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The Biology of *Callianassa (Trypaea) australiensis* Dana 1852 (Crustacea, Thalassinidea)

BY

T. S. HAILSTONE and W. STEPHENSON

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I. SUMMARY

Methods are described for collecting burrowing crustacea from intertidal sand flats by the use of "yabby pumps".

Ecological observations indicate the dominance of *Callianassa australiensis* in intertidal sand flats on parts of the east Australian coast.

Biometric data collected at different sampling sites over several years are analysed for growth and breeding activities, and the main events of the life cycle are outlined.