The Coconut Crab

The Australian Centre for International Agricultural Research (ACIAR) was established in June 1982 by an Act of the Australian Parliament. Its mandate is to help identify agricultural problems in developing countries and to commission collaborative research between Australian and developing country researchers in fields where Australia has a special research competence.

ACIAR Monograph Series
This peer-reviewed series contains the results of original research supported by ACIAR, or material deemed relevant to ACIAR's research objectives. The series is distributed internationally, with an emphasis on developing countries.

Reprinted 1992

G.P.O. Box 1571, Canberra, ACT, Australia 2601

Brown, I.W. and Fielder, D.R. 1991. The Coconut Crab: aspects of the biology and ecology of *Birgus latro* in the Republic of Vanuatu. ACIAR Monograph No. 8, 136 p.

ISBN 1 86320 054 1

Technical editing: Apword Partners, Canberra
Production management: Peter Lynch
Design and production: BPD Graphic Associates, Canberra, ACT

Printed by: Goanna Print, Fyshwick

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

Editors

I.W. Brown and D.R. Fielder

Australian Centre for International Agricultural Research,
Canberra, Australia 1991

The Authors

I.W. Brown. Queensland Department of Primary Industries,
Southern Fisheries Centre, PO Box 76, Deception Bay,
Queensland, Australia

D.R. Fielder. Department of Zoology, University of Queensland,
St Lucia, Queensland, Australia

W.J. Fletcher. Western Australian Marine Research Laboratories,
PO Box 20, North Beach, Western Australia, Australia

S. Lavery. Department of Zoology, University of Queensland,
St Lucia, Queensland, Australia

A. Obed. Fisheries Department, Ministry of Agriculture,
Forests and Fisheries, PO Box 211, Port Vila, Republic of
Vanuatu

C. Schiller. Department of Zoology, University of Queensland,
St Lucia, Australia

Contents

Introduction vi

1. Project Overview and Literature Survey
I.W. Brown and D.R. Fielder 1

2. Reproduction, Early Life-History and Recruitment
C. Schiller, D.R. Fielder, I.W. Brown and A. Obed 13

3. Moulting and Growth Characteristics
W.J. Fletcher, I.W. Brown, D.R. Fielder and A. Obed 35

4. Structure and Dynamics of Populations
W.J. Fletcher, I.W. Brown, D.R. Fielder and A. Obed 61

5. Genetic Characteristics
S. Lavery and D.R. Fielder 87

6. Conclusions
I.W. Brown, D.R. Fielder and W.J. Fletcher 99

7. Annotated Bibliography
I.W. Brown and D.R. Fielder 103

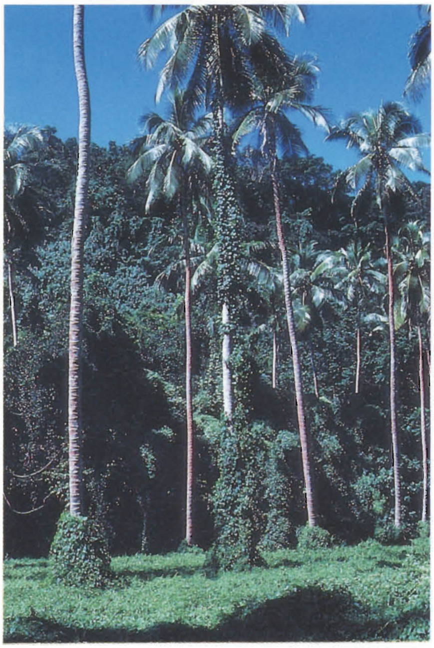
Introduction

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.

