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

Methods

Enclosures

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

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

Freeze-branding

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

Heat-branding

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

Introduction of crabs to Bier Island

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

Purchases of crabs

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

Abdomen expansion

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

Shell condition

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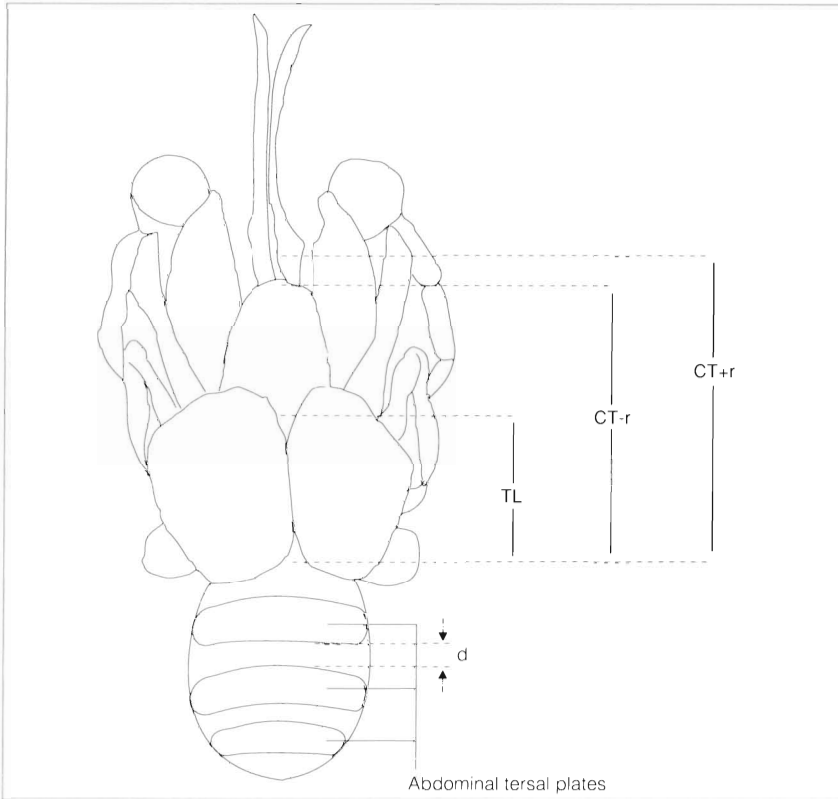
Figure 1. Dorsal (top) view of a coconut crab showing the standard size measurements taken. TL = thoracic length, used in the calculation of abdominal expansion index. CT refers to cephalothoracic length, including (+r) or excluding (-r) the rostrum. d is the distance (mm) between the first and second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

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

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

Market surveys

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

Buried crab searches

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

Results

Moulting behaviour

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

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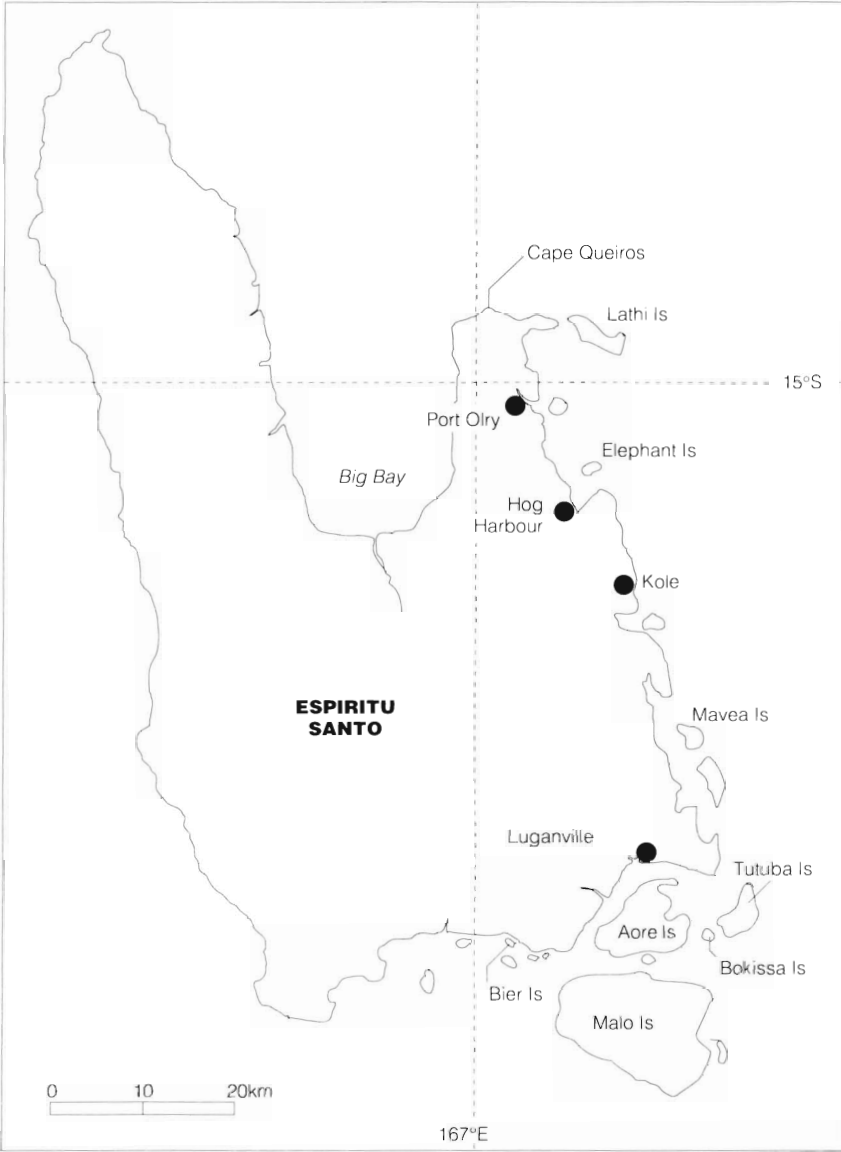
Figure 2. Espiritu Santo (Vanuatu) showing the sampling sites at Hog Harbour and Elephant Island.

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

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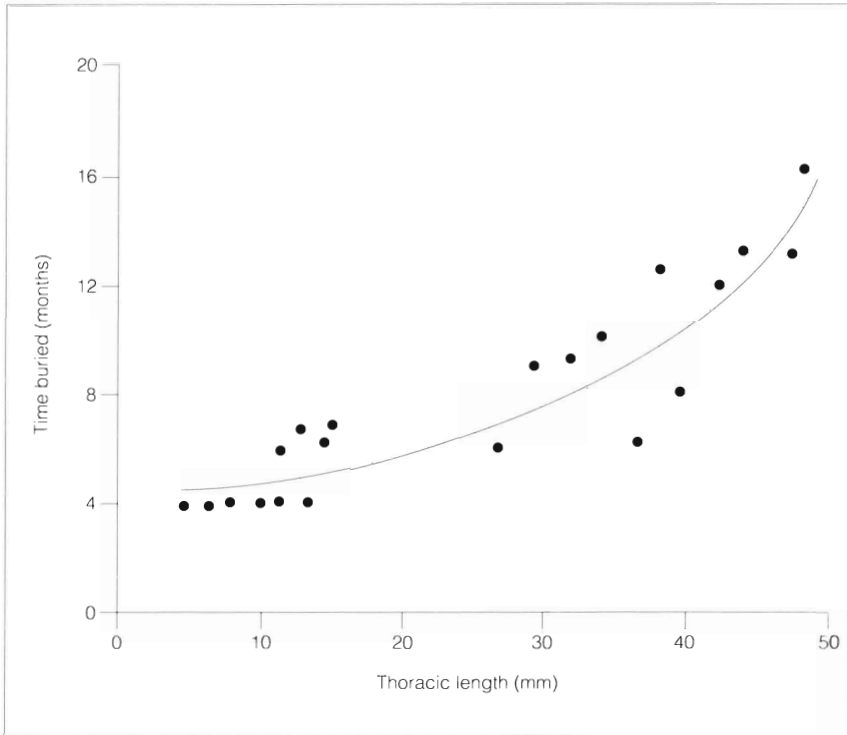
Figure 3. Relationship between the size of the crab and the length of time it remains underground to moult.

