moulting behaviour is discussed, together with an apparent relationship between abdominal swelling and the onset of ecdysis. Feeding habits, diel activity patterns, and inter- and intra-specific interactions are outlined, with reference to the literature. A life history model for *Birgus* is developed, primarily with reference to probable sources of natural mortality at various points in the species' life cycle. The status of coconut crab stocks in the Marianas is reviewed, and possible management strategies presented. Various pieces of existing legislation are documented, and finally there is a discussion of the general feasibility of rearing *Birgus latro* on a large scale.

ANDREWS, C.W. 1899. A description of Christmas Island (Indian Ocean). Geographical Journal, 13, 17–35.

——1900. A Monograph of Christmas Island. London.

——1909a. Account of his first visit to Christmas Island 1908. Proc. Zool. Soc. Lond., 101–103.

——1909b. Exhibition of a photograph of the robber crab (*Birgus latro*) on Christmas Island with an account of its habits. Proc. Zool. Soc. Lond., (1909), 887–889; Pl. LXXXIII.

A very brief and general discourse on the natural history of the robber crab.

ANON. 1969. Coconut crabs. Science (New York Academy of Science), 9(3), 26–27.

——1973a. Villagers begin to breed coconut crabs. Aust. Fisheries, 32, 15.

A short report reprinted from a SPIFDA (South Pacific Islands Fisheries Development Agency) newsletter on a coconut breeding venture located in the village of Fanafo on the island of Santo, New Hebrides (Republic of Vanuatu).

——1973b. Breeding of coconut crabs (*Birgus latro*) in the New Hebrides. South Pacific Islands Fisheries Development Agency Newsl., 8, 27.

This is a reprint of a news bulletin published by the French Residency in the New Hebrides (now Republic of Vanuatu) (p.10 of the issue dated 23 March 1973). The release describes an operation at the Santo village of Fanafo in which young crabs brought in from the wild are held in captivity, and fed with sprouted coconut and bread until they grow to marketable size. The title is misleading, since the operation was obviously not set up to breed the crabs at all, only to grow them in captivity.

——1973c. Pacific Island Mariculture Conference, University of Hawaii, Hawaii Institute of Marine Biology, Coconut Island, Kaneohe, Hawaii, February 6–8 1973, 21 p.

The conference recommended priorities for the establishment of mariculture programs in the Pacific islands. *Birgus latro* was one of a number of invertebrate species considered (p. 10). Top priority species included Malaysian prawn, brine shrimp, marine shrimp and oysters. *Birgus* ranked with the second priority species, which also included northern lobster, mangrove crab, pearl oyster and tridacnid clams. The probability of expanding markets for coconut

crabs, their ability to be shipped alive, and the possible need for culture as a long-term conservation measure were mentioned.

——1975. R-0010 Coconut Crab. Guam Agricultural Experimental Station (University of Guam), Research Report 1, 10–14.

Progress report on a project to investigate the biology and feasibility of culture of *Birgus latro*, a species highly marketable in Guam. The project's objectives were to establish methods for collecting large numbers of juvenile crabs, to develop holding techniques for juveniles and adults, to carry out food and growth trials, to estimate growth in wild crabs, and to assess natural recruitment rates. Feeding trials were inconclusive since moult growth-increments were very small. Various explanations for the poor growth rates are discussed. Tagging trials (employing anchor tags as used on lobsters) were about to commence, as were electrophoretic experiments aimed at finding a biochemical way of identifying the onset of moulting. Attempts to locate very small shelled juveniles met with little success, suggesting low recruitment levels on Guam. The potential for the culture of coconut crabs on Guam was not considered very high, at least on a commercial scale.

ATTENBOROUGH, D. 1979. Life on Earth: A Natural History. Collins/BBC, London. 319 p.

Brief mention is made (p. 58) of the robber crab's size, terrestrial habits, ability to climb coconut trees, and dependence on access to the sea for reproduction.

BAGNIS, R. 1970. A case of coconut crab poisoning. Clin. Toxicol., 3(4), 585–588.

A case of poisoning from the ingestion of the flesh of a large *Birgus latro* is documented. The crab was caught in a swampy area on the atoll of Kauehi in the central Tuamotus. After cooking, the flesh was reported to taste bitter. First symptoms appeared about twelve hours after ingestion, and the illness persisted for five days. Local reports indicated knowledge of other cases (one fatal) and a belief that the toxicity derives from the crabs eating roots of *Ceodos umbraculifera*. The author also cites cases from southern Japan reported by Hashimoto et al. (1968).

BATES, M. and ABBOTT, D. 1958. Coral Island, Portrait of an Atoll. Scribner, New York.

BAYNE, C.J., COGAN, B.H., DIAMOND, A.W., FRAZIER, J., GRUBB, P., HUTSON, A., POORE, M.E.D., STODDART, D.R., and TAYLOR, J.D. 1970a.

Geography and ecology of Cosmoledo Atoll. Atoll Res. Bull., 136, 37–56.

Reports the occurrence of *B. latro* on Cosmoledo Atoll and cites Honegger's (undated) records of *B. latro* on Wizard, Grand Polyte and South Islands.

——1970b. Geography and ecology of Astove. Atoll Res. Bull., 136, 83–99.

B. latro is cited as being conspicuous among the land crustaceans of this atoll.

BORRADAILE, L.A. 1898. On some Crustaceans from the South Pacific. Part II. *Macrura anomala*. Proc. Zool. Soc. Lond. 1898, 457–468.

Discusses tree-climbing habits of *B. latro* and its use of coconuts and Pandanus fruit as food.

——1900a. On the young of the robber crab. In: Willey, A., ed., Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere. Part V, 585–589.

Defines breeding seasons as May (Philippines), January – February (Loyalty Islands), and the beginning of the year (Christmas Island). The first zoea larva

is described from those hatched by ripe females on Christmas Island. Behaviour of egg-carrying females and hatching are briefly described.

——1900b. A note on the hatching-stage of the Pagurine landcrabs. Proc. Roy. Soc. Lond., 937–938.

BOURN, D. and COE, M.J. 1979. Features of tortoise mortality and decomposition on Aldabra. Phil. Trans. R. Soc. Lond. B, 286, 189–193.

Of those crustaceans considered as scavengers, *B. latro* was considered to have major importance. As many as 14 crabs were seen near tortoise carcasses at one time. Coconut crabs were active almost exclusively at night or during the early morning. They were seen tearing the flesh from dead tortoises, and even carried bones and entrails away.

BOURNE, G.C. 1886. General observations on the fauna of Diego Garcia, Chagos Group. Proc. Zool. Soc. Lond., 331–334.

BOUVIER, E.L. 1891. Le crabe des cocotiers ou *Birgus larron*. Le Naturalist, 13me Anee, 81–85.

BURGGREN, W.W., and McMAHON, B.R. 1981. Haemolymph oxygen transport, acid base status and hydro mineral regulation during dehydration in three terrestrial crabs, *Cardisoma*, *Birgus*, and *Coenobita*. J. Exp. Zool., 218(1), 53–64.

The interaction between haemolymph water and ion content, and respiration and acid base balance during dehydration and recovery are described for *Cardisoma carnifex*, *Birgus latro* and *Coenobita brevimanus*.

CAMERON, J.N. 1981a. Brief introduction to the land crabs of the Palau Islands—stages in the transition to air breathing. J. Exp. Zool., 218(1), 1–6.

An introduction to a series of papers arising from a cruise of the 'Alpha Helix' to Palau. The principal land crabs of Palau are described and their distributions are outlined. The gill area and gill structure of *Callinectes sapidus*, *Ocypode albicans*, *Cardisoma carnifex* and *Birgus latro* are compared.

——1981b. Acid base responses to changes in CO_2 in two Pacific crabs: the coconut crab, *Birgus latro*, and a mangrove crab, *Cardisoma carnifex*. J. Exp. Zool., 218(1), 65–74.

The acid-base regulating ability is described for the completely terrestrial *Birgus latro* and the amphibious *Cardisoma carnifex* during experimental manipulation of blood pH and CO_2 partial pressure. Terrestrial crabs are able to respond to acid-base disturbance by compensatory mechanisms. However without a means of carrying out branchial ion exchange their ability to regulate blood pH is strictly limited.

CAMERON, J.N. and MECKLENBURG, T.A. 1973a. Aerial gas exchange in the coconut crab *B. latro* with some notes on *Gecarcoidea lalandii*. Respir. Physiol., 19(3), 245–261.

Measurements were made on blood pH, and partial pressures of CO_2 and O_2, ventilation rates and volume, acid-base characteristics, and diffusion gradient across the lungs in *Birgus latro* from Eniwetok Atoll (Marshall Islands). The importance of the scaphognathites and their function in ventilation is described. Increases in ventilation flow (e.g. following disturbance) are achieved by increasing scaphognathite beat frequency rather than amplitude. Blood chemistry parameters are discussed with regard to the crabs' evolutionary transition to terrestriality.

——1973b. Air breathing in the coconut crab *Birgus latro*. Physiologist, 16(3), 278.

This is evidently an abstract of a conference presentation, and covers the same ground as Cameron and Mecklenburg 1973a.