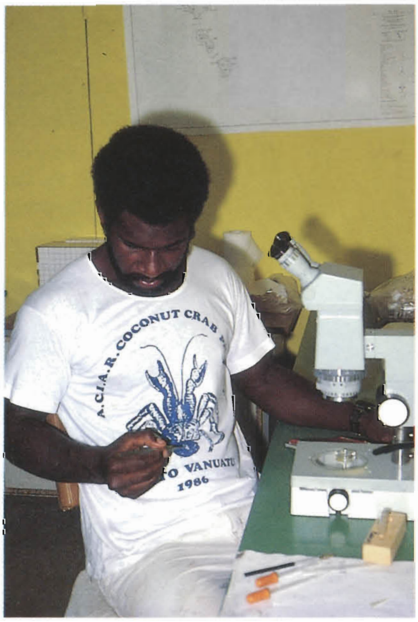
Collecting plankton samples.

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.

References

Abdulali, H. 1971. Narcondam Island and notes on some birds from the Andaman Islands. J. Bomb. Nat. Hist. Soc., 68, 385-411.

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

Altevogt, R. and Davis, T.A. 1975. *Birgus latro*, India's monstrous crab: a study and an appeal. Bulletin Department Marine Science, University, Cochin, 7, 11-24.

Amesbury, S.S. 1980. Biological studies on the coconut crab (*Birgus latro*) in the Mariana Islands. University of Guam Marine Laboratory Technical Report 66, 39 p.

Andrews, C.W. 1900. A Monograph of Christmas Island. London.

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

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

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

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

Borradaile, L.A. 1900. 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.

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.

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.

——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.

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.

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

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

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.

Davis, T.A. and R. Altevogt 1978. Is the coconut crab a pest of coconut? World Crops: July/August 1978, 157-162 and p. 172.

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.

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

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

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

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.

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.

Hashimoto, Y. 1979. Coconut crab poisoning. In: Marine Toxins and other Bioactive Marine Metabolites. Japan Scientific Societies Press. 68-69.

Held, E.E. 1963. Moulting behaviour of *Birgus latro*. Nature, London, 200, 799-800.

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.

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

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

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.

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

——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.

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

——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.

Johnson, D.S. 1965. Land crabs. J. Malaysian Branch, Royal Asiatic Society, 38(2), 43-66.

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.

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

Linsley, N.L. 1934. Curious things about Guam. The Guam Recorder, September 1934, 115-116.

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.

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.

McMahon, B.R. and Burggren, W.W. 1981. Acid base balance following temperature acclimation in land crabs. J. Exp. Zool., 218(1), 45-52.

Motoh, H. 1980. Field guide for the edible crustaceans of the Philippines. SEAFDEC Aquaculture Department Publication (Iloilo, Philippines).

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

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

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

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.

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

Schultz, L.P. 1948. The biology of Bikini Atoll with special reference to the fishes. Ann. Report, Board of Regents, Smithsonian Institute, 1947.

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.

Storch, V., Cases, E. and Rosito, R. 1979. Recent findings on the coconut crab *Birgus latro* (L.). Philippine Scientist, 16, 57-67.

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.

Wells, Susan M., Pyle, R.M. and Collins, N.M., 1983 (eds). Coconut or robber crab. I.U.C.N. Invertebrate Red Data Book, I.U.C.N.; Gland, Switzerland. 632 p.

Wiens, H.J. 1962. Atoll terrestrial fauna: terrestrial crabs. Atoll Environment and Ecology. Yale University Press, New Haven and London, 532 p.

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

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'.

---

[1]. Christmas Island research funded by Australian National Parks and Wildlife Service (1987–88) and McQuade Dredging Pty Ltd (1988–89 and 1989–1990). Niue research funded by FAO-United Nations–South Pacific Agriculture Department Project.

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) microlecithal (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 $c=b$.

		Morphometrics			Osmolality	
Egg Stage	No.	Dimensions (mm)	Surface Area (mm^2)	Volume (mm^3)	No	Osmolality (mOsm kg/H_2O)
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

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.