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

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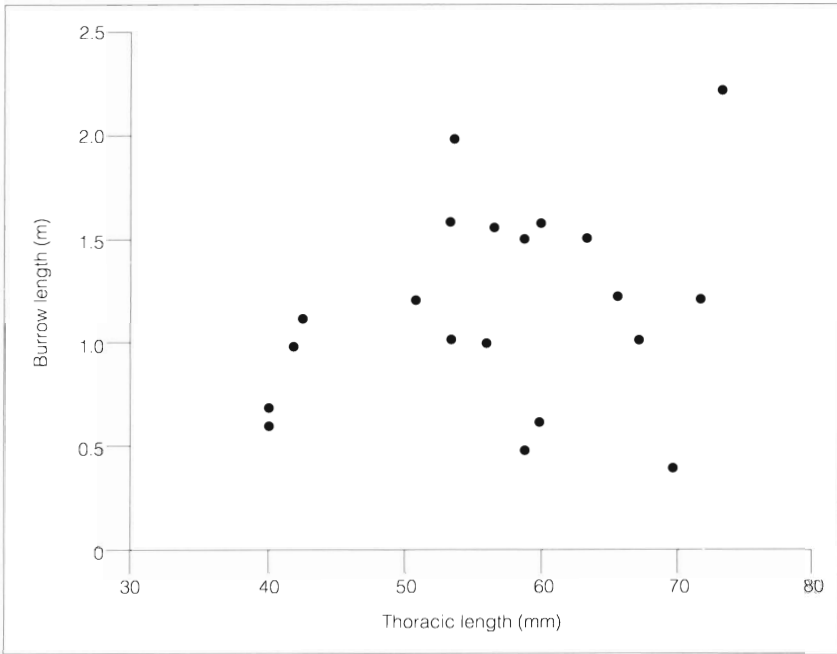
Figure 4. Relationship between crab size and the length of the moulting burrow.
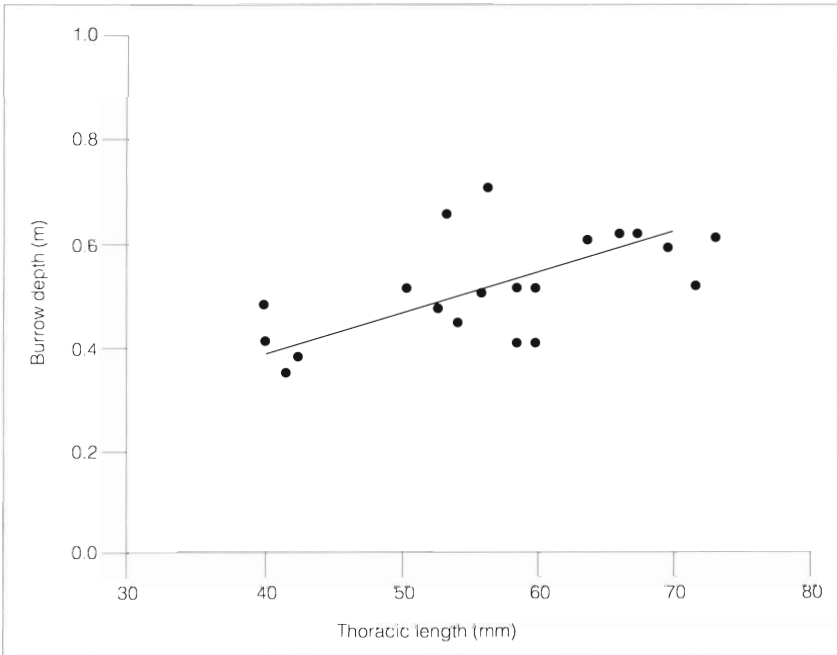

Figure 5. Relationship between crab size and the depth of the moulting burrow.
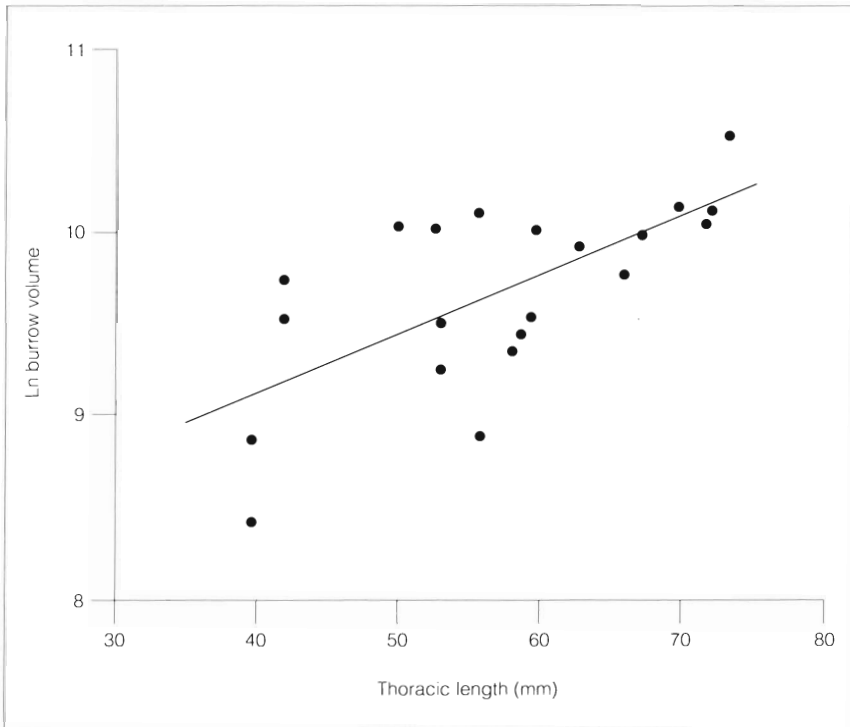
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Figure 6. Relationship between crab size and the natural logarithm of the moulting burrow volume.

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

Growth increment estimation

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

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

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

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

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

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

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

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

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

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

$Y = 13.44 - 0.176 \times X$

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

increase in length at each moult would be expected to conform to a quadratic function, with small increments at small body sizes, large increments at intermediate sizes and small increments again at large sizes. This appeared to be the case, as is shown by the dome-shaped curve in Fig. 8a.
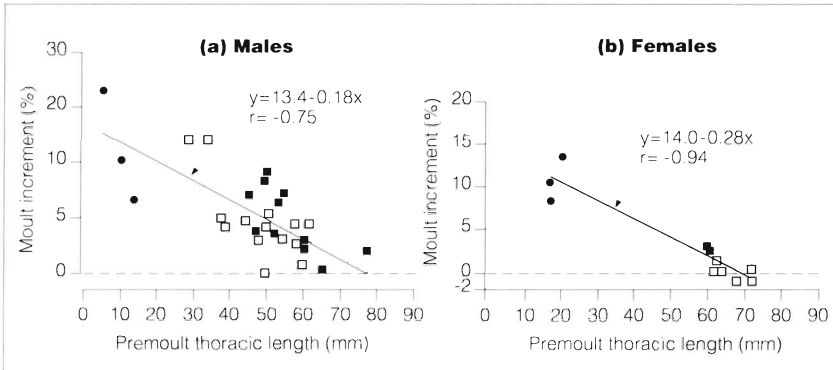

Figure 7. Changes in the magnitude of the moult increment (as a proportion of pre-moult body size) and increasing thoracic length in male and female coconut crabs. Data from enclosure experiments are represented by solid circles, from measurements on excavated crabs by solid squares, and from mark – recapture experiments by open squares.
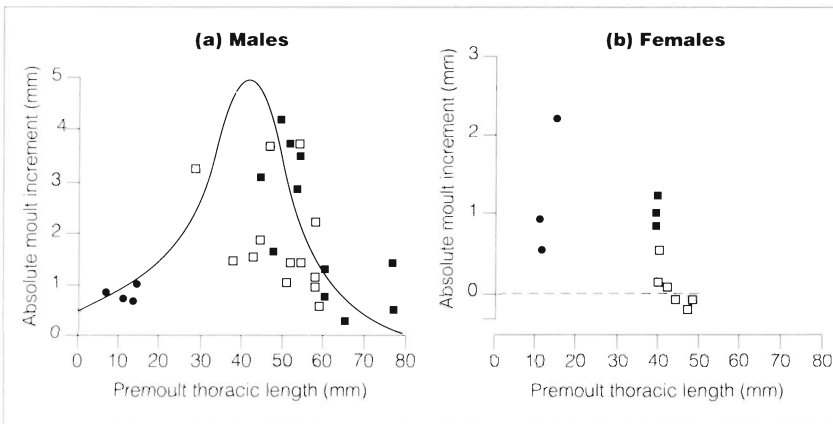

Figure 8. Changes in absolute moult increment with increasing body size in male and female coconut crabs. The curve in (a) was fitted by eye. See Fig. 7 for explanation of symbols.