CARSON, H.L. and WHEELER, M.R. 1973. A new crab fly from Christmas Island, Indian Ocean (Diptera:Drosophilidae). Pacific Insects, 15, 199–208.

A description of a new species of drosophilid fly, *Lissocephala powelli*, found breeding on *Gecarcoidea humei* and *Birgus latro* at Christmas Island.

CATALA, R.L.A. 1957. Report on the Gilbert Island: some aspects of human ecology. Atoll Res. Bull., 59, 1–187.

Discounts the proposition that coconut crabs cause extensive damage to coconut palms (page 30).

CHAKRAVARTI, D. and EISLER, R. 1961. Strontium-90 and gross beta activity in the fat and non-fat fractions of the liver of the coconut crab (*Birgus latro*) collected at Rongelap Atoll during March 1958. Pacific Science XV, 155–159.

Radioactivity resulting from nuclear weapon-testing in the Pacific immediately following World War II was measured in various organisms. This paper explains why radioactivity in *B. latro* liver samples should be compared on the basis of non-fat solids.

CHAPMAN, W.M. 1948. Coconut-eaters. Pacific Discovery, 1(2), 3–6.

A conversational discourse about the probable mechanism by which *Birgus latro* removes and eats the nuts from coconut trees. Reference is made to their chiefly nocturnal habits and to their seaward spawning migration. The unexpected effect of building a wartime airstrip across the migration trails of coconut crabs on the island of Munda (Solomons) is described.

CHEKE, A.S. and LAWLEY, J.C. 1983. Biological history of Agalega, with special reference to birds and other land vertebrates. Atoll Res. Bull., 273, 65–108.

This paper describes the history of introduction and current status of a number of animals on Agalega, one of a pair of small islands under Mauritian administration situated some 560 km south of the Seychelles. A note on the coconut crab appears as an appendix, commenting on some earlier literature which suggested that *Birgus* had been introduced. *Birgus* populations appear to have declined during the 1940s, and disappeared entirely during the subsequent decade.

COE, M.J. and SWINGLAND, I.R. 1984. Giant tortoises of the Seychelles. In: Stoddart, D.R., ed., Biogeography and Ecology of the Seychelles Islands. W. Junk, Netherlands. 309–330.

B. latro is cited as the main nest predator of tortoise eggs. A plate on page 320 shows *B. latro* eating a tortoise egg.

COHEN, E. 1968. Immunologic observations on the agglutinins of the haemolymph of *Limulus polyphemus* and *Birgus latro*. Trans. N.Y. Acad. Sci., 30, 427–443.

Describes the presence, in the haemolymph of *Limulus polyphemus* and *Birgus latro*, of avid agglutinins for erythrocytes of a variety of vertebrate species. It is speculated that these agglutinins may have provided some selective advantage to the animals during the course of their evolution. Alternatively they may be part of the saccharide transport or storage mechanisms associated with the shell formation of the animals.

——1970. A review of the nature and significance of haemagglutinins of selected invertebrates. In: Bianchi, C.P. and Hilf, R., ed., Protein Metabolism and Biological Function. Rutgers University Press, New Brunswick.

Non-haemolytic agglutinins were found in all adults tested but were not found in young moulting coconut crabs.

COHEN, E., ROZENBERG, M., and MASSARO, E.J. 1974. Agglutinins of *Limulus polyphemus* (horseshoe crab) and *Birgus latro* (coconut crab). Ann. N.Y. Acad. Sci., 234, 28–33.

A short paper which compares the ability of *Limulus* and *Birgus* agglutinins to compete for the same erythrocyte membrane determinant. Cells MM, MN and NN, when coated with *Limulus* or *Birgus* agglutinins will primarily inhibit the absorption of specific anti-M or anti-N sera.

CROPP, B. 1982. Coconut cracking crabs. Oceans, 15(3), 14–15.

During a filming visit to Lisilus Island, part of an atoll at the eastern extremity of Papua New Guinea, the author witnessed a duel between two large robber crabs, apparently over a coconut which had been ingeniously cracked open by one of the antagonists. The contest ended with one crab losing a leg and a claw. The author claims to have seen (and filmed) the crab de-husking the coconut, then carrying it up a nearby tree. The nut was dropped from a height of about 10 metres, and it split perfectly in two upon striking a second coconut lying on the ground. Two interesting colour photographs accompany this conversational article.

CUZENT, G. 1884. Archipel de Pomotu. Bull. de la Société Academique de Brest II., 9, 49–90.

DANA, J.D. 1849. Geology. 'U.S. Exploring Expedition' (Vol. 10) Putnam, New York. p. 9.

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(3), 574–580.

Galathea Bay is apparently the only locality on Great Nicobar Island where *Birgus* is found. Several crabs collected during 1966 were studied, and detailed accounts of their diet (from direct observation, stomach contents analysis, examination of food remains, and feeding experiments) are given. The crabs readily consumed the coconut flesh offered, but the normal diet appeared to consist mainly of *Barringtonia*, *Pandanus*, and arecanut fruits. Coastal Nicobarese believed that observed damage to fallen coconuts was due to rats rather than coconut crabs.

The crabs' tree-climbing ability is described in detail, and the general comment made that declining populations may be linked to predation on (small) crabs by introduced domesticated animals such as pigs. The eggs from one berried female coconut crab were hatched and the eggs and first zoeal larval stage described and illustrated. No further observations on the larvae were made, presumably because none survived.

DARWIN, Charles 1845. The Voyage of the Beagle. Dent, London.

The occurrence of *Birgus latro* on Keeling Island is recorded along with some observations on the habits of the crab.

DARWIN, C. 1972. A monstrous crab. In: Animals (London) 14(9), 405–407.

DAVIS, T.A. 1984. Observations on the giant coconut crab (*Birgus latro*). Festschrift zum 60. Geburtstag von R. Altevogt. 8 Seiten, 6 Abbildungen. Manuscript, Munster.

DAVIS, T.A. and ALTEVOGT, R. 1976. Giant turtles and robber crabs of the South Sentinel. Yojana, 20, 75–79.

——1978. Is the coconut crab a pest of coconut? World Crops: July/August 1978, 157–162 and p. 172.

A very detailed and comprehensive review of the literature on the utilisation of coconuts by coconut crabs. References to the crabs' ability to climb trees and pick coconuts, strip off the husks and break open the kernels, are provided. Contradictory views, mostly resulting from observations on captive crabs, are

also discussed. Additional observations were made by the authors during visits to South Sentinel Island (Indian Ocean) in 1973 and 1974 (see also Altevogt and Davis 1975). Circumstantial evidence of the animals' capacity to de-husk and break open coconuts was obtained, but no crabs were actually observed in the act. Some discussion follows on a theory relating the possible origin and dispersal of the coconut palm with the distribution of *Birgus*. However the theory is discredited as there is ample evidence that *Birgus* is not dependent upon coconuts. Many diverse dietary items are listed. Interestingly, there is neither any firm evidence, discussion, nor conclusion presented as to whether *Birgus* is or is not a pest of the coconut.

DELSMAN, H.C. 1923. De krabben van Christmas-Eiland. Tropische Natuur., 12, 1–10.

EDMONSON, C.H. 1923. Crustacea from Palmyra and Fanning Islands. Bernice P. Bishop Museum (Honolulu) Bull. 5.

ELLIS, A. 1936. Adventuring in Coral Seas. Angus and Robertson, Sydney.

FARRELL, A. 1928. John Cameron's Odyssey. Macmillan, New York.

FELDER, D.L., MARTIN, J.W. and GOY, J.W. 1985. Patterns in early postlarval development of decapods. In: Wenner, A.M., ed., Crustacean Issues 2: Larval Growth. A.A. Balkema, Rotterdam & Boston. 236 p.

A single sentence on p. 207 refers to Reese's (1968) hypothesis regarding the retention of ancestral hermit crab behavioural patterns by early postlarval coconut crabs.

FLETCHER, W.J., FIELDER, D.R. and BROWN, I.W. 1989. Comparison of freeze- and heat-branding techniques to mark the coconut crab *Birgus latro* (Crustacea, Anomura). J. Exp. Mar. Biol. Ecol., 127, 245-251.

This paper is the result of early experimental work during the ACIAR Coconut Crab Project in Vanuatu. The effectiveness of freeze- and heat-branding as methods to individually identify post-moult coconut crabs was assessed in captive and free-ranging animals. The success of freeze-branding was dependent on the material used in the branding tool and the length of application. A maximum of 80% success was attained. Heat-branding was always successful but the resolution of the marks was often poor. The authors discuss the applicability of these methods to studies on other crustaceans.

FLETCHER, W.J., BROWN, I.W. and FIELDER, D.R. 1990a. Movement of coconut crabs, *Birgus latro*, in a rainforest habitat in Vanuatu. Pac. Sci., 44, 407–416.

