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

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

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

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

Very few small crabs were found in this study, and these included only two individuals smaller than 10 mm TL. This is not uncommon, as most major field studies have also reported an extreme paucity of juveniles (Held 1963; Amesbury 1980; Reese 1987). Reese (1987) believes that small juveniles are in fact present, but that they are very secretive and difficult to find. This does not, however, explain the fact that some of the larger size groups (e.g. 15-30 mm TL) were scarce at some sites but abundant at others. Such situations may be caused by intraspecific interactions: the larger size-classes were often most abundant in areas where small crabs were sparse, but this was not universally true. Helfman (1973) found a much younger population on his Ngerkersiul study site (where many crabs were smaller than 25 mm TL) than at Igurin, and only on one island (Cocos) in Guam was Amesbury (1980) able to find small crabs.

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

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5 GENETIC CHARACTERISTICS

S. Lavery and D.R. Fielder

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

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

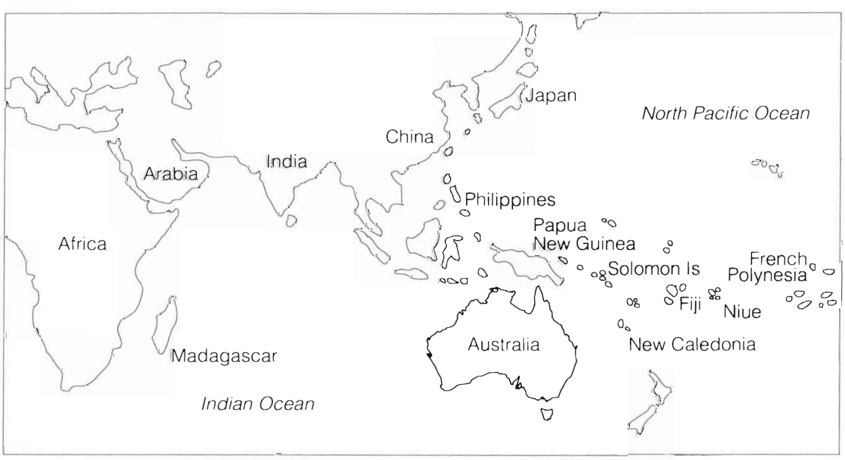

Figure. 1. Indo-Pacific distribution of the coconut crab.

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

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

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

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

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

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

Methods

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

Considerable effort was involved in organising the collection of samples from as wide a range of locations as possible. The primary sampling locations were in Vanuatu, the base for the ACIAR coconut crab project. In other parts of the Pacific, the results of a mail survey throughout the Indo-Pacific were used initially as a basis for likely sources of specimens. Countries targeted for approach were those which appeared to have a readily-available supply of coconut crabs, which had indicated they may be interested in coconut crab research, and which lay in a strategic position. For Indian Ocean samples, a variety of contacts was used, including personnel in the CSIRO Division of Fisheries Research, ACIAR, the University of Queensland and the University of New South Wales. In addition, other relevant contacts in Indian Ocean countries were canvassed. Personal contact was also made with biologists from six locations (Seychelles, Maldives, Christmas Island, Papua New Guinea, Solomon Islands and Kiribati). Initial letters were sent to 15 locations requesting assistance, with further communication taking place with the five locations shown in Figure 2 giving a positive response (Vanuatu, Solomon Islands, Christmas Island, Cook Islands and Niue).

Figure 2. Indo-Pacific collection sites.