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

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

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

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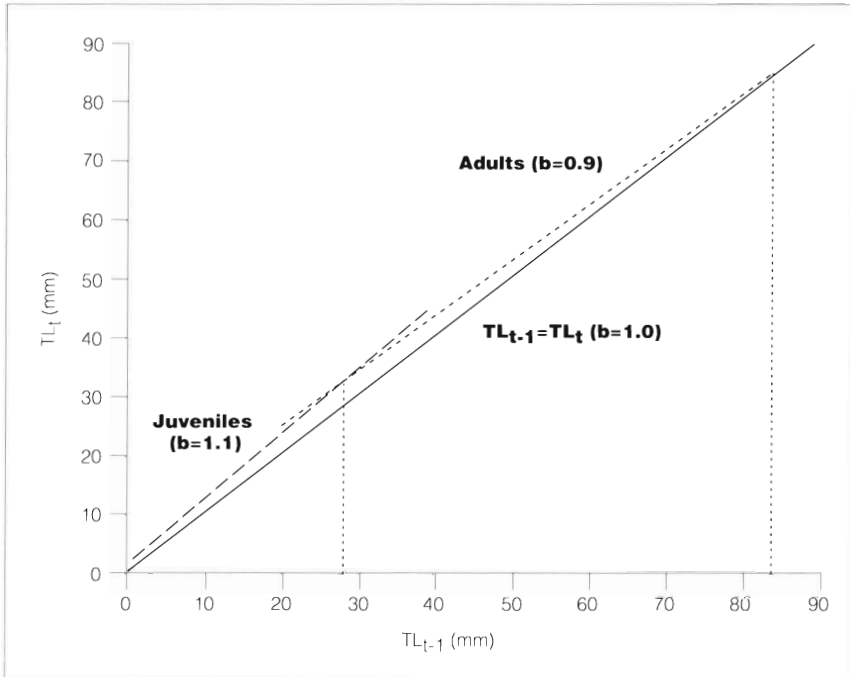

Figure 9. Walford plot of size at time t against size at time t-1. Note differences in slope between juvenile and adult stages, and that the regression lines intersect at approximately 28 mm TL.

Abdomen Expansion

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

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

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

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

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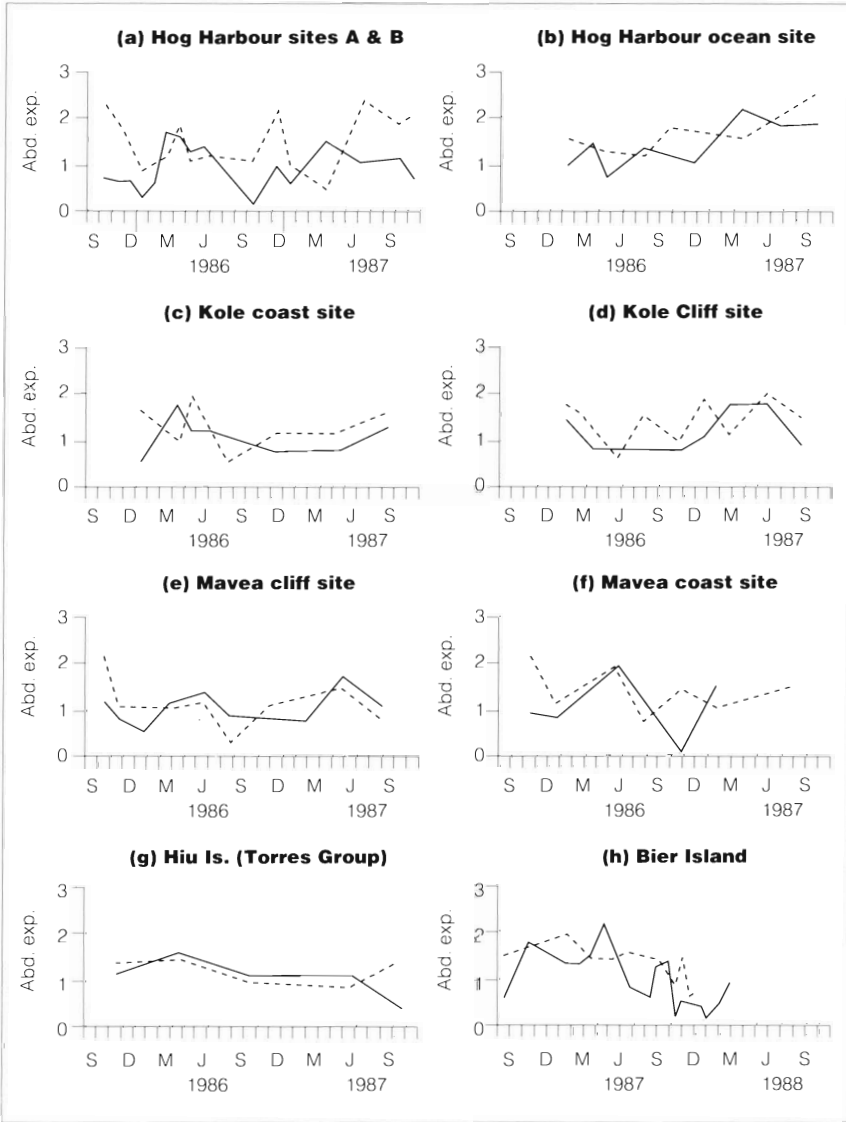
Figure 10. Seasonal changes in abdominal expansion index of male and female coconut crabs (males: solid line; females: dotted line) at the major sampling sites in northern Vauatu.

Shell condition

Another assessment of seasonality in the moulting activity of coconut crab populations was based on visual analysis of plots of the proportion of crabs which had recently moulted (as estimated from the shell index) against time. Shell indices of 1.5 or less were considered to be indicative of recent moulting.
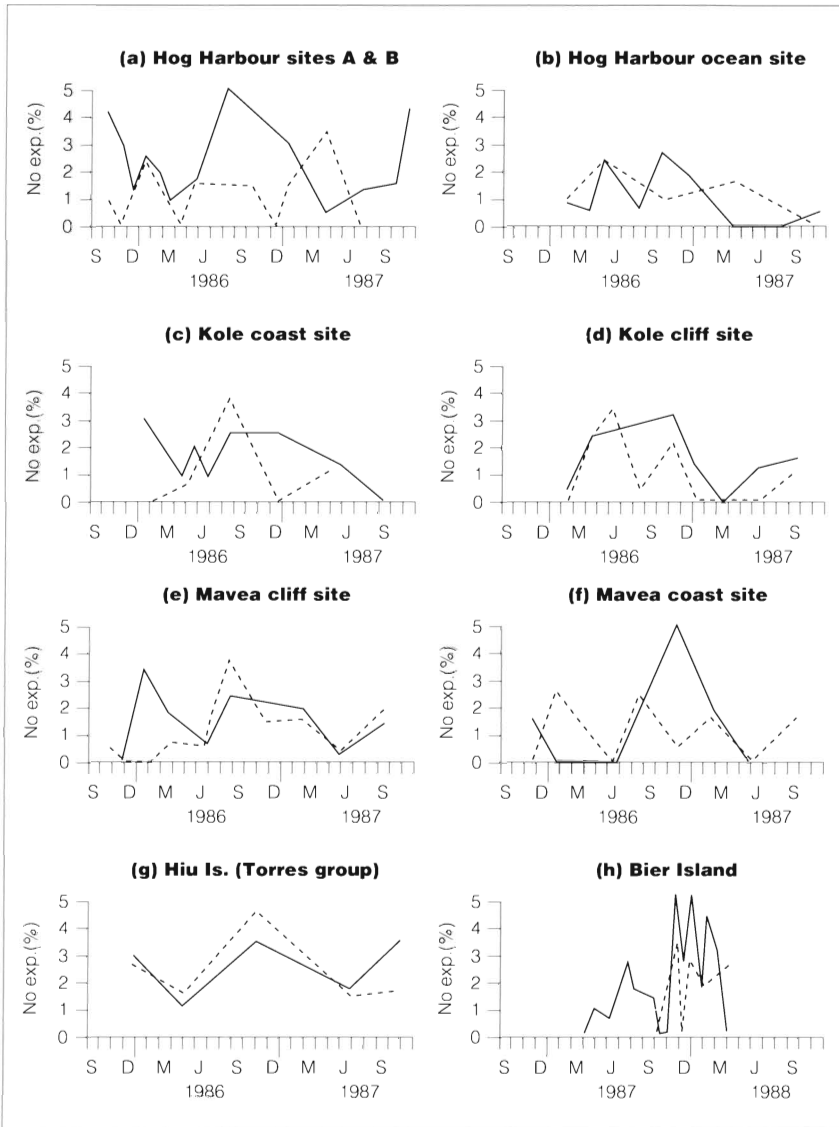
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Figure 11. Seasonal changes in the proportion of sampled coconut crabs at the major sampling sites showing no abdominal expansion (males: solid line; females: dotted line).

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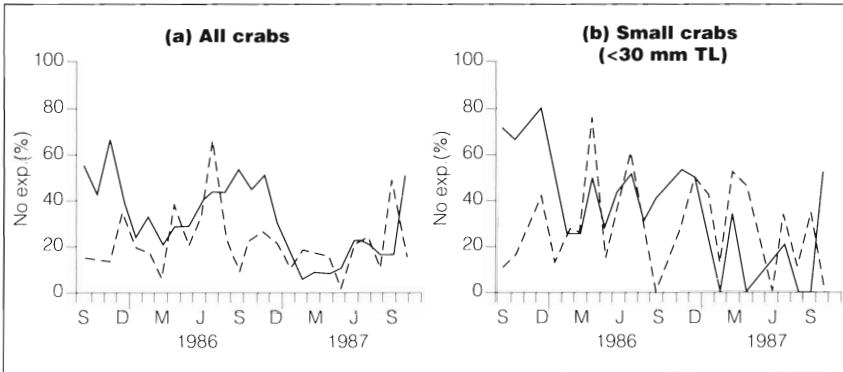
Figure 12. Seasonal changes in the proportion of crabs (at all sites pooled) showing no abdominal expansion (males: solid line; females: dotted line).