As part of the Vanuatu project the movement patterns of coconut crabs were studied using mark–recapture and radio-tracking methods in eastern Santo. No significant correlation was observed between the minimum possible distance moved and time at liberty. Individual size evidently had no effect on distance moved among crabs which were 'indigenous' to the experimental area (Bier Island), but there was a negative correlation among crabs introduced from other areas. Recapture rates of both groups (indigenous and introduced) were similar, but the introduced animals tended to move somewhat further from their point of release. Only two of the five radio-tagged crabs released on Santo were located again, and both had moved more than 250 m away from their release point. On the island site, however, all radio-tagged crabs were encountered again at least once, and frequently at sites which they had occupied previously. The species appears to have a flexible home range, and may tend to disperse from a particular area after capture and handling.

——1990b. The use of standard and inverse Leslie experiments to estimate the abundance of the coconut crab (*Birgus latro* L.) in Vanuatu.

Catchability coefficients (the relationship between stock size and catch per unit effort) were estimated for coconut crabs caught by the baited transect method. The experiments were done in conjunction with a Petersen mark–recapture study at one of the sites to determine absolute density. The predicted increase in density from changes in CPUE was compared with the known value (i.e. the number of crabs added to the population in the inverse experiment) and also with changes in the Petersen estimates. The technique is now being used as a tool in the management of coconut crab stocks.

——1990c. Growth of the coconut crab *Birgus latro* in Vanuatu. J. Exp. Mar. Biol. Ecol., 141, 63–78.

Aspects of the growth of coconut crabs were studied in northern Vanuatu where they form an important cash crop. Moult behaviour and growth increment were studied using captive crabs, but with limited success. The best information on moult increment was derived from tagged free-ranging crabs and moulting crabs excavated from their burrows. Moult frequency was estimated primarily from assessment of shell age and abdominal expansion in wild-caught crabs and animals on sale at municipal markets. Asymptotic thoracic lengths were estimated as about 80 mm (males) and 50 mm (females). Adults appeared to moult only once per year, during the dry season, but juveniles (<30 mm TL) moulted more frequently. The computed growth rate indicates that crabs may take more than 10 years to attain the current minimum legal size in Vanuatu, and they may live to more than 40 years of age. The significance of these characteristics on the exploitation of coconut crab stocks is discussed. Additional material on this aspect of the biology of *Birgus latro* may be found in Section 3 of this volume.

FOSBERG, F.R. 1956. Military Geography of the Northern Marshalls, prepared under the direction of the Chief of Engineers, US Army, and the US Geological Survey.

FRIEDERICI, G. 1910. Ein Beitrag zur Kentniss der Tuamotu Inseln. Mitteilungen der Gesellschaft fur Erdkunde zu Leipzig, 7, 97–176.

FRYER, J.C.F. 1911. Reports of the Percy Sladen Trust Expedition to the Indian Ocean in 1905—The structure and formation of Aldabra and neighbouring islands—with notes on their flora and fauna. Trans. Linn. Soc. Lond. (2) Zool., 14, 397–442; plates 22-29.

Coconut crabs were abundant, especially at Takamaka where they carried off loose property at night and destroyed household components. Eighty crabs were killed in the first three nights. An overturned turtle on the beach was believed to have been killed by *B. latro*.

FUSETANI, N., HASHIMOTO, K., MIZUKAMI, I., KAMIYA, H. and YONABARU, S. 1980. Lethality in mice of the coconut crab *Birgus latro*. Toxicon, 18(5-6), 694–698.

A high proportion of the inhabitants of the Yaeyama archipelago (Ryukyu Islands) have experienced poisoning by *Birgus latro*. The problem is also known in the Tuamotu, Palau and Yap Islands. The authors note that poisoning occurred (in the Ryukyus) only on ingestion of the viscera. Water-soluble toxin (lethality between 0.5 and 1 MU) was extracted from the hepatopancreatic and intestinal tissue of *Birgus latro* specimens from Ishigaki Island, but muscle, gonads and viscera other than hepatopancreas and intestine did not contain toxin. These findings support the theory that the toxicity is derived from the crabs' food. However two of the plants (*Diospyros maritima* and *Hernandia sonora*) often implicated in coconut crab poisoning were found to contain no toxin.

GARDINER, J.S. 1907–1909. The Percy Sladen Trust Expedition to the Indian Ocean in 1905. Trans. Linn. Soc. Lond. Second series., 12, 1–56.

A brief description of the occurrence of *Birgus latro* on the Island of Salomon (Chagos Archipelago). Includes a photograph of *B. latro* attacking a coconut.

GEORGE, R.W. 1978. The land and freshwater crabs of Christmas Island. Unpublished report to Australian National Parks and Wildlife Service, Perth. 22 p.

GERARD, E. 1893. Composition chimique de la graisse du foie de ... *Birgus latro*. Journ. de Pharm. et de Chimie, 5me serie., 28, 443-450.

GIBSON-HILL, C.A. 1947. Field notes on the terrestrial crabs (Christmas Island). Bull. Raffles Museum, 18, 43–52.

Anecdotal discourse on distribution, feeding and reproductive and aggressive behaviour. It is proposed that *B. latro* is not capable of using undamaged coconuts for food.

——1948. The robber crab. Malayan Nature J., 3(1), 10–14.

A general account of *Birgus latro* is given, based on available literature at the time, as well as observations on crabs in the Christmas and Cocos-Keeling Islands. Distribution, affinities with the hermit crabs, maximum size, colour patterns, and some behavioural aspects are discussed. In a brief outline of the crab's early development the author cites Harms (1932) as saying that the young animals abandon their protective mollusc shell at about nine months of age. The crabs' tree-climbing habits, varied diet, and capacity for opening coconuts are described, the latter with reference to previous documented accounts by Rumphius, Darwin, Forbes and Guppy. William Dampier's (1688) comments on the edible qualities of Christmas Island coconut crabs are related.

——1949. The Robber Crab. Zoo Life, 4, 58–60.

GILL, W. 1876. Life in the Southern Isles. Religious Tract Society, London.

GILLETT, K. 1974. Raymond Burr's island. Australian Women's Weekly, August 7th, 22-23.

This magazine article is primarily an account of the author's visit to Naitauba, an island in the Lau Group east of Fiji. The main purpose of the visit was to photograph the coconut crab and investigate some of the conflicting reports regarding its behaviour. Crabs were hard to find, but a recently-occupied 'nest' in a small crevice in a rocky cliff face was found about a mile inland. Eventually a local islander captured a male crab at night in a rocky area, and the animal was photographed climbing a coconut tree and starting to open a fallen nut (photos included in article).

GORDAN, J. 1956. A bibliography of pagurid crabs, exclusive of Alcock, 1905. Bull. Am. Mus. Nat. Hist., 108, 253–352.

A comprehensive bibliography on hermit crabs. A list of works included on *Birgus latro* appears on page 304.

GORE, R.H. 1985. Moulting and growth in decapod larvae. In: Wenner, A.M., ed., Crustacean Issues 2: Larval Growth. A.A. Balkema, Rotterdam and Boston, 236 p.

The author refers (p. 17) to Reese and Kinzie's (1968) work indicating that the final zoeal stage of *Birgus* exhibits a mixture of larval and glaucothoeal characteristics, and to Provenzano's interpretation of such 'extra' stages as resulting from non-uniform internal growth coupled with a regular moulting cycle.

GRAY, H.S. 1981. Christmas Island—Naturally. Howard Gray Publication, Geraldton, Western Australia, 133 p.

A brief popular account of coconut crab natural history, including some good photographs. Nuisance behaviour such as scavenging at campsites is mentioned, as is the animal's habit of thrusting its unprotected abdomen into crevices, logs, etc. when approached. Coconut crabs are found throughout the island and are usually nocturnal. Any vegetable material or carrion may be used as food. Females migrate to the overhanging sea-cliffs to spawn during the early months of the year, but males apparently do not migrate similarly. The smallest free-living forms (5-10 cm in length) are common on the shore terrace during the early part of the year. The largest specimens had a leg span of 50 cm, and stood 30 cm high. It is suggested that 8-10 moults are required to attain this size. In most inhabited places throughout their range coconut crabs have been hunted virtually to extinction.

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.

Crabs collected on Christmas Island were air-freighted live to Sydney where they were maintained in captivity under controlled laboratory conditions. Their food supply included dog-biscuits, fruits and sweet corn. Crabs provided with fresh water drank far less than those provided only with saline water. Primary urine is formed by filtration in the crabs' antennal organ. The authors mentioned that the feeding regime was adequate to sustain growth and promote moulting, but no data on either process are presented.

GROSS, W.J. 1955. Aspects of osmotic regulation in crabs showing the terrestrial habit. Amer. Nat., LXXXIX, 205–222.

B. latro has special adaptations to terrestrial life. It can drink water from small puddles, moisten its gill-chambers without immersion, and control body fluid concentrations by selecting water of appropriate salinity.

——1957. An analysis of response to osmotic stress in selected decapod Crustacea. Biol. Bull., 112, 43–62.

——1964. Water balance in anomuran land crabs on a dry atoll. Biol. Bull., 126, 54–68.

A study on water balance in *Birgus latro*, *Coenobita perlatus* and *C. brevimanus*. *Birgus* are normally found in wooded areas in association with piles of rotten coconuts. They do not depend on seawater for their water source. Coconut crabs forced to inhabit exposed dry islets probably do utilise seawater as a water source or tolerate slow desiccation within sealed burrows.