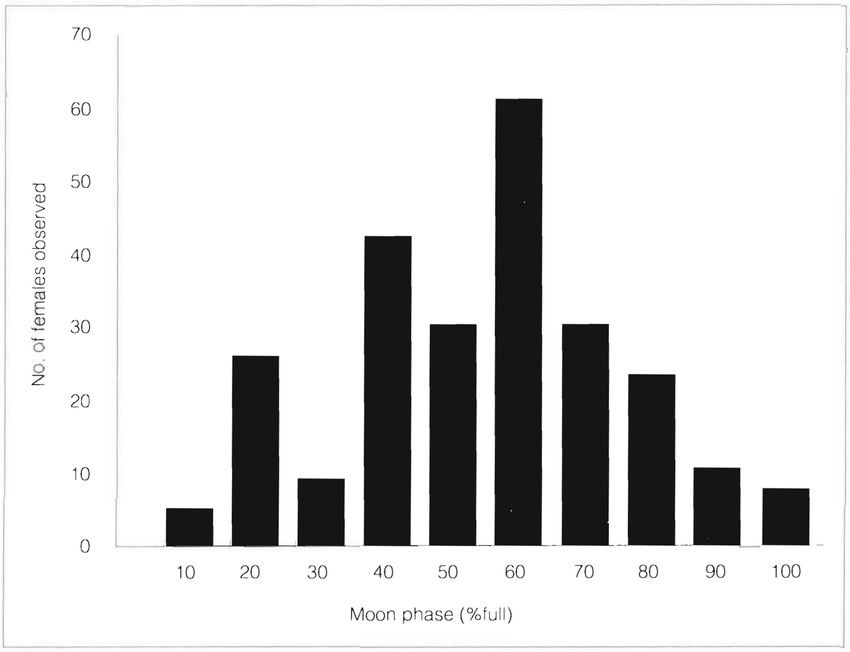


Figure 1. Number of female *Birgus latro* bearing mature eggs observed at different phases of the moon at the Espiritu Santo study area in Vanuatu (November 1985 to April 1987).

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

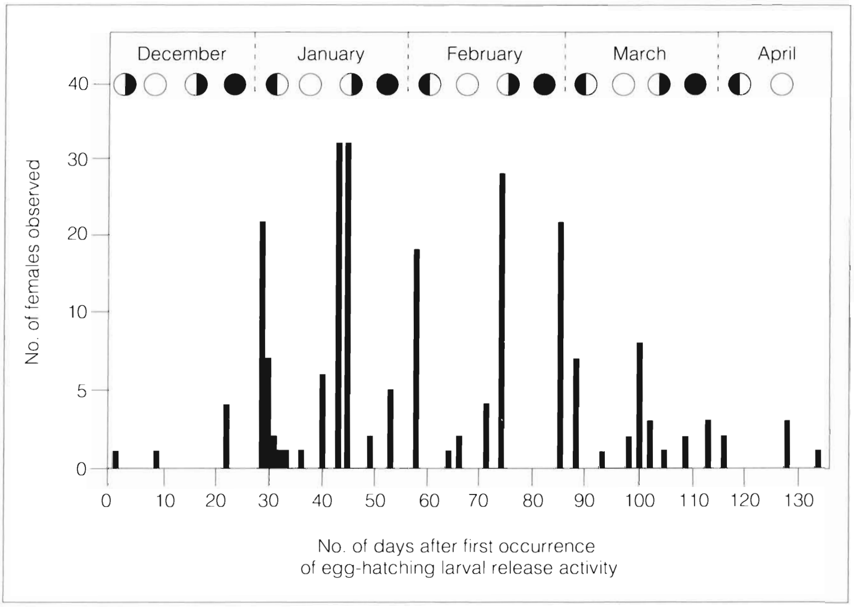


Figure 2. Number of female *Birgus latro* observed releasing larvae during the 1986-87 reproductive period at the Espiritu Santo Study area in Vanuatu. The X-axis indicates the number of days since the first recorded release of larvae on 17/12/86. Lunar phases are indicated with the solid circle representing new moon.