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

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

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

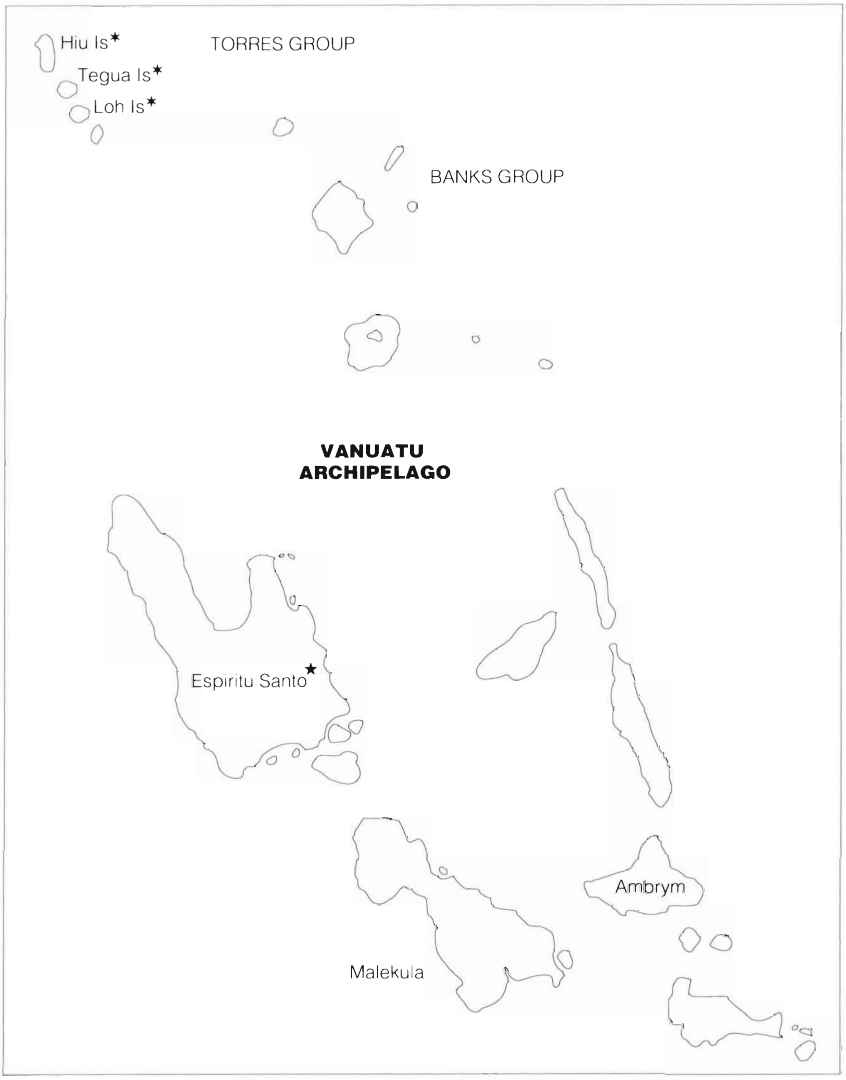

Figure 3. Vanuatu collection sites (*).

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

Table 1. Coconut crab collection details

Location		Sample size
Christmas Island		82
Solomon Islands		44
Vanuatu (total)		169
Santo	82	
Tegua	41	
Hiu	21	
Loh		25
Niue		18
Cook Islands		11