GRUBB, P. 1970. Ecology of terrestrial decapod crustaceans on Aldabra. Phil. Trans. Roy. Soc. Lond. Ser. B. Biol. Sci., 260, 411-416.

B. latro is the second most abundant terrestrial decapod on Aldabra. An account is given of its burrows and shelters and on its feeding habits, especially those concerned with eating *Pandanus* fruits.

——1971. The growth, ecology and population structure of giant tortoises on Aldabra. Phil. Trans. R. Soc. Lond. B, 260, 327-372; plates 24–25.

Robber crabs were abundant in *Pandanus* thickets and climbed these trees to eat the ripe fruit. Tortoises ate the bodies of *Birgus* if they were offered to them and they also scavenged egg-carrying crabs dying on the dunes.

GUNTHER, A. 1874. A contribution to the fauna of Savage Island. Proc. Zool. Soc. Lond., 295–297, 1 plate.

GUPPY, H.B. 1882. Note on the coconut-eating habit of the *Birgus* in the Solomon Group. Proc. Linn. Soc. N.S.W. First Series, 7, 661–665.

Describes an individual *B. latro* found eating a fallen coconut and its subsequent eating habits while held captive on board ship. A brief description of the crab's defensive behaviour is also given.

'H., Dr' 1923. Eenige opmerkingen over den klapperdief (*Birgus latro*). Trop. Natuur., 12, 77–78.

HAGEN, H.O. von 1977. The tree-climbing crabs of Trinidad. Stud. Fauna Curacao, 54, 25–59.

HAIG, J. 1984. Land and freshwater crabs of the Seychelles and neighbouring islands. In: Stoddart, D.R., ed., Biogeography and Ecology of the Seychelles Islands. W. Junk, The Netherlands. 123–139.

B. latro was the largest and one of the most abundant terrestrial crabs. It was found in the supra-littoral beach vegetation, coconut groves and *Pandanus* thickets, where it sheltered in rock-holes and crevices, between tree roots and in *Cardisoma* holes. On Aldabra *B. latro* is a scavenger on dead tortoises and preys on tortoise eggs and hatchlings.

HARMS, J.W. 1932. Die Realisation von Genen und die Konsekutive Adaption II. *Birgus latro* L., als landkrebs und seine Bezeihungen zu den Coenobitiden. Zeitschr. wiss. Zool., 140, 167–290.

——1937. Lebensablauf und Stammesgeschicte des *Birgus latro* L. von der Weinachts-insel. Zeitschr. fur 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(3), 131–137.

Speculates on the origin of Darwin's account of *B. latro* at the Keeling or Cocos Islands in 1836. Dispersal of coconut crabs by way of floating coconuts is also suggested.

HARRIS, R.R. and KORMANIK, G.A. 1981. Salt and water balance and antennal gland function in 3 Pacific species of terrestrial crab (*Gecarcoidea lalandii, Cardisoma carnifex, Birgus latro*). 2. The effects of desiccation. J. Exp. Zool., 218(1), 107–116.

This paper describes the rates of water loss, changes in haemolymph and urine concentration and the role of the antennal gland in water conservation and osmoregulation during dehydration of the three terrestrial crab species.

HASHIMOTO, Y. 1979. Coconut crab poisoning. In: Marine Toxins and other Bioactive Marine Metabolites. Jap. Sci. Soc. Press, Tokyo. 68-69.

Several cases of intoxication from the ingestion of coconut crabs are reported, mainly from the Ryukyu Islands south of Japan. One case involved a small crab whose 'abdominal part', eaten by three children, resulted in a rapid onset of vomiting and diarrhoea. No ill-effects were experienced by a neighbouring family which ate the claws, but two pigs, fed some leftovers, became sick and died in a few days. Several plant species (listed) are believed to be implicated in the crabs' toxicity. The author cites Holthuis' 1968 reference to the procedure on Yap where crabs are starved for several days before they are eaten, and recommends that this may be an effective means of clearing the toxic substances from the animal.

HASHIMOTO, Y., KONOSU, S., and YASUMOTO, T. 1968. La ciguatera dans les iles Ryukyu et Amami. Doc. 7., presented at the Seminar on Ichthyosarcotoxism at Papeete, Tahiti, August 16–22, 1968.

HEDLEY, C. 1896. General account of the atoll of Funafuti. Aust. Mus. Mem. III (Sydney), 1896–1900.

HELD, E.E. 1963. Moulting behaviour of *Birgus latro*. Nature, London, 200, 799–800.

An aquarium-held specimen of *B. latro* moulted four times during a period of 463 days, increasing in cephalothoracic length from 20.8 to 30 mm, and in weight from 6.8 to 20.2 g. Ecdysis occurred in a burrow (excavated by the crab), the entrance of which was plugged with loosely-packed soil. Ecdysis was not observed, but the moulted crab ate its exuvium before emerging from its burrow.

HELFMAN, G.S. 1973. Ecology and behaviour of the coconut crab, *Birgus latro* (L.). M.Sc. thesis, University of Hawaii (Zoology). (University Microfilms M-5452). 158 p.

This dissertation represents the most comprehensive study to date on the behaviour and ecology of *Birgus latro*. The material presented forms the basis of the author's three subsequent papers (1977a, b, 1979). Coconut crab populations in Palau (Ngerskersiul Islet) and Eniwetok (Igurin Islet) were studied by attracting individuals to staked coconuts and recording behavioural interactions at the baits. Size-structure and sex ratios were examined, and population density estimated from tagging (with spray paint). Fecundity, breeding cycle and copulatory behaviour are described in detail, as are various aspects of their feeding, communicative and agonistic behaviour. Temporal and spatial changes in distribution and diel changes in behaviour are discussed. Population differences between the two study sites are interpreted with reference to competition for limited resources (burrow sites and food). It is suggested that this regulatory mechanism is mediated through behavioural interaction and possibly cannibalism.

——1977a. Agonistic behaviour of the coconut crab, *Birgus latro* (L.). Z. Tierpsychol., 43, 425–438.

B. latro is not gregarious. Large crabs dominate and are avoided by small crabs and agonistic displays help maintain individual distances of about one metre. The number of visual displays is reduced but amplitude of retained displays increases with age. This may be linked with evolutionary loss of a protective mollusc shell and to visual limitations of nocturnal habits.

——1977b. Copulatory behaviour of the coconut or robber crab *Birgus latro* (L.) (Decapoda, Anomura, Paguridea, Coenobitidae). Crustaceana, 33, 198–202.

Copulatory behaviour of *B. latro* is described from a single observation of a copulating pair. Copulation occurred on land, lasted only a few minutes, and resulted in the deposition of spermatophores on the ventral coxal surfaces of the female's second and third walking legs. Egg extrusion and fertilisation were not observed.

——1979. Coconut crabs and cannibalism. Natural History, 88, 76–83

A popular account of the ecology of *Birgus latro*. The author gives logical explanations for the coconut crabs' simplified behavioural repertoire, its ability to achieve a large size, and its success on isolated islands. Cannibalism is put forward as the major means available to *B. latro* for regulating population sizes. The article is illustrated with excellent colour photographs.

HENRY, R.P. and CAMERON J.N. 1981. A survey of blood and tissue nitrogen compounds in terrestrial decapods of Palau. J. Exp. Zool., 218(1), 83–88.

The contribution of intracellular free amino acids to intracellular osmolality is discussed for *Gecarcoidea lalandii*, *Cardisoma carnifex*, *Birgus latro*, *Coenobita brevimanus* and *C. perlatus*. A profile of the major nitrogen compounds in blood and tissue is also given.

HERMS, W.B. 1926. *Diocalandra taitensis* (Guerin) and other coconut pests of Fanning and Washington Islands. Philippine J. Sci., 30, 243–274.

Birgus latro is listed as a pest of coconut trees but as long ago as 1926 coconut crabs were virtually extinct on Fanning Island, and were not considered in pest control measures (page 254).

HICKS, J. 1980. An annotated bibliography of the natural history of Christmas Island, Indian Ocean. Australian National Parks & Wildlife Service Report (mimeo). 25 p. + index.

HICKS, J., RUMPFF, H. and YORKSTON, H. 1984. Christmas Crabs. Christmas Island Natural History Association, Christmas Island, Indian Ocean.

A popular account of coconut crab biology including anatomy, activity, feeding, and spawning, particularly with reference to the Christmas Island populations. A well-presented chapter in a spectacular book containing many excellent colour photographs of the island's extensive terrestrial crab fauna.

HINCKLEY, A.D. 1969. Ecology of terrestrial arthropods on the Tokelau Atolls. Atoll Res. Bull., 124, 1–18.

Records the presence of *B. latro* on all three of the Tokelau atolls.

HOLTHUIS, L.B. 1953. Enumeration of the decapod and stomatopod Crustacea from Pacific coral islands. Atoll Res. Bull., 15(24), 1–66 + appendices.

Distributional records for *Birgus latro* are listed from several localities in the Marshall Islands, as well as the Gilberts (now Kiribati), and Raroia Atoll in the Tuamotus. The habitats from which the crabs were recorded are also described very briefly.