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

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

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

The seasonal pattern in the frequency of moulting crabs found on the Elephant Island transects were at variance, however, with the hypothesis of one moult during the winter (Fig. 15). This figure shows the number of burrow sites which were searched and in which a moulting crab was located and the number of sites at which the crabs could not be located. During 1986 large numbers of burrowed moulting crabs were found in
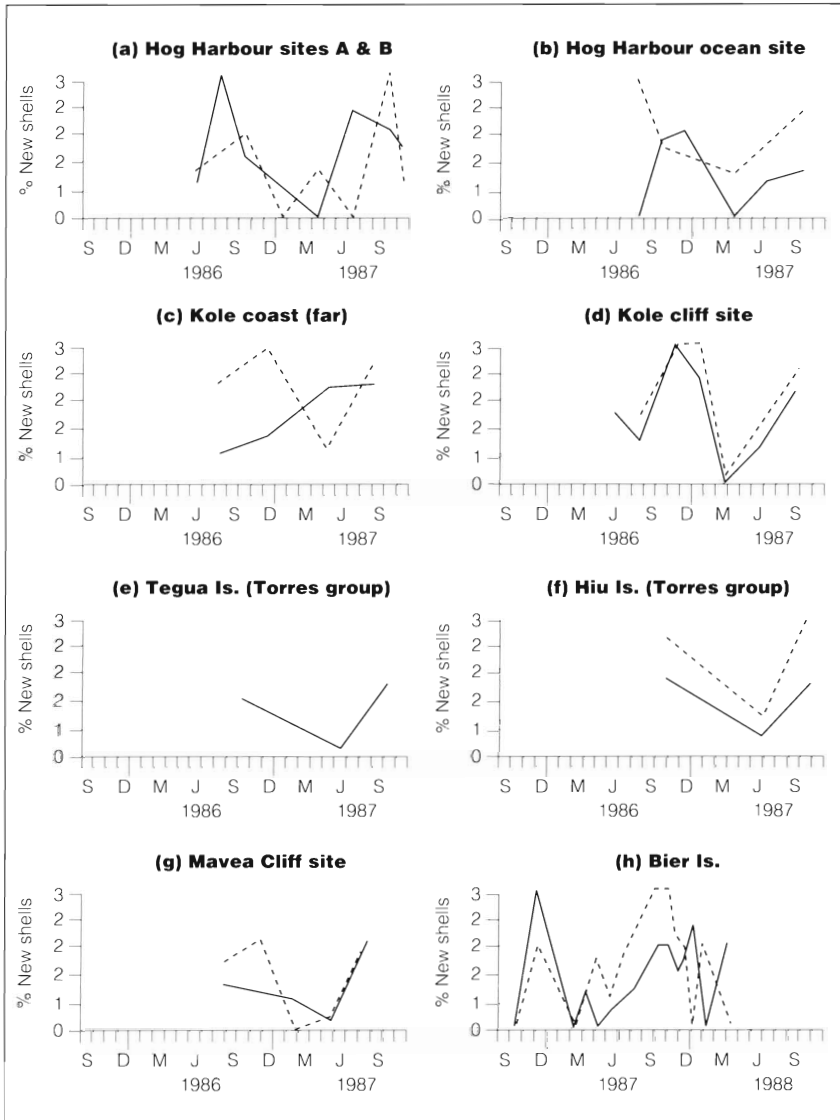
Figure 13. Seasonal changes in the proportion of coconut crabs with 'new' shells (i.e. with a shell index of 1.5 or less) at the major sampling sites (males: solid line; females: dotted line).

June and July but few in November, but in 1987 the pattern was less easy to interpret, as only one moulting crab was located in June. In the second year of sampling the largest numbers of moulting crabs were found in March-April, and there was a second subsidiary peak in early September. The fact that on many occasions (despite evidence of fresh burrow workings) no crab could be found indicates that the probing

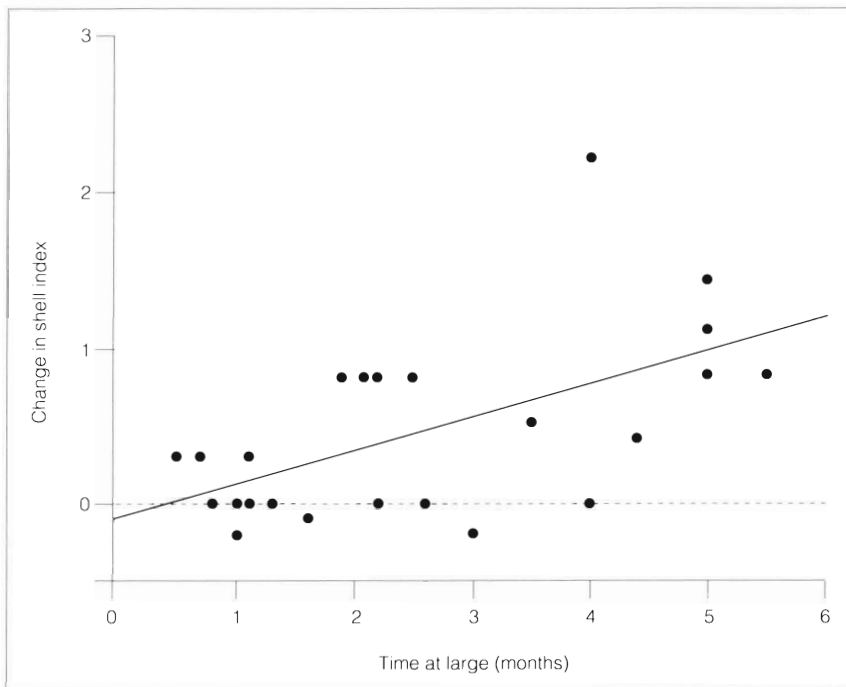**Figure 14.** Relationship between change in shell index and the time at large (i.e. interval between time of release and time at recapture).
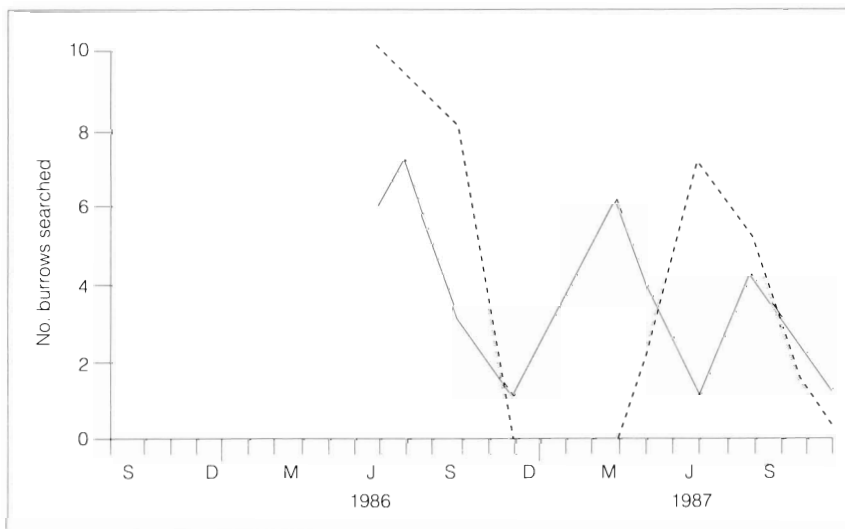

Figure 15. Seasonal changes in the number of searched moulting burrows in which crabs were found (solid line) and in which no crabs were located (dotted line).