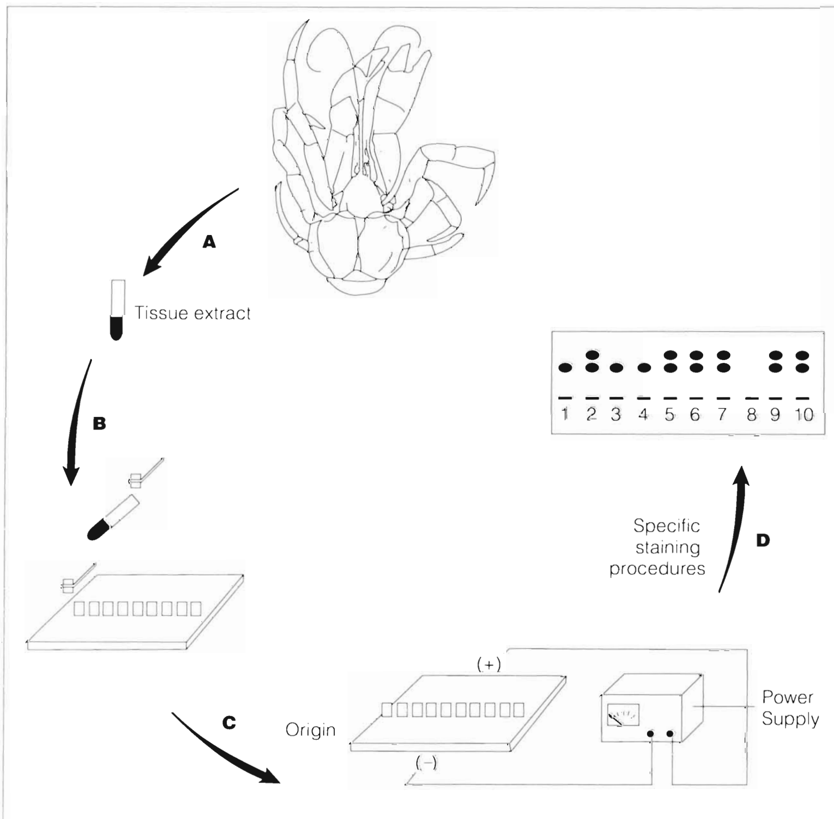

Figure. 4. Electrophoretic procedure. (Adapted from Utter et al. 1987. Used with permission.)

Results

Of the 76 enzyme systems initially screened, 83 different enzyme loci were detected in the range of tissues employed. Of these, 22 loci proved to be uninterpretable and 54 loci were monomorphic, while only seven loci were polymorphic.

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

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

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

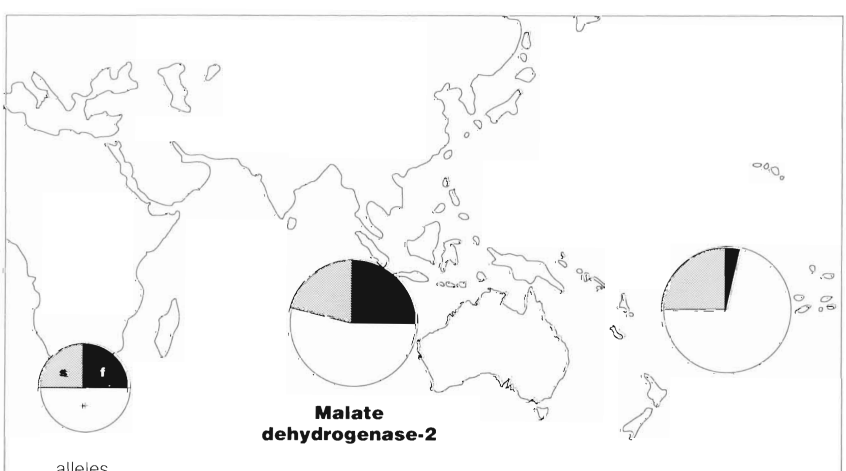

Figure 5. Mdh-2 allele frequency differences between Indian and Pacific Oceans.

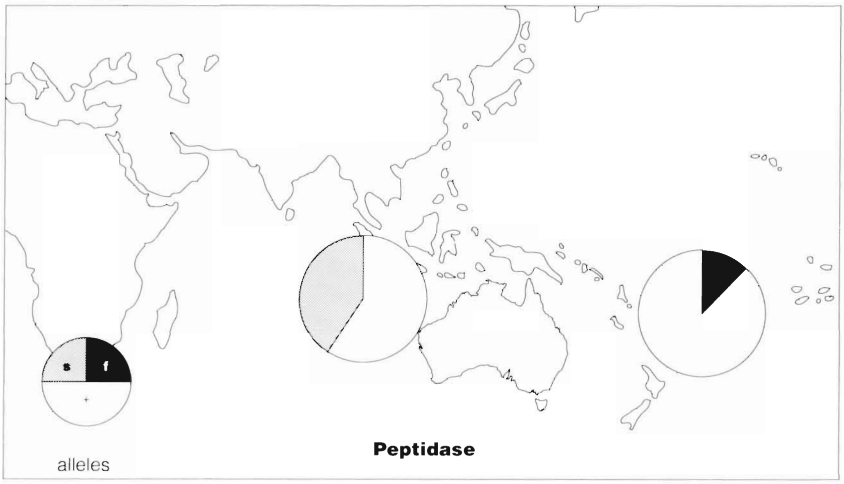

Figure 6. Pep allele frequency differences between Indian and Pacific Oceans.