——1959. Contributions to New Guinea carcinology. III: The occurrence of *Birgus latro* (L.) in Netherlands New Guinea. Nova Guinea (new ser.), 10, 303–310.

Discusses the distribution of *B. latro* in western New Guinea. Habitat, habits, methods used to capture coconuts and their value as food are discussed briefly.

——1963. Contributions to New Guinea Carcinology. IV. Further data on the occurrence of *Birgus latro* (L.) in west New Guinea (Crustacea, Decapoda, Paguridea). Nova Guinea, 18, 355–359.

Lists known occurrences of *B. latro* in western New Guinea. Native names, details of habitat and food gathering, together with methods for catching *B. latro* are discussed.

——1968. Are there poisonous crabs? Crustaceana, 15, 215–222.

This general treatise on crab toxicity makes passing reference to the practice among the Yap islanders (Federated States of Micronesia) of starving coconut crabs for several days before they are eaten. The object of this is to ensure that any toxic plant materials which may have been consumed by the crab are voided from its alimentary canal.

HORST, R. 1902. On the habits of the cocoa-nut (sic) crab or palm thief. Notes from the Leyden Museum, 23, 143–146.

HORSTMANN, U. 1976. Some aspects on the culture of the coconut crab (*Birgus latro*). National Research Council of the Philippines Bull., 60, 8-13.

The salient features of the life history of *Birgus latro*, including predators, reproduction and early development, and habitat are summarised. An instance is cited of a coconut crab being found in the stomach of a marine crocodile in Palau. Rearing and holding experiments were conducted on Mactan Island (Philippines), but problems were experienced with crabs escaping from a 'semi-natural' corrugated-iron walled pen. Cannibalism also presented problems. Development of different types of enclosures eventually resulted in much-decreased mortality. The captive crabs were fed a wide variety of foods, but none moulted. It was felt perhaps that the rearing conditions were not conducive to ecdysis. No growth rates were established. The author believes that 'there might be a possibility of culturing *Birgus* in farms', but not until the characteristics of the early crab stages have been described. Recommendations 'to protect coconut crabs in the Philippines' included introduction of seasonal and size restrictions, area closures, and eventually the development of a hatchery.

——1980. Some aspects on the culture of the coconut crab *Birgus latro*. Abstract In: Kurian, C.V. et al., ed. Symposium of Coastal Aquaculture, 12–18 January 1980. Mar. Biol. Assn India, Cochin.

Precis of the work outlined in the author's 1976 paper, relating to cage experiments and feeding trials. None of the crabs moulted, and the author concludes that successful cultivation of *Birgus* will depend on an ability to induce and control moulting.

HUCKLEY, A.D. 1969. Ecology of terrestrial arthropods on the Tokelau atolls. Atoll Res. Bull., 124, 1–18.

This paper provides a distributional reference to the presence of *Birgus* in Tokelau.

HUME, A.O. 1874. The islands of the Bay of Bengal. Stray Feathers, 2, 91.

JOHNSON, D.S. 1965. Land crabs. J. Malaysian Branch R. Asiat. Soc., 38(2), 43–66.

This article reviews some of the literature on the food and feeding habits of *Birgus latro*, with particular reference to the crabs' reputed ability to cut down and de-husk coconuts. The main features of the reproductive cycle, moulting behaviour and early life-history are described, with appropriate references to the literature. The geographical distribution of *Birgus* is outlined briefly, and finally there is a short discussion of the relative importance of various known predators.

JUNGMICHEL. 1862. De St. Davids-of-Mapia eilanden, benoorden Nieuw-Guinea. Tijdschrift voor Indische Taal-Land-en Volkenkunde. (Batavia, The Hague), II. Ser. 4, 2, 155–156.

KEMM, V. 1982. More about the coconut crab. 'Naika', Journal of the Vanuatu Natural History Society, 5, 5–6.

A descriptive article based largely on Davis and Altevogt (1978) and a 1981 I.U.C.N. report which may have been the precursor to Wells et al. (1983). It summarises the main features of the coconut crab's morphology, size (including an unreferenced report of a crab weighing 15 kg!), climbing ability, early life history and burrowing behaviour. Reference is made to I.U.C.N.'s classification of coconut crabs as being vulnerable but not endangered. Predators and dietary items are listed, and the process of breaking open coconuts is described. The species is said to be cannibalistic. Brief mention is

made of the importance of *Birgus* in Vanuatu, and of the recently enacted minimum legal size of 140 mm (sic) thoracic length.

KNOTT, N.P. 1971. Meet *Birgus latro*: Mrs Coconut Crab. Land Res. Brch., Div. Lands & Surveys, Dept. Resources & Development (Saipan, T.T.P.I.) extension publication (mimeo.), 5 p.

This extension document promotes the concept of conservation of natural coconut crabs resources in the Saipan area. Specific conservation measures include i) only taking crabs with a carapace width of at least three inches, ii) not taking ovigerous females, iii) not setting wild fires (which kill many crabs), iv) not taking female crabs or males with CW<5.5" between June 15 and August 15 (the local breeding season), and v) reserving specified areas as permanently closed to the capture of crabs. A simple point-by-point summary of the animal's life history, diet, and moulting behaviour is provided. The author finally indicates that further information is required on the following points: i) catch statistics, ii) dates when females are ovigerous, iii) size at first maturity, and iv) whether shrews prey on small crabs.

KOPSTEIN, P.F. 1925 Bilder aus den Molukken: II. Der Kokosrauber (*Birgus latro*). Natuurk. Tijdschr. Ned. Indie. 85: 95–101.

——1929. Zoologische Tropenreise. Batavia, Leiden.

KORMANIK, G.A. and HARRIS, R.R. 1981. Salt and water balance and antennal gland function in three Pacific species of terrestrial crab (*Gecarcoidea lalandii*, *Cardisoma carnifex*, *Birgus latro*). 1. Urine production and salt exchanges in hydrated crabs. J. Exp. Zool., 218(1), 97–105.

Salt and water losses via urine were assessed in *Birgus latro*, *Gecarcoidea lalandii* and *Cardisoma carnifex*. The negative role of the antennal gland in sodium excretion was also studied.

LAWRENCE, J.M. 1970. Lipid content of the organs of the coconut crab *Birgus latro* (Decapoda: Paguridae). Crustaceana, 19(3), 264–266.

Previous work on lipids in cold-water crustaceans suggested that low environmental temperatures were associated with high fat levels. Lipids were extracted from the hepatopancreas, testis, intestine, gills, and muscle of two male *Birgus latro* collected from Eniwetok Atoll (Marshall Islands). The comparatively high lipid levels found in the coconut crabs failed to support the high fat, low temperature hypothesis.

LEVER, R.A. 1968. What sort of a thief is the robber crab? Pacific Island Monthly, August 1968.

LINSLEY, N.L. 1934. Curious things about Guam. The Guam Recorder, September 1934, 115–116.

One of a series of articles about curiosities in Guam which might escape the attention of the casual observer. The coconut crab's evolutionary affinity with the hermit crab, and its aquatic larval stage, are described. A brief discussion follows about the animals' ability to cut down coconuts for food; reports of this behaviour were apparently supported by local photographic evidence. Coconut crab numbers in Guam had already declined to the point where they were considered rather rare. Besides man, the author mentions monitor lizards as preying on the crabs, and describes mortality due to ants. In contrast to many other reports, the crabs on Guam appear to be active during the day rather than at night.

LIONNET, J.G. and PETTIT, G. 1922. Un crabe mangeur de noix de coc. Revue de bot. appl. et d'agric. Coloniale, 2, 518–519.

LISTER, J.J. 1888. On the Natural History of Christmas Island, in the Indian Ocean. Proc. Zool. Soc. Lond., 1888, 512–531.

A short article discussing geology, flora, and fauna of Christmas Island. *Birgus latro* is the only crustacean mentioned. It was the most conspicuous invertebrate on the island. A brief description of replenishing water supplies in branchial cavities is given.

LUCAS, H. 1883. Note sur le *Birgus latro*. Ann. Soc. Entom. de France, 6me serie, 3(2), Bull. de seances, Plates 39–40.

MACGINITIE, G.E. and MACGINITIE, N. 1949. Natural History of Marine Animals. McGraw-Hill Book Co., New York.

The biology of coconut crabs, including their feeding habits and the use of broken coconut shells as abdominal shelters, is described briefly (Page 301).

McMAHON, B.R. and BURGGREN, W.W. 1980. Regulation of acid–base status at different temperatures in bimodal and in terrestrial crustaceans. Am. Zool., 20, 802.

An abstract only in which it is suggested that pH is regulated in *B. latro* (highly terrestrial) by variation of CO_2 partial pressure as in air-breathing vertebrates. Land hermit crabs (*Coenobita brevimanus* and *Cardisoma carnifex*) probably switch between aquatic and terrestrial modes of acid-base regulation as environmental and physical conditions change.

——-1981. Acid–base balance following temperature acclimation in land crabs. J. Exp. Zool., 218(1), 45–52.