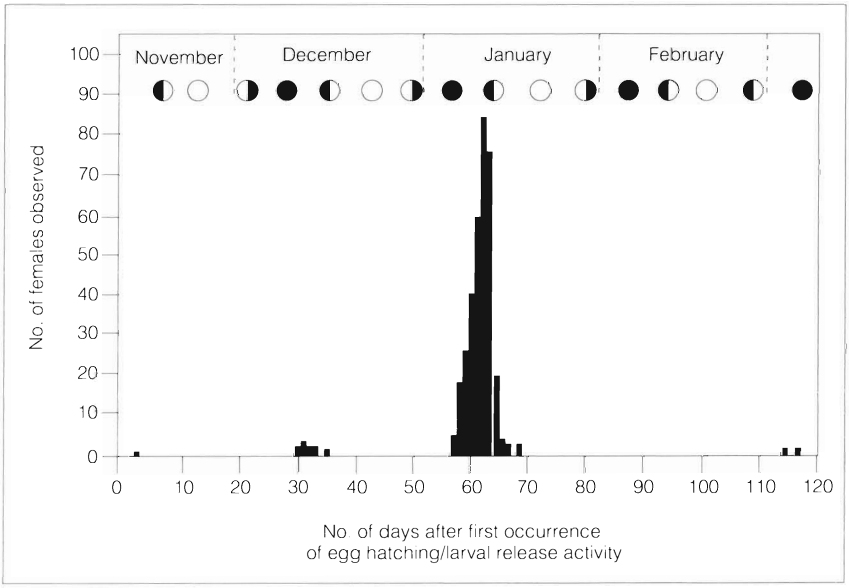


Figure 3. Number of female *Birgus latro* observed releasing larvae during the 1988-89 reproductive period on Christmas Island. The X-axis indicates the number of days since the first recorded release of larvae on 12/11/88. Lunar phases are indicated with the solid circle representing new moon.

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).

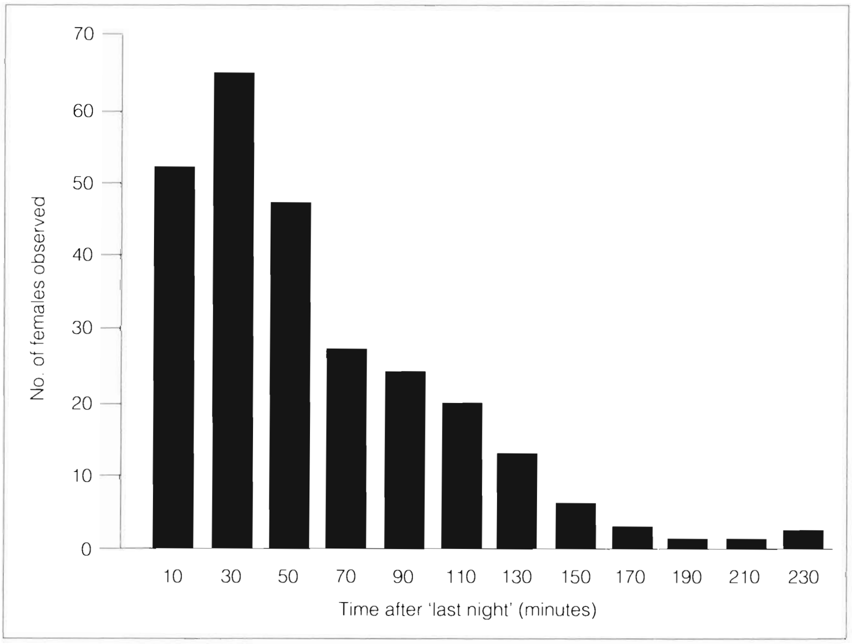


Figure 4. Number of female *Birgus latro* observed releasing larvae during the evening as a function of time (minutes) after last light.

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.

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.