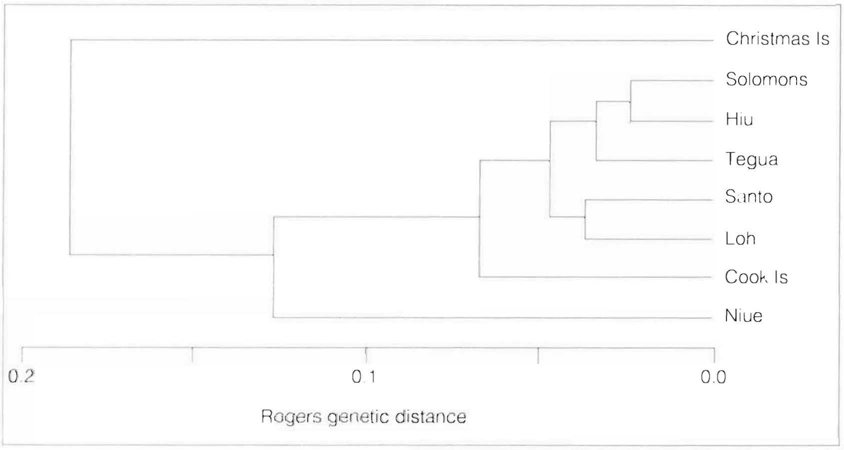

Figure 7. Dendrogram of genetic distances between sites.

Discussion

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

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

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

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

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

Conclusions

Population structure

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

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

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

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

Genetic implications for artificial culture

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

Although the latter goal may be worthwhile in itself, there are many possible risks involved in translocating individuals throughout the range (Utter et al. 1989). The process of artificial rearing, almost unavoidably, will result in a loss of genetic diversity, and perhaps survival traits, in the reared population compared to the source population (Sbordoni et al. 1986; Quattro and Vrijenhoek 1989). Also, the movement of reared animals from one population to another may swamp the existing gene pool with introduced alleles, resulting in an overall loss of genetic variation. Each population may be adapted to its own environmental conditions, and therefore the introduction of many individuals from another region may lower the overall fitness of the population. The consequences of this may be that we become tied to continual artificial stocking of an area to ensure continued survival, or even that large amounts of money are spent producing animals that will not survive in different conditions from their parent region. A further problem is that if genetic variation is lost through artificial rearing and stocking, then this means a loss of the raw genetic material which could be used for future genetic improvement of stocks through breeding (e.g. faster growth rates).

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

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

Acknowledgments

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6 Conclusions

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

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

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

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

Because of the slow growth rates and probable low rates of natural mortality it would take monitoring of 10–20 years at the one location to reconcile these two hypotheses conclusively. In order to test the hypothesis that recruitment is dependent on environmental factors which determine pelagic larval dispersion patterns, a long term program would be required to monitor oceanic current speeds and directions in the vicinity of the islands. Obviously this would have to be carried out in conjunction with a program to monitor the abundance of postlarval and juvenile crabs in a variety of terrestrial habitats.

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

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

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

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

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

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

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

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

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

This arrangement essentially involved a quota system, with collectors taking a maximum of 600 kg of crabs per month from each of the islands Tegua and Hiu. Sales were permitted only to the government fish market, which would pay a standard price of 500 vatu per kg. Once the monthly quota had been reached, the airline would be instructed not to transport any more crabs. In any case the airline was requested not to carry crabs that were consigned anywhere but to the Fish Market. The village chiefs on each of the two islands would decide how the quota was to be divided up between collectors.