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

Growth rates

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

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

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

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

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

Discussion

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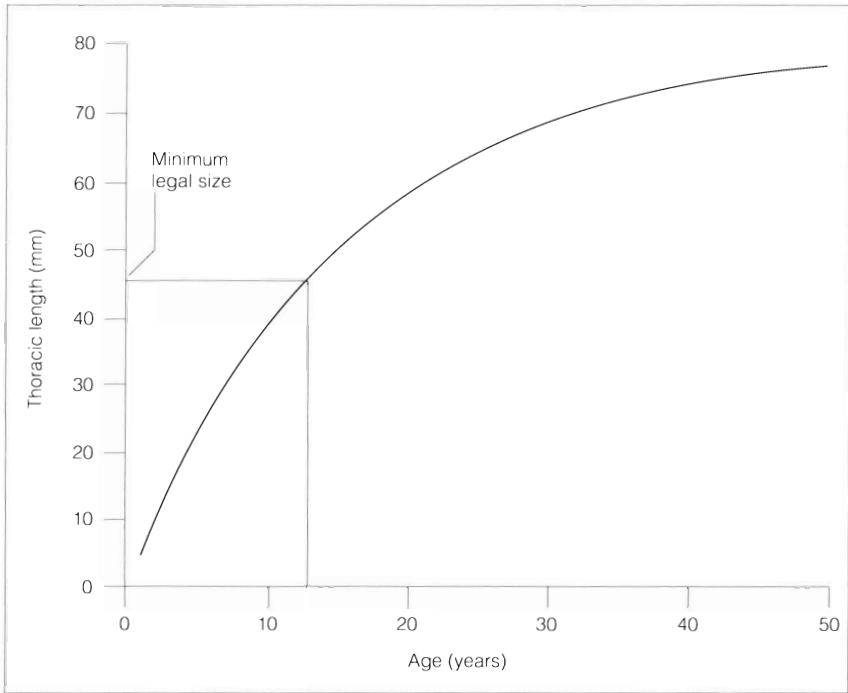
Figure 16. Von Bertalanffy growth curve for the coconut crab *Birgus latro* showing approximate age at the current minimum legal size in Vanuatu.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

References

Aiken, D.A. 1980. Moulting and growth. In: Cobb, J.S. and Phillips, B.F., ed., The Biology and Management of Lobsters. Vol. 1, Physiology and behaviour. Academic Press, New York.

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

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

Breitler, W.C.M.K. 1970. Laboratory experiments on the influence of environmental factors on the frequency of moulting and the increase in size at moulting of juvenile shore crabs *Carcinus maenas*. Neth. J. Mar. Res., 9, 100-120.

Brown, C.G. and Bennett, D. 1978. Population and catch structure of the edible crab *Cancer pagurus* in the English Channel. J. Cons. Int. Explor. Mer., 39, 88-100.

Campbell, A. 1983. Growth of tagged American lobsters (*Homarus americanus*) in the Bay of Fundy. Can. J. Fish. Aquat. Sci., 40, 1667-1675.

Chapman, C.J., and Rice, A.L. 1971. Some direct observations on the ecology of the Norway lobster *Nephrops norvegicus*. Mar. Biol., 51, 157-165.

Cleaver, F.C. 1949. Preliminary results of the coastal crab (*Cancer magister*) investigation. Wash. State Dep. Fish. Biol. Rep. 49, 49-82.

Farmer, A.S. 1973. Age and growth in *Nephrops norvegicus* (Decapoda: Nephropidae).Mar. Biol., 23, 315-325.

Fielder, D.R. 1964. The spiny lobster, *Jasus lalandei* (Milne-Edwards) in South Australia. Aust. J. Mar. Freshwater. Res., 15, 77-92.

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.

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(4), 407-416.

Fletcher, W.J., Brown, I.W. and Fielder, D.R. 1990b. Growth of the coconut crab *Birgus latro* in Vanuatu. J. Exp. Mar. Biol. Ecol., 141, 63-78.

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

Gross, W.J., 1955. Aspects of osmotic regulation in crabs showing the terrestrial habit. Am. Nat., 89, 205-222.

Haefner, P.A., and van Engel, W.A. 1975. Aspects of moulting, growth and survival of male rock crabs, *Cancer irroratus*, in Chesapeake Bay. Chesapeake Sci., 16, 253-265.

Hartnoll, R.G. 1982. Growth. In: Abele, L.G., ed., The biology of Crustacea, Vol. 2. Academic Press, New York. 111-197.

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

Helfman, G.S. 1973. Ecology and behaviour of the coconut crab, *Birgus latro* (L.). M.Sc. thesis, University of Hawaii (Zoology);

University Microfilms M-5452, 158 p.

Hiatt, R.W. 1948. The biology of the lined shore crab, *Pachygrapsus crassipes* Randall. Pac. Sci., 2, 135-213.

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

Keating, A.S. 1835. Account of the Cocos-Keeling Islands. In: A Voyage around the World, 4, 374-388.

Kurata, H. 1962. Studies on the age and growth of crustacea. Bull. Hokkaido Reg. Fish. Res. Lab., 22, 1-48.

Mauchline, J. 1977. Growth in shrimps, crabs and lobsters — an assessment. J. Cons. Int. Explor. Mer., 37, 162-169.

Newman, G.G. and Pollock, D.E. 1974. Growth of the rock lobster *Jasus lalandei* and its relationship to benthos. Mar. Biol., 24, 339-346.

Pauly, D. 1980. On the interrelationship between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer., 39, 175-192.

Pollock, D.E., and Roscoe, M.J. 1977. The growth at moulting of crayfish *Jasus tristani* at Tristan da Cunha, South Atlantic. J. Cons. Int. Explor. Mer, 37, 144-146.

Reese, E.S. 1968. Shell use: an adaptation for emigration from the sea in the coconut crab. Science, 161, 385-386.

Reese, E.S. 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.

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

Rice, A.L. 1968. Growth 'rules' and the larvae of decapod crustaceans. J. Nat. Hist.,2, 525-530.

Seurat, L.G. 1905. Sur le crabe des cocotiers, *Birgus latro* L. Bull. Mus. nat. Hist. naturelle (Paris), 11, 146-147.

Smith, E. 1980. Growth. In: Proceedings of the Canada-U.S. workshop on the status of assessment science for N.W. Atlantic lobster (*Homarus americanus*) stocks, St Andrews, NB. Can. Tech. Rep. 932.

4 Structure and Dynamics of Populations

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and A. Obed

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

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

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

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

Methods

Study areas

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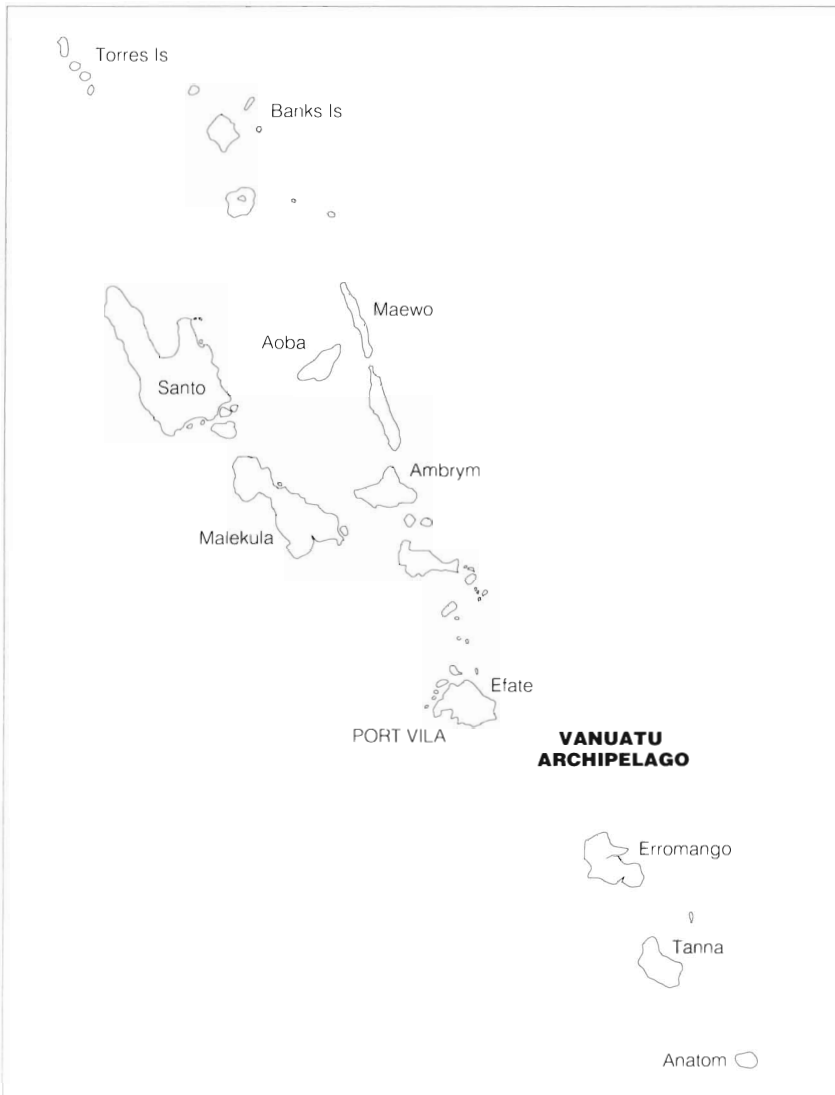

Figure 1. The Vanuatu Archipelago, showing the main study areas.