References

Amesbury, S.S. 1980. Biological studies on the coconut crab (*Birgus latro*) in the Mariana Islands. University of Guam Marine Laboratory Technical Report 66, 39 p.

Barnes, R. 1980. Invertebrate Zoology. Saunders College, Holt, Rinehart and Winston, Philadelphia. 1089 p.

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

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

Chapman, W.M. 1948. Coconut-eaters. Pacific Discovery 1. 3-6.

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.

Davis, C.C. 1964. A study of the hatching process in aquatic invertebrates. 8. Events of eclosion in the American lobster *Homarus americanus* Milne-Edwards (Astacura, Homaridae). Am. Midl. Nat. 72, 203-210.

Fletcher, W.J. Growth and recruitment of the coconut crab *Birgus latro* (L.) in Vanuatu. A report. Australian Centre for International Agricultural Research. Canberra, Australia. Unpublished.

Gibson-Hill, C.A. 1949. The robber crab. Zoo. Life 4. 58-60.

Gifford, C.A. 1962. Some observations on the general biology of the land crab *Cardisoma guanhumi* (Latreille) in south Florida. Biol. Bull. Mar. Biol. Lab., Woods Hole 123. 207-223.

Gray, H.S. 1981. Christmas Island—Naturally. Howard Gray Publ. Geraldton, W.A. 133 p.

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.

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.

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

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

Henning, H.G. 1975. Aggressive, reproductive and moulting behaviour, growth and maturation of *Cardisoma guanhumi* Latreille (Crustacea,Brachyura). Forma. Functio., 8, 563-610.

Henry, R.P. and Cameron, J.N. 1981. A survey of blood and tissue compounds in terrestrial decapods of Palau. J. Exp. Zool. 218(1), 83-88.

Hicks, J., Rumpff, H. and Yorkston, H. 1984. Christmas Crabs. Christmas Island Natural History Association, Christmas Island, Indian Ocean.

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

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

Orlamunder, J. 1942. Zur Entwicklung und formbildung des *Birgus latro* L. mit Besonderei Berucksichtigung des X-organs. Zeitschr. wiss. Zool., 155, 280-316.

Panadian, T.J. 1970. Yolk utilisation and hatching time in the Canadian lobster *Homarus americanus*. Mar. Biol., 7, 249-254.

Paula, J. 1989. Rhythms of larval release of decapod crustaceans in the Mira Estuary, Portugal. Mar. Biol., 199, 309-312.

Reese, E.S. 1965. The ecology of the coconut crab *Birgus latro* (L.). Abstract in Bull. Ecol. Soc. Amer., 46(4), 191-192.

——1987. Terrestrial environments and ecology of Enewetak Atoll. *In:* The Natural History of Enewetak Atoll Volume 1 The Ecosystem: Environments, Biotas and Processes. Devaney, D.M., E.S. Reese, B.L. Burch and P. Helfrich (ed.) Office of Scientific and Technical Information, U.S. Department of Energy. 228p.

Reese, E.S. and Kinzie 111, R.A. (1968) The larval development of the coconut or robber crab *Birgus latro* (L.) in the laboratory (Anomura, Paguridea). Crustaceana Suppl. 2. 117-144.

Saigusa, M. and Hidaka, T. 1978. Semilunar rhythm in the zoea release activity of the land crabs *Sesarma*. Oecologia 37, 163-176.

Sandifer, P.A. 1975. The role of pelagic larvae in recruitment to populations of adult Decapod crustaceans in the York River estuary and adjacent lower Chesapeake Bay, Virginia. Est. Coast. Mar. Science. 3. 269-279.

Schiller, C.B. 1988. Pilot stock survey of the coconut crab (Birgus latro) on Niue Island, Pacific Ocean. Consultancy report. Food and Agriculture Organisation of the United Nations. Rome, Italy. 42p.

3

Moulting and Growth Characteristics

W.J. Fletcher, I.W. Brown, D.R. Fielder
and A. Obed

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).