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

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

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

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

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

7 Annotated Bibliography

I.W Brown and D.R. Fielder

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

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

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

ALCOCK, A. 1902. A naturalist in Indian seas. London.

——1905. Catalogue of the Indian decapod crustacea in the collection of the Indian Museum. Part 2: Anomura, Fasc. I. Pagurides. Calcutta.

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

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

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

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

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

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

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

A comprehensive account of studies carried out on coconut crabs primarily on the island of Guam during 1973 and 1974. Field surveys were also undertaken on other islands in the Northern Marianas (Pagan, Asuncion, and Guguan), and Palau (Ngariungs Is., Kayangel Atoll). Features of the species' reproductive behaviour and development are reviewed, including the relationship between larval release and moon phase (and tide). Early life history is summarised (primarily from Reese and Kinzie 1968); amongst the numerous small shell-bearing coenobitids examined at Guam none was referable to *Birgus*. The pooled length-weight relationship is given, there being no significant difference in regression parameters between the sexes. Some captive crabs in small enclosures moulted, but no size-increase resulted. Crabs in a large enclosure failed to moult at all. Burrowing and moulting behaviour is discussed, together with an apparent relationship between abdominal swelling and the onset of ecdysis. Feeding habits, diel activity patterns, and inter- and intra-specific interactions are outlined, with reference to the literature. A life history model for *Birgus* is developed, primarily with reference to probable sources of natural mortality at various points in the species' life cycle. The status of coconut crab stocks in the Marianas is reviewed, and possible management strategies presented. Various pieces of existing legislation are documented, and finally there is a discussion of the general feasibility of rearing *Birgus latro* on a large scale.

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

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

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

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

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

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

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

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

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

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

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

The conference recommended priorities for the establishment of mariculture programs in the Pacific islands. *Birgus latro* was one of a number of invertebrate species considered (p. 10). Top priority species included Malaysian prawn, brine shrimp, marine shrimp and oysters. *Birgus* ranked with the second priority species, which also included northern lobster, mangrove crab, pearl oyster and tridacnid clams. The probability of expanding markets for coconut crabs, their ability to be shipped alive, and the possible need for culture as a long-term conservation measure were mentioned.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Defines breeding seasons as May (Philippines), January – February (Loyalty Islands), and the beginning of the year (Christmas Island). The first zoea larva is described from those hatched by ripe females on Christmas Island. Behaviour of egg-carrying females and hatching are briefly described.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

DANIEL, A. and PREM-KUMAR, V.K. 1967. The coconut crab *Birgus latro* (L.) (Crustacea: Paguridae) in the Great Nicobar Island. J. Bombay Nat. Hist. Soc., 64(3), 574–580.

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

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

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

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

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

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

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

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

A very detailed and comprehensive review of the literature on the utilisation of coconuts by coconut crabs. References to the crabs' ability to climb trees and pick coconuts, strip off the husks and break open the kernels, are provided. Contradictory views, mostly resulting from observations on captive crabs, are also discussed. Additional observations were made by the authors during visits to South Sentinel Island (Indian Ocean) in 1973 and 1974 (see also Altevogt and Davis 1975). Circumstantial evidence of the animals' capacity to de-husk and break open coconuts was obtained, but no crabs were actually observed in the act. Some discussion follows on a theory relating the possible origin and dispersal of the coconut palm with the distribution of *Birgus*. However the theory is discredited as there is ample evidence that *Birgus* is not dependent upon coconuts. Many diverse dietary items are listed. Interestingly, there is neither any firm evidence, discussion, nor conclusion presented as to whether *Birgus* is or is not a pest of the coconut.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

GREENAWAY, P., TAYLOR, H.H. and MORRIS, S. 1990. Adaptations to a terrestrial existence by the robber crab *Birgus latro*. VI. The role of the excretory system in fluid balance. J. Exp. Biol., 152, 505-519.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

——1937. Lebensablauf und Stammesgeschicte des *Birgus latro* L. von der Weinachts-insel. Zeitschr. fur Naturwissen (Jena), 71, 1–34.