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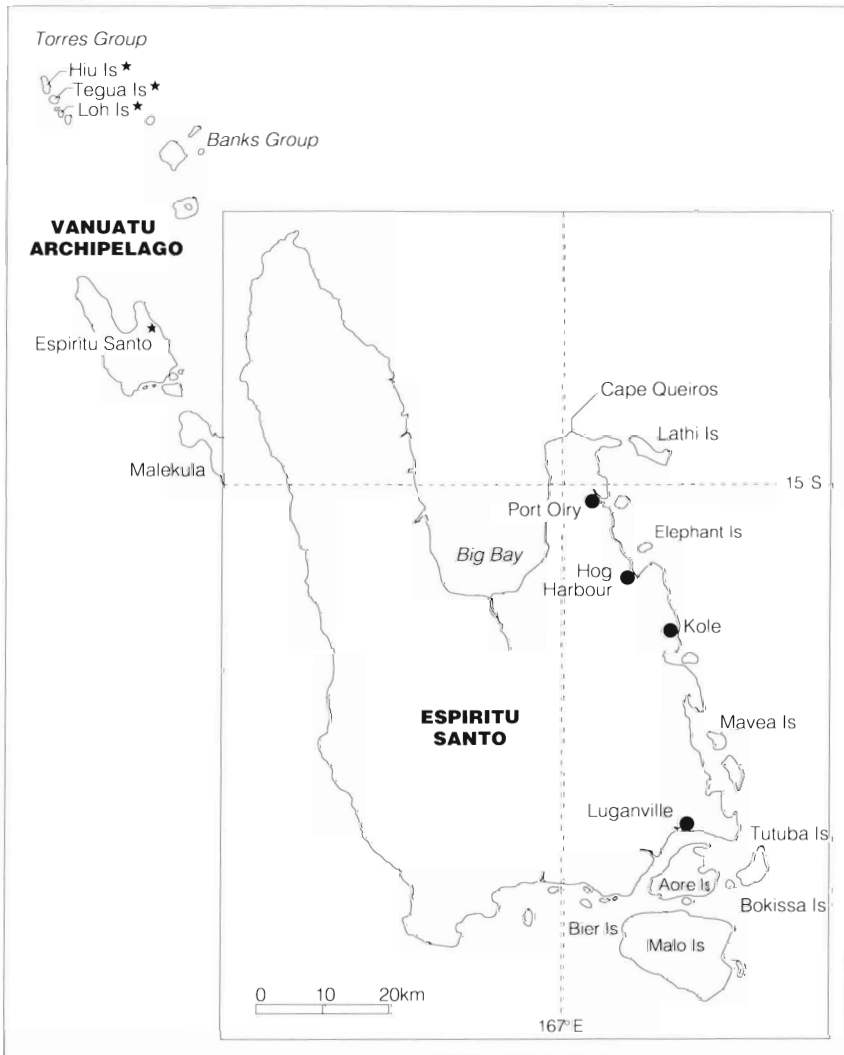

Figure 2. Primary study sites on Santo and in the Torres Group.

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

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

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

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

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

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

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

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

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

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

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

Catch per unit effort

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

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

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

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

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

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

Estimation of abundance

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

Activity levels

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

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

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

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

Results

Analysis of catch per unit effort (CPUE)

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Pooled catch rates

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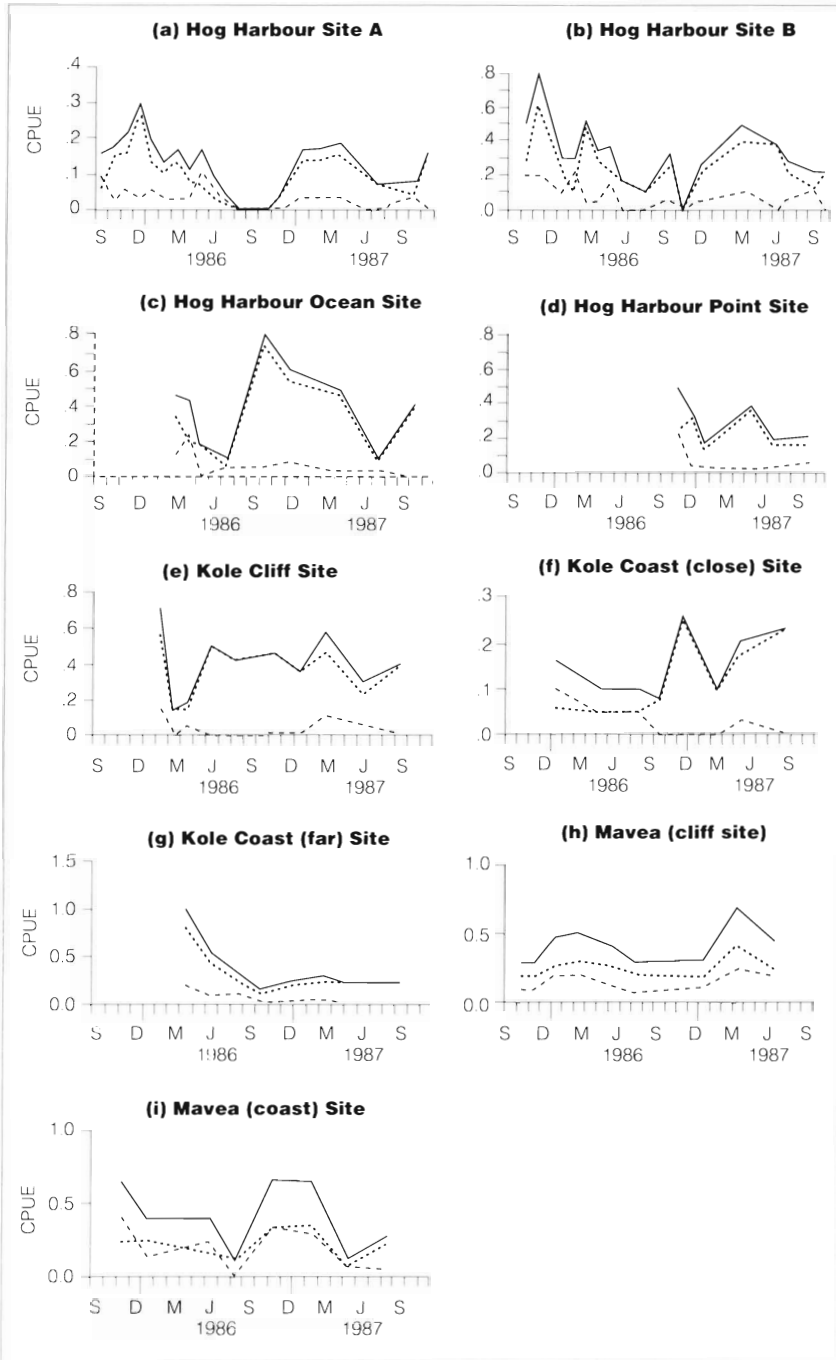
Figure 3. Seasonal changes in CPUE (catch per unit effort) at the primary study sites. The catch rate of legal-sized crabs is represented by a dashed line; that of undersize crabs by a dotted line, and that of the total by the solid line.

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

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

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

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

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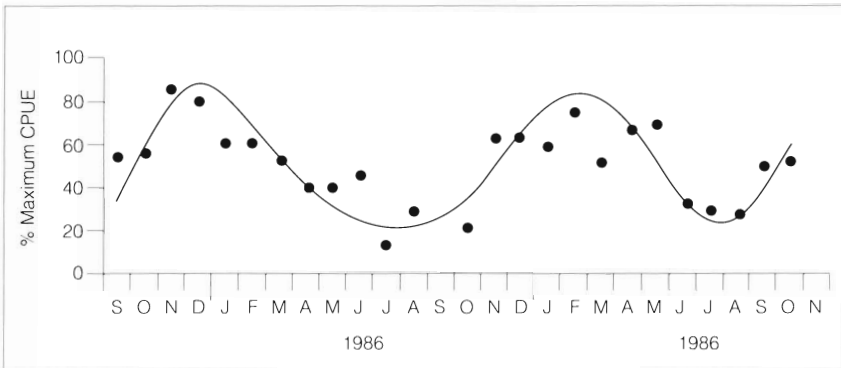
Figure 4. Seasonal changes in CPUE at all Santo sites pooled, expressed as a percentage of the maximum value recorded at any site.