Acid–base responses to change in body temperature are described for three species of supra-littoral crustaceans—the land hermit crab *Coenobita brevimanus*, a brachyuran (*Cardisoma carnifex*) and the coconut crab *Birgus latro*. The latter, the most terrestrial of the three species apparently controls acid - base status in a manner similar to that of most terrestrial ectothermic vertebrates. The other two species, which have water available in their burrow or shell, also utilise mechanisms typical of aquatic ectotherms.

McNEILL, F. 1961. The robber crab—a crustacean mystery. Aust. Mus. Mag., 13, 283–286.

A brief discussion of the habits of *B. latro* stressing the controversial nature of available reports. The article concentrates on food and feeding behaviour.

MANGUM, C.P. 1977. The analysis of oxygen uptake and transport in different kinds of animals. J. Exp. Mar. Biol. Ecol., 27, 125–140.

B. latro is chosen as an example of a large terrestrial crustacean to compare indices of oxygen uptake and transport with 12 other invertebrate species from eight phyla.

MARSHALL, J.T. 1951. Vertebrate ecology of Arno Atoll, Marshall Islands. Atoll Res. Bull., 3.

MASSARO, E.J. and COHEN, E. 1978. An electrophoretic analysis of selected enzymes of the coconut crab, *Birgus latro*. Comp. Biochem. Physiol., 60B, 151-152.

Various enzymes from five specimens of *Birgus latro* collected from Henry Island, Eniwetok Atoll (Marshall Islands) were screened using starch-gel electrophoresis as the first step in a biochemical investigation of evolutionary relationships in the anomura. Isozymes of LDH, MDH, G6PDH, IDH, SDase, PGM, GK, CPK, AK, CA and esterases were analysed from gill, gonad, heart, hepatopancreas, intestine, lung, pericardial gland, skeletal muscle and sperm duct tissue. Esterases and superoxide dismutase were active in all tissues, but most of the enzymes showed remarkably little general

activity. It was noted that increased storage time degraded the enzyme activity. The authors concluded that either the enzymatic activities sought were naturally very weak, or that problems existed with the analytical process.

MATTHEWS, D.C. 1956. The probable method of fertilization in terrestrial hermit crabs based on a comparative study of spermatophores. Pac. Sci., 10, 303–309.

Macroscopic and microscopic structures of the spermatophores of truly aquatic (*Dardanus punctulatus*), 'transitional' terrestrial (*Coenobita rugosus*), and truly terrestrial (*Birgus latro*) species of hermit crabs are described and compared. Possible methods of fertilisation in terrestrial hermit crabs are discussed.

MIYAKE, S. 1965. The Crustacean Anomura of Sagami Bay. Biological Laboratory of the Imperial Household, Japan. 161 p.

Contains a taxonomic description of the family Coenobitidae, and presents a key to the Japanese genera of Coenobitidae including *Birgus*, which apparently does not occur in Sagami Bay itself.

MOTOH, H. 1980. Field guide for the edible crustaceans of the Philippines. SEAFDEC Aquaculture Dept. Publn (Iloilo, Philippines).

A two-paragraph description of the morphology, aspects of behaviour, and distribution of *B. latro*, opposite a photograph of a crab at the top of a coconut tree.

MOUL, E.T. 1957. Preliminary report on the flora of Onotoa Atoll, Gilbert Islands. Atoll Res. Bull., 57.

NAPOLI, F. 1904. Sopra alcuni caratteri e sulle abitudini del *Birgus latro*. Fabr. Boll. della Soc. zool. Italiana, 13, 193–197.

NIERING, W.A. 1956. Bioecology of Kapingamarangi Atoll, Caroline Islands: terrestrial aspects. Atoll Res. Bull., 49, 1–32.

Records (Page 18) coconut crabs as inhabiting either cavernous bedrock areas, puraka banks, or large hollow breadfruit trees. *Birgus latro* is the only one of a large number of land crustaceans eaten by the native people, and harvesting pressure keeps the numbers of crabs to a minimum.

——1963. Terrestrial ecology of Kapingamarangi Atoll, Caroline Islands. Ecol. Monogr., 33, 131–160.

A section on land crustacea within an extensive study of the atoll makes mention of *B. latro* as being a delicacy and is therefore scarce. The role that *B. latro* might play in controlling coconut dispersion is discussed.

ORLAMUNDER, J. 1942. Zur Entwicklung und Formbildung des *Birgus latro* L. mit Besonderei Berucksichtigung des X-Organs. Zeitschr. wiss. Zool., 155, 280–316.

PAGE, H.M. and WILLASON, S.W. 1982. Distribution patterns of terrestrial hermit crabs at Eniwetok Atoll, Marshall Islands. Pac. Sci., 36(1), 107–118.

Birgus latro receives only a very small mention in this study. Most observations were made on *Coenobita perlatus* and *C. rugosus*. *Coenobita brevimanus* and *Birgus latro* were both apparently uncommon on Eniwetok. Both species were found primarily in the interior of the island whereas the other two coenobitids were apparently more abundant on the beach and in the nearshore vegetation.

PRINCE, J.H. 1968. Animals in the night: Senses in action after dark. Angus & Robertson Ltd., Sydney. 111 p.

RABALAIS, N.N. and GORE, R.H. 1985. Abbreviated development in

decapods. pp 67–126 In: Wenner, A.M., ed., Crustacean Issues 2: Larval Growth. A.A. Balkema, Rotterdam and Boston. 236 p.

Birgus is listed (p. 109) among several terrestrial and semi-terrestrial decapods whose larvae show no evidence of significant developmental abbreviation. This is contrary to the theory that evolution towards a terrestrial lifestyle is accompanied by a reduction in the number and/or duration of the larval stages.

REESE, E.S. 1965a. The ecology of the coconut crab *Birgus latro* (L.). Bull. Ecol. Soc. Amer., 46(4), 191–192.

An abstract of a conference paper describing research on *B. latro* on Eniwetok Atoll, Marshall Islands. Population size, structure, and movement were studied using tag–recapture methods. The author reports that very small animals were difficult to find, and that females were ovigerous in early summer.

——1965b. The larval development of the coconut crab *Birgus latro* (L.) in the laboratory (motion picture). Am. Zool. 5, 638.

An abstract in which the times spent in each larval stage and distinguishing features of *B. latro* zoeae are outlined.

——1968. Shell use: an adaptation for emigration froM the sea by the coconut crab. Science, 161, 385–386.

B. latro glaucothoes enter empty gastropod shells as a necessary part of their successful emigration from a marine to a terrestrial habitat. This is an excellent example of retention of ancestral behaviour during development.

——1969. Behavioural adaptations of intertidal hermit crabs. Am. Zool., 9, 343–355.

A very brief mention of *B. latro* as hermit crabs which carry snail shells to protect their abdomens and prevent desiccation during the glaucothoe and early crab stages. Strongly developed nocturnal habits eliminate the need for such 'shell' protection as adults.

——1987. Terrestrial environment and ecology of Eniwetok Atoll. In: Devaney, D.M. et al., ed. The Natural History of Eniwetok Atoll, Vol. 1, 187–202.

REESE, E.S. and KINZIE, 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.

The four zoeae larvae and one glaucothoe of *Birgus latro* reared at the Hawaii Institute of Marine Biology from eggs hatched at a collecting site on Eniwetok Atoll are described and figured. *B. latro* zoea larvae and glaucothoe are compared with those described for the coenobitids *C. perlatus*, *C. rugosus*, and *C. brevimanus*, which may be collected at the same sites as *B. latro*.

REYNE, A. 1938. On the distribution of *Birgus latro* L. in the Dutch East Indies. Arch. Neerl. Zool., 3 (suppl.), 239-247.

——1939. On the food habits of the coconut crab (*Birgus latro* L), with notes on its distribution. Arch. Neerland. Zool., 3, 283-320.

A largely anecdotal paper concerned mainly with the question of whether *B. latro* feeds on coconuts. Reyne's conclusion is that *B. latro* is omnivorous. It subsists mostly on vegetable matter and it eats coconuts only fortuitously. A world distribution is defined for coconut crabs.

ROCK, J.F. 1916. Palmyra Island, with a description of its flora. Bull. College of Hawaii (Honolulu), 4, 1–53.

RUMPHIUS, G.E. 1705. D'Amboinsche Rariteitkamer. F. Halma, Amsterdam (Ch. 5). Pagination various; approx. 450 p.

SCHNEE, P. 1905. Die kokoskrabbe in der Freiheit und im Terrarium. Blatter fur Aquarien und Terrarienkunde, 16, 185–188 & 193–196.

SCHULTZ, L.P. 1948. The biology of Bikini Atoll with special reference to the fishes. Ann. Rept Board of Regents, Smithson. Inst., 1947.

SEMPER, C. 1878. Ueber die Lunge von *Birgus latro*. Zeitschr. f. wiss. Zoologie, 30, 282–287.

SEURAT, L.G. 1905. Sur le crabe des cocotiers, *Birgus latro* L. Bull. du Mus. nat. d'Hist. naturelle (Paris), 11, 146–147.

SHEPPARD, C.R.C. 1979. Status of three rare animals on Chagos. Environmental Conservation, 6(4), 310.