HARRIES, H.C. 1983. The coconut palm, the robber crab and Charles Darwin: April Fool or a curious case of instinct? Principes, 27(3), 131–137.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

——1929. Zoologische Tropenreise. Batavia, Leiden.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Various enzymes from five specimens of *Birgus latro* collected from Henry Island, Eniwetok Atoll (Marshall Islands) were screened using starch-gel electrophoresis as the first step in a biochemical investigation of evolutionary relationships in the anomura. Isozymes of LDH, MDH, G6PDH, IDH, SDase, PGM, GK, CPK, AK, CA and esterases were analysed from gill, gonad, heart, hepatopancreas, intestine, lung, pericardial gland, skeletal muscle and sperm duct tissue. Esterases and superoxide dismutase were active in all tissues, but most of the enzymes showed remarkably little general activity. It was noted that increased storage time degraded the enzyme activity. The authors concluded that either the enzymatic activities sought were naturally very weak, or that problems existed with the analytical process.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

RABALAIS, N.N. and GORE, R.H. 1985. Abbreviated development in decapods. pp 67–126 In: Wenner, A.M., ed., Crustacean Issues 2: Larval Growth. A.A. Balkema, Rotterdam and Boston. 236 p.

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

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

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

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

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

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

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

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

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

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

REESE, E.S. and KINZIE, R.A., 1968. The larval development of the coconut or robber crab *Birgus latro* (L.) in the laboratory (Anomura, Paguridae). Crustaceana, Suppl. 2, 117–144.

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

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

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

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

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

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

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

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

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

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

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

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

SMATRESK, N.J. and CAMERON, J.N. 1981. Post-exercise acid–base balance and ventilatory control in *Birgus latro* the coconut crab. J. Exp. Zool., 218(1), 75-82.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Subject Classification

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

Distribution/abundance/dispersal
Alexander 1979
Altevogt and Davis 1975
Amesbury 1980
Andrews 1909
Anon. 1975
Bagnis 1970
Borradaile 1900a
Cameron 1981a
Cameron and Mecklenburg 1973a, b
Carson and Wheeler 1973
Catala 1957
Chakravarti and Eisler 1961
Chapman 1948
Cheke and Lawley 1983
Daniel and Prem-Kumar 1967
Darwin 1845
Davis and Altevogt 1978
Fletcher et al. 1990a, b
Fusetani et al. 1980
Gardiner 1909
Gibson-Hill 1947, 1948
Gray 1981
Grubb 1970
Guppy 1882
Harries 1983
Helfman 1973
Henry and Cameron 1981
Herms 1926
Holthuis 1959, 1963
Johnson 1965
Linsley 1934
Lister 1888
Niering 1956, 1963
Page and Willason 1982
Reese 1965a
Reyne 1939
Sheppard 1979
Storch, Cases and Rosito 1979
Swingland and Coe 1979
Taylor 1968
Tinker 1965
Wells, Pyle and Collins 1983
Wiens 1956, 1962
Wood Jones 1909
Yaldwin and Wodzicki 1979

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

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

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

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

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

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

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

Diet
Alexander 1979
Anon. 1975
Bourn and Coe 1979
Chapman 1948
Coe and Swingland 1984
Davis and Altevogt 1978
Gardiner 1909
Gray 1981
Haig 1984
Hashimoto 1979
Helfman 1979
Herms 1926
Hicks, Rumpff and Yorkston 1984
Holthuis 1968
Horstmann 1976, 1980
Johnson 1965
Kemm 1982
Knott 1971
Linsley 1934
MacGinitie and MacGinitie 1949
McNeill 1961
Reyne 1939
Storch, Cases and Rosito 1979
Swingland and Coe 1979
Wells, Pyle and Collins 1983
Wiens 1962
Wilson 1913
Wood Jones 1909

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

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

Storch, Cases and Rosito 1979
Wilson 1913

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

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

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

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