Activity levels

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

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

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

Hermit crab abundance

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

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

Size structure

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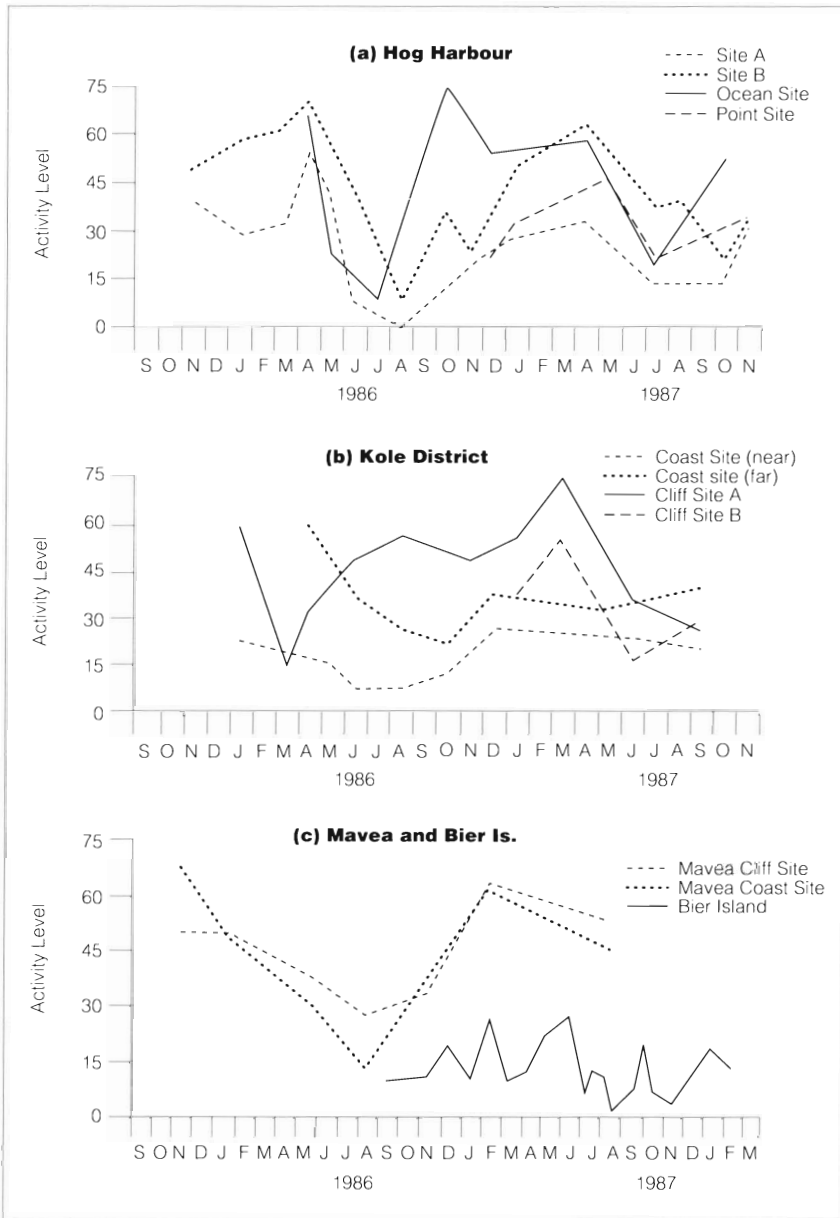
Figure 5. Seasonal changes in activity level index (estimated from the proportion of baits which had been eaten by coconut crabs) at the major sites.

(Bokissa Island) and 55 mm (Tegua Island), while that of females ranged from 29 mm (Bokissa Island) to 39 (Kole Coast). The maximum size of male crabs found at the various sites ranged from
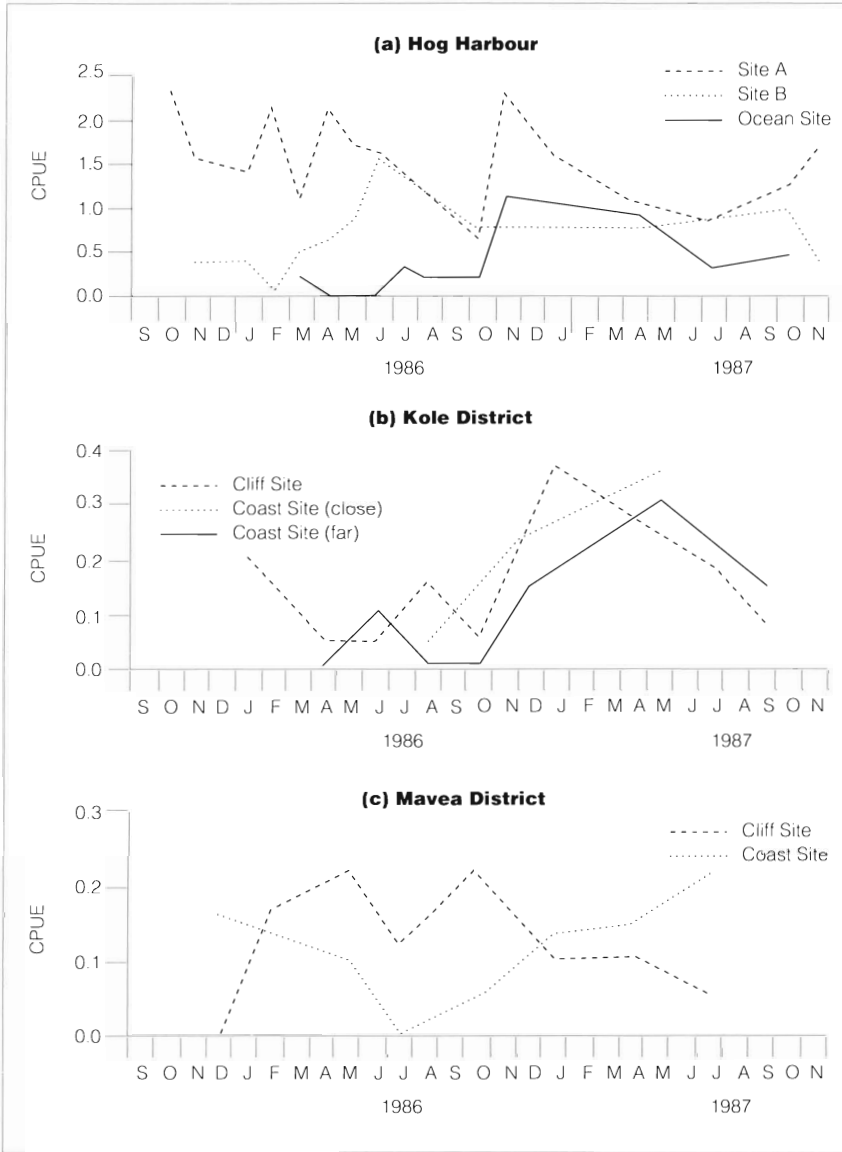
Figure 6. Seasonal change in relative abundance (CPUE) of coenobitid hermit crabs (nakato) at the major sampling sites.

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

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

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

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

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

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

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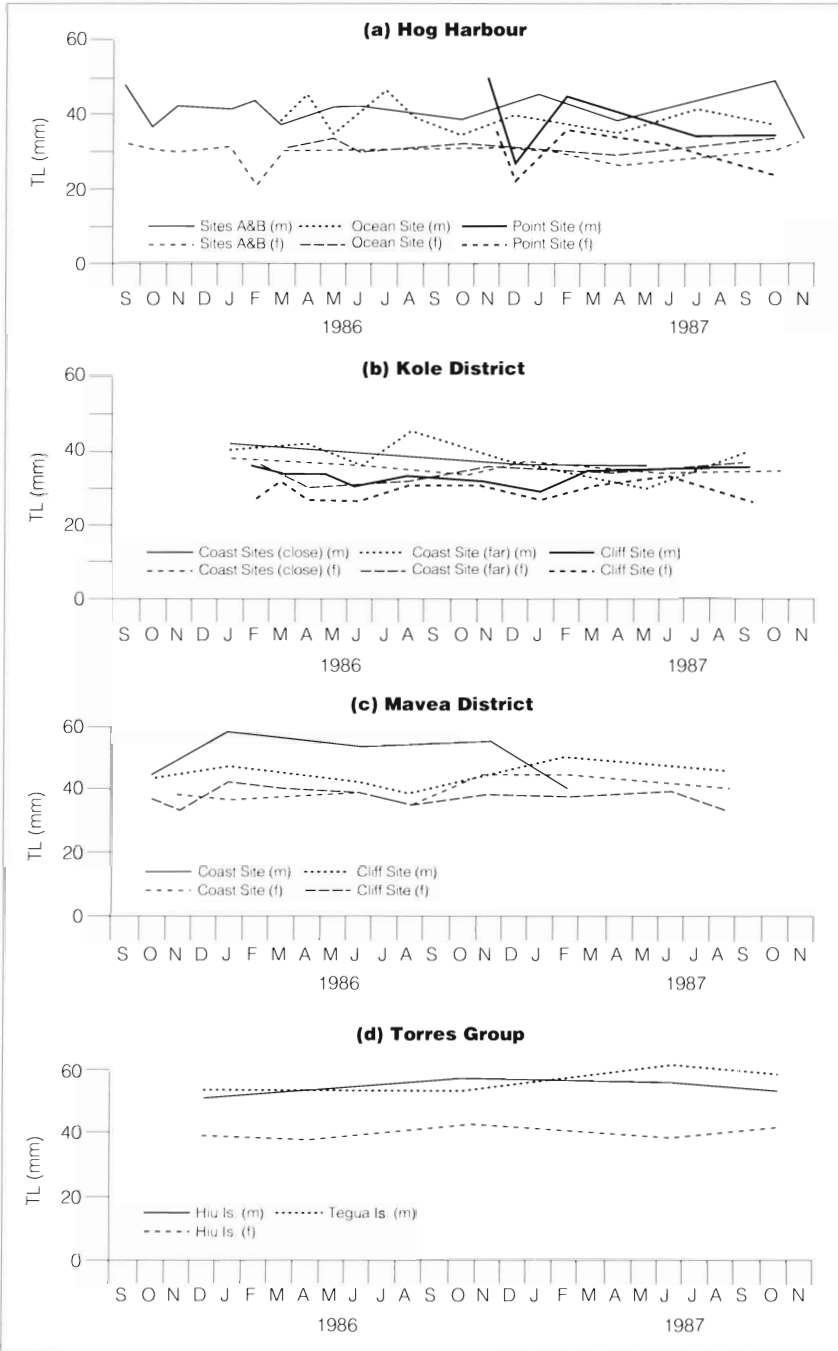
Figure 7. Seasonal changes in mean size (thoracic length) of male (m) and female (f) coconut crabs at each of the major sites on Santo, Hiu and Tegua during the project period.