A very brief assessment of the status of *Birgus latro*, the green turtle and the hawksbill turtle on the islands and atolls of Chagos Archipelago during 1975 and 1978–79. There appeared to be a link between the length of time the islands had been uninhabited and the numbers and average size of crabs living there.

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(1), 75-82.

In *Birgus latro* hyperventilation following exercise causes respiratory alkalosis which helps restore acid–base balance after post-exercise acidosis. Use of a branchial lung is the dominant method of gas exchange.

STODDART, D.R., BENSON, C.W. and PEAKE, J.F. 1970. Ecological change and effects of phosphate mining on Assumption Island. Atoll Res. Bull., 136, 121–145; plts 18–35.

Birgus latro is noted as being among the terrestrial crustaceans of Assumption Island.

STORCH, V., CASES, E. and ROSITO, R. 1979. Recent findings on the coconut crab *Birgus latro* (L.). Philippine Scientist, 16, 57–67.

A brief and general resume of the morphology, life history and behaviour of *Birgus latro* (summarised from the literature) precedes an account of coconut crab burrows, diet, and methods of capture on the island of Olango (off Cebu, Philippines). Anecdotal reports indicate substantial declines in crab population density over the past two decades. Digging behaviour among the Olango crabs is described. Other behavioural features, as well as diet and distribution, are summarised from the literature. Finally, a significant account of the ultrastructure of certain tissues (including gills, lungs, blood, and hepatopancreas) is given. This work was done by transmission electron microscopy, and is accompanied by diagrams of gill, blood and lung ultra-structure, and electron micrographs of the mid-gut gland.

STORCH, V., JANSSEN, H.H. and CASES, E. 1982. The effects of starvation on the hepatopancreas of the coconut crab, *Birgus latro* (L.) (Crustacea, Decapoda). Zoologischer Anz, 208(3–4), 115–123. (in English)

STREETS, T. 1877. Some account of the natural history of the Fanning group of islands. Amer. Naturalist, 11.

SUDHAUS, W. 1974. Recapitulation in the etho-ecology of *Cinclus cinclus*. Beitr. Vogelkd, 20(6), 461–466.

SWINGLAND, I.R. and COE, M.J. 1979. The natural regulation of giant tortoise populations on Aldabra Atoll: recruitment. Phil. Trans. R. Soc. Lond. B, 286, 177–188.

On Malabar the major nest predator of tortoises is *B. latro*. Moreover the density of coconut crabs increases as the density of tortoise nests increases.

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This is not the case on Grand Terre, where the major nest predator is another land crab (*Cardisoma carnifex*). *B. latro* is also one of the main predators of tortoise hatchlings.

TAYLOR, J.D. 1968. Coral reef and associated invertebrate communities (mainly molluscan) around Mahe, Seychelles. Phil. Trans. R. Soc. Lond. B, 254, 129–206.

An occasional coconut crab was found in the supralittoral vegetation. *B. latro* numbers have been severely reduced by human predation.

TINKER, S.W. 1965. Pacific Crustacea. Charles E. Tuttle Co., Vermont and Tokyo.

A brief note on the natural history of *Birgus latro* printed opposite a black and white photograph of the crab as an aid to identification.

TOWLE, D.W. 1981. Transport-related ATPase as probes of tissue function in 3 terrestrial crabs of Palau. J. Exp. Zool., 218(1), 89-96.

Blood osmolality and chloride levels were measured in *Birgus latro*, *Gecarcoidea lalandii* and *Cardisoma carnifex* after exposure to seawater and fresh water. Sodium and potassium-dependent ATPase activity was measured in intestine and antennal gland tissue as well as three branchial cavity tissues—gill, lung and pericardial sac—to identify the major sites of ion transport. Gill and antennal gland exhibited the highest level of enzyme activity in the three terrestrial crab species. The pericardial sac and branchial chamber lining (lung) are not greatly involved in Na and water transport. The possible roles of the intestine and antennal gland in water uptake and retention are discussed.

VAN WELSEN, J.W.A. 1916. Herinneringen uit de Molukken: II. Klapperkreeft, ketam kanarie, *Birgus latro*. Tropische Natuur., 5, 14–16.

VERRILL, A.H. 1940. Wonder Creatures of the Sea. Appleton-Century, New York.

VOGEL, H.H. and KENT, J.R. 1970a. Life history, behaviour, and ecology of the Coconut Crab, *Birgus latro*. Amer. Zool., 10(3), 289–290.

An abstract in which the use of night vision equipment, luminescent paint, radioactive and radio tags to study *B. latro* is explained. Crabs were observed interacting with others of the same species, other crustaceans, and rats. *B. latro* is said to be able to open coconuts. The authors maintain that *Birgus* grows up to two or three feet (sic) across the shell.

VOGEL, H.H. and KENT, J.R. 1970b. Life history, behaviour and ecology of the Coconut Crab, *Birgus latro*. Bull. Ecol. Soc. Amer., 51, 40.

An abstract, evidently of a conference presentation. It is a verbatim duplication of the previous abstract (Vogel and Kent 1970a).

——1971a. A curious case: the coconut crab. Fauna (Rancho Mirage, Calif.), 2, 4–11.

——1971b. The behaviour, ecology, life-history and control of the coconut crab *Birgus latro*. Am. Zool., 11(4), 640.

An abstract, evidently of a conference presentation. It is a verbatim duplication of previous abstracts (Vogel and Kent 1970a and b).

WELLS, S.M., PYLE, R.M. and COLLINS, N.M., 1983. ed. Coconut or robber crab. I.U.C.N. Invertebrate Red Data Book, I.U.C.N.; Gland, Switzerland. 632 p.

This is perhaps the most comprehensive published survey of the literature on *Birgus latro* in recent times. It contains a general description of the species

(morphological characteristics, maximum size and weight), a detailed geographical distribution summary, and an account of its habitat and ecology (including feeding, and diurnal and reproductive behaviour patterns). A summary of the species' early life history follows, as well as brief synopses of scientific interest in and the potential value of the crab, and threats to its survival. Various instances are given of conservation measures already implemented or planned. The paper concludes with a comment about the potential for the commercial farming of coconut crabs. The authors indicate that further research on growth and mass larval culture are needed. Forty-six references are provided in the bibliography.

WIENS, H.J. 1956. The geography of Kapingamarangi Atoll in the Eastern Carolines. Atoll Res. Bull., 48, 1–86.

Briefly mentions (page 27) that coconut crabs are the only land crabs eaten and they grow to a large size. They are caught around the bases of breadfruit trees and they prowl through adjacent taro fields.

——1962. Atoll Environment and Ecology. Yale University Press, New Haven and London, 532 p.

Includes a short but comprehensive review of *B. latro* distribution and food habits.

WIERSMA, C.A.G. 1948. The innervation of the legs of the coconut crab, *Birgus latro* L. Physiologia comparata et oecologia, 1, 68–75.

The distribution of leg muscles and their innervation is described for *B. latro* and compared with that previously described for Palinura, Astacura, and Brachyura.

WILLEMOES-SUHM, R. von 1876. Von der Challenger-Expedition V. Zeitschr. wiss. Zool., 26, LIX–LXXV.

——1877. Von der Challenger-Expedition V. Zeitsch. wiss. Zool., 29, CIX–CXXXVI.

WILSON, C.B. 1913. Giant coconut crab of mid-Pacific Islands. Paradise of the Pacific, 26(11), 13–16.

This article was written in reply to correspondence which apparently questioned the veracity of a previous newspaper report on the coconut crabs of Palmyra Is. The author maintains that the sight of a coconut crab climbing a tree, nipping off a few coconuts, then sliding down again, while uncommon, ceases (after two or three sightings) to be a curiosity. He then describes how the crab de-husks the nut and cracks it open by pounding it with the 'striking claw', and claims that young green coconuts are eaten in their entirety (husk, meat and shell). The general morphology, size and colour of *Birgus* is described, and its diet is said to include bananas, plantains and pandanus fruit as well as coconuts. The author reports that two or three crabs typically inhabit a single den (a hole, cave or hollow in a tree-trunk); rarely is a lone crab found in a den. The use of a stick for extracting crabs from their dens is described.

WOOD, E.M., GEORGE, J.D., GEORGE, J. and WOOD, C.R. 1987. The coral reefs of the Bodgaya Islands (Sabah: Malaysia) and Pulau Sipadan. 6. Scientific conclusions, conservation issues and recommendations. Malay. Nat. J., 40 (3&4), 311–324.

Passing reference is made to the fact that *B. latro* lives and scavenges among the strand vegetation around Pulau Sipadan, an uninhabited, densely forested island regularly visited by fishermen collecting turtle eggs.

WOOD JONES, F. 1909. The fauna of the Cocos-Keeling Atoll, collected by F. Wood Jones. Proc. Zool. Soc. Lond. 1909, 132–160.

This article briefly discusses the probability of fallen coconuts being eaten by rats rather than by *B. latro* as is often supposed.