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

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

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

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

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

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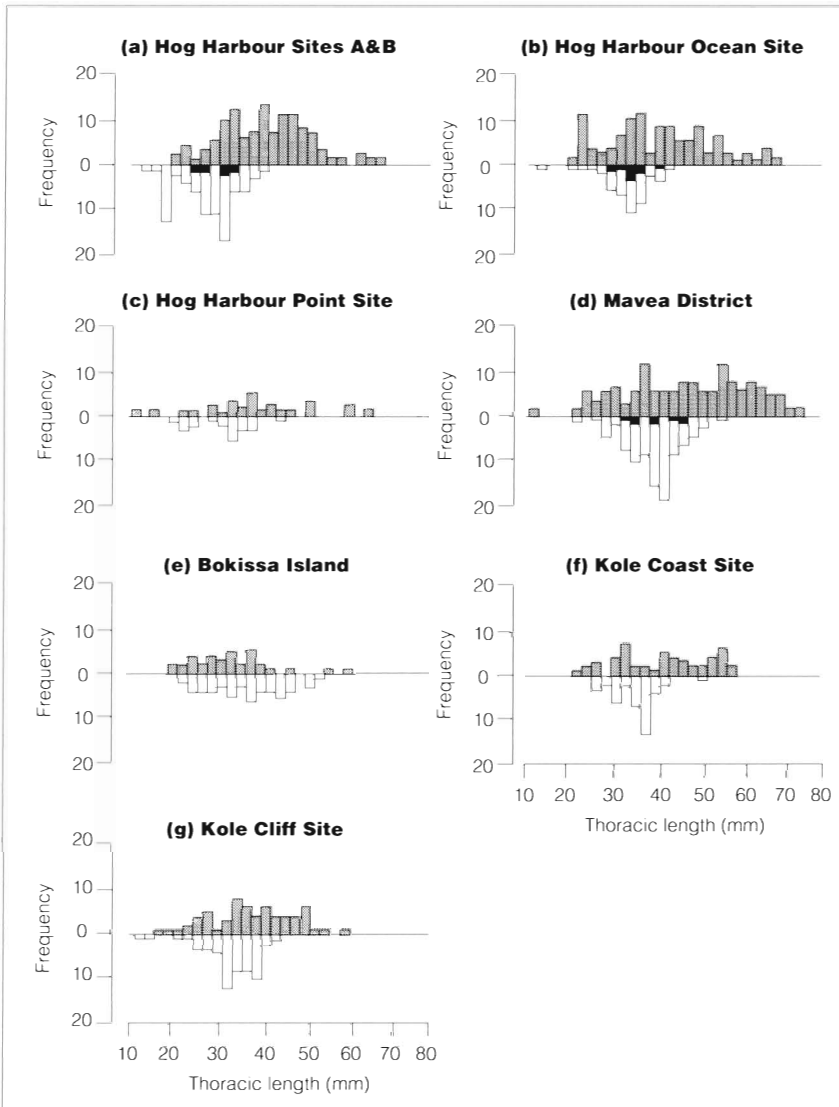
Figure 8. Pooled size—frequency distributions of coconut crabs at each of the major sampling sites. Males are represented by stippled bars, females by open bars, and ovigerous (egg-bearing) females by solid bars.

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

Discussion

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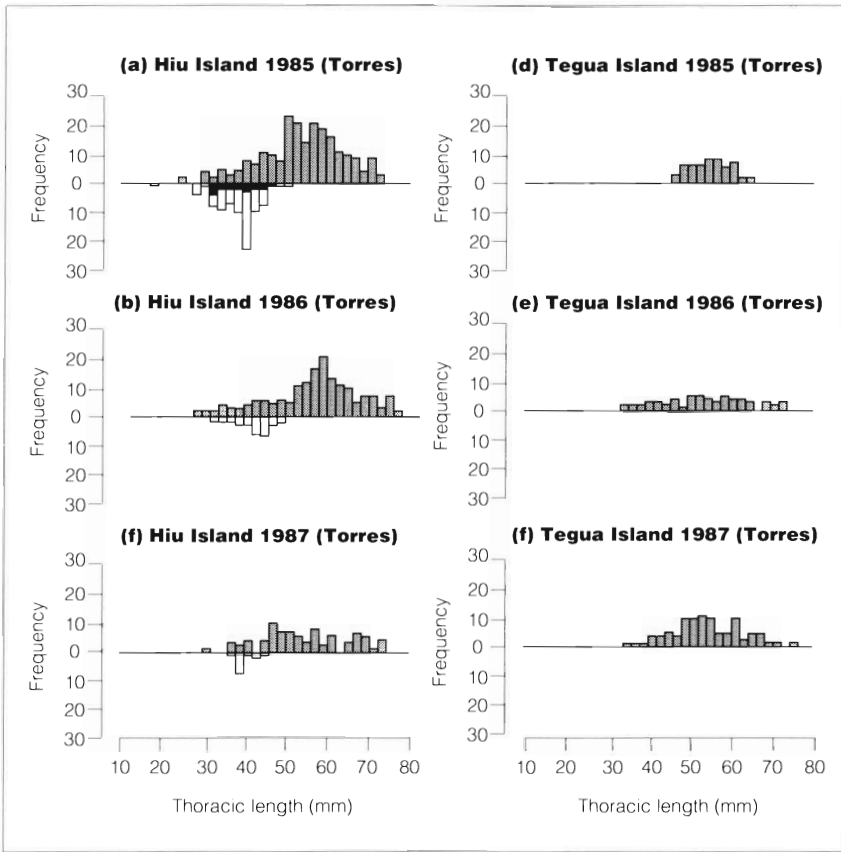
Figure. 9. Pooled annual size-frequency distributions of coconut crabs at sites on Hiu Island (a-c) and Tegua Island (d-f) in the Torres Group. Males are represented by stippled bars, females by open bars, and ovigerous (egg-bearing) females by solid bars.

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

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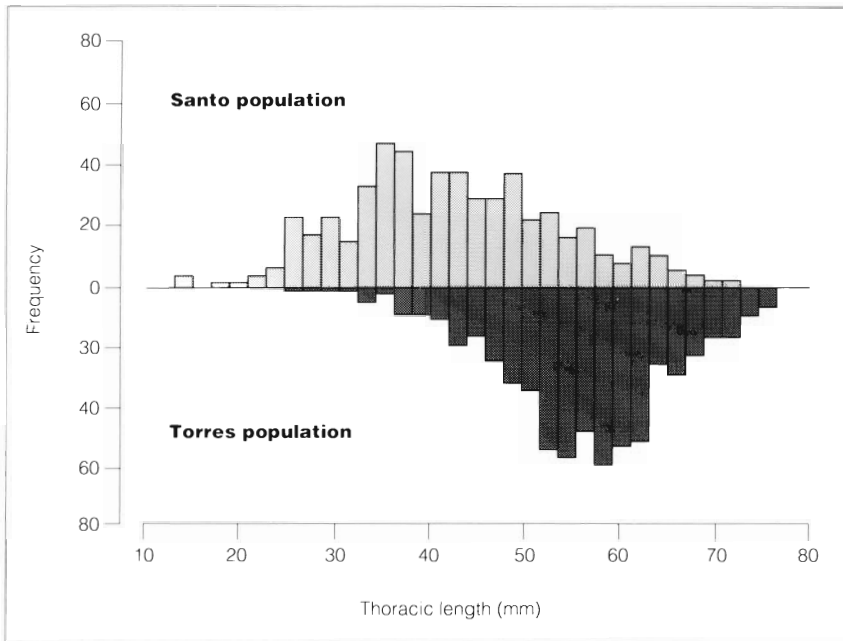
Figure 10. Geographical differences in the pooled size–frequency distributions of coconut crabs between the Santo and Torres populations.

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

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

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

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

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

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

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

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

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

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

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

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

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