YALDWYN, J.C., and WODZICKI, K. 1979. Systematics and ecology of the land crabs (Decapoda: Coenobitidae, Grapsidae and Gecarcinidae) of the Tokelau Islands, central Pacific. Atoll Res. Bull., 235, 1–58.

A comprehensive discourse on the various roles played by land crabs (including *B. latro*) in the ecology of the Tokelaus. The systematics, distribution, vernacular names, population numbers and crab - rat relationships are all discussed.

Subject Classification

Locality record/taxonomic key
Bayne, Cogan et al. 1970a, b
Hinckley 1969
Holthuis 1953
Huckley 1969
Miyake 1965
Stoddart, Benson and Peake 1970

Distribution/abundance/dispersal
Alexander 1979
Altevogt and Davis 1975
Amesbury 1980
Andrews 1909
Anon. 1975
Bagnis 1970
Borradaile 1900a
Cameron 1981a
Cameron and Mecklenburg
  1973a, b
Carson and Wheeler 1973
Catala 1957
Chakravarti and Eisler 1961
Chapman 1948
Cheke and Lawley 1983
Daniel and Prem-Kumar 1967
Darwin 1845
Davis and Altevogt 1978
Fletcher et al. 1990a, b
Fusetani et al. 1980
Gardiner 1909
Gibson-Hill 1947, 1948
Gray 1981
Grubb 1970
Guppy 1882
Harries 1983
Helfman 1973
Henry and Cameron 1981
Herms 1926
Holthuis 1959, 1963
Johnson 1965
Linsley 1934
Lister 1888
Niering 1956, 1963
Page and Willason 1982
Reese 1965a
Reyne 1939
Sheppard 1979
Storch, Cases and Rosito 1979
Swingland and Coe 1979
Taylor 1968
Tinker 1965
Wells, Pyle and Collins 1983

Wiens 1956, 1962
Wood Jones 1909
Yaldwin and Wodzicki 1979

Habitat/ecology
Altevogt and Davis 1975
Andrews 1909
Fletcher et al. 1990a
Gillett 1974
Grubb 1970, 1971
Haig 1984
Holthuis 1959
Horstmann 1976, 1980
Niering 1956, 1963
Page and Willason 1982
Reese 1965a
Storch, Cases and Rosito 1979
Taylor 1968
Wells, Pyle and Collins 1983
Wiens 1956
Wilson 1913
Wood, George, George and Wood
  1987
Yaldwin and Wodzicki 1979

Morphology/anatomy
Altevogt and Davis 1975
Andrews 1909
Cameron 1981a
Gibson-Hill 1948
Hicks, Rumpff and Yorkston 1984
Johnson 1965
Kemm 1982
Matthews 1956
Motoh 1980
Reese 1965b
Storch, Cases and Rosito 1979
Tinker 1965
Vogel and Kent 1970a, b, 1971b
Wells, Pyle and Collins 1983
Wiens 1956
Wiersma 1948
Wilson 1913

Movement
Altevogt and Davis 1975
Amesbury 1980
Attenborough 1979
Borradaile 1898
Cropp 1982
Davis and Altevogt 1978
Fletcher et al. 1990a

Gibson-Hill 1948
Gillett 1974
Grubb 1971
Kemm 1982
Wilson 1913

Histology
Matthews 1956
Storch, Cases and Rosito 1979
Towle 1981
Wiersma 1948

Respiration/metabolism
Burggren and McMahon 1981
Cameron 1981b
Cameron and Mecklenburg
  1973a, b
Mangum 1977
McMahon and Burggren 1981
Smatresk and Cameron 1981
Towle 1981

Salt and water balance/pH/blood
Burggren and McMahon 1981
Greenaway et al. 1990
Gross 1955, 1964
Harris and Kormanik 1981
Henry and Cameron 1981
Kormanik and Harris 1981
Lister 1888
McMahon and Burggren 1980,
  1981
Reese 1969
Smatresk and Cameron 1981
Towle 1981

Diet
Alexander 1979
Anon. 1975
Bourn and Coe 1979
Chapman 1948
Coe and Swingland 1984
Davis and Altevogt 1978
Gardiner 1909
Gray 1981
Haig 1984
Hashimoto 1979
Helfman 1979
Herms 1926
Hicks, Rumpff and Yorkston 1984
Holthuis 1968
Horstmann 1976, 1980
Johnson 1965
Kemm 1982
Knott 1971

Linsley 1934
MacGinitie and MacGinitie 1949
McNeill 1961
Reyne 1939
Storch, Cases and Rosito 1979
Swingland and Coe 1979
Wells, Pyle and Collins 1983
Wiens 1962
Wilson 1913
Wood Jones 1909

Toxicity
Bagnis 1970
Borradaile 1898
Fusetani et al. 1980
Hashimoto 1979
Holthuis 1968
Storch, Cases and Rosito 1979

Behaviour (including feeding)
Altevogt and Davis 1975
Amesbury 1980
Attenborough 1979
Bourn and Coe 1979
Catala 1957
Coe and Swingland 1984
Cropp 1982
Davis and Altevogt 1978
Fletcher et al., 1990a
Fryer 1911
Gibson-Hill 1947, 1948
Gillett 1974
Grubb 1970
Guppy 1882
Helfman 1973
Hicks, Rumpff and Yorkston
  1984
Holthuis 1959
Johnson 1965
Kemm 1982
Linsley 1934
Lister 1888
MacGinitie and MacGinitie
  1949
McNeill 1961
Niering 1963
Reese 1965a, 1968, 1969
Reyne 1939
Storch, Cases and Rosito 1979
Tinker 1965
Vogel and Kent 1970a, b, 1971b
Wiens 1962
Wilson 1913
Wood Jones 1909
Yaldwin and Wodzicki 1979

Predators
  Horstmann 1976, 1980
  Johnson 1965
  Kemm 1982
  Linsley 1934

Tagging/marking
  Anon. 1975
  Fletcher et al. 1989, 1990a, b
  Helfman 1973
  Reese 1965a
  Vogel and Kent 1970a, b, 1971b

Moulting
  Amesbury 1980
  Anon. 1975
  Fletcher et al. 1990c
  Held 1963
  Horstmann 1976, 1980
  Johnson 1965
  Knott 1971
  Wiens 1962

Growth
  Alexander 1979
  Amesbury 1980
  Anon. 1975
  Fletcher et al. 1990c
  Gore 1985
  Gray 1981
  Held 1963
  Helfman 1979
  Horstmann 1976, 1980

Copulation
  Helfman 1973, 1977b
  Horstmann 1976, 1980
  Matthews 1956

Reproduction/spawning
  Amesbury 1980
  Attenborough 1979
  Borradaile 1900a
  Chapman 1948
  Daniel and Prem-Kumar 1967
  Gibson-Hill 1947
  Gray 1981
  Helfman 1973
  Hicks, Rumpff and Yorkston
    1984
  Horstmann 1976, 1980
  Johnson 1965
  Knott 1971
  Matthews 1956
  Reese and Kinzie 1968

Eggs/larvae/postlarvae/embryology
  Alexander 1979
  Amesbury 1980
  Borradaile 1900a
  Daniel and Prem-Kumar 1967
  Felder, Martin and Goy 1985
  Gibson-Hill 1948
  Gore 1985
  Horstmann 1976, 1980
  Johnson 1965
  Kemm 1982
  Matthews 1956
  Rabalais and Gore 1985
  Reese 1965b, 1968
  Reese and Kinzie 1968

Activity patterns
  Altevogt and Davis 1975
  Amesbury 1980
  Bourn and Coe 1979
  Chapman 1948
  Davis and Altevogt 1978
  Fletcher et al. 1990a
  Gray 1981
  Helfman 1973
  Hicks, Rumpff and Yorkston
    1984
  Holthuis 1963
  Kemm 1982
  Linsley 1934
  Storch, Cases and Rosito 1979
  Yaldwin and Wodzicki 1979

Territoriality
  Altevogt and Davis 1975
  Amesbury 1980
  Fletcher et al. 1990a
  Gibson-Hill 1947
  Guppy 1882
  Helfman 1973, 1977a

Parasites/diseases/commensals
  Amesbury 1980
  Carson and Wheeler 1973

Population structure
  Helfman 1973
  Reese 1965a

Capture methods
  Anon. 1975
  Davis and Altevogt 1978
  Fletcher et al. 1990c
  Helfman 1973
  Holthuis 1959

Storch, Cases and Rosito 1979
Wilson 1913

Culture potential
Amesbury 1980
Anon. 1973a, b, c, 1975
Horstmann 1976, 1980

**Conservation/management/
economics**
Amesbury 1980
Anon. 1973c
Horstmann 1976, 1980
Kemm 1982
Knott 1971
Wells, Pyle and Collins 1983
Radioactivity
Chakravarti and Eisler 1961
Wells, Pyle and Collins 1983

**Immunology/electrophoresis/
tissue chemistry**
Cohen 1968, 1970
Cohen, Rozenberg and Massaro
1974
Lawrence 1970
Massaro and Cohen 1978

Significant literature review
Davis and Altevogt 1978
Gordan 1956
Johnson 1965
Reyne 1939
Storch, Cases and Rosito 1979
Wells, Pyle and Collins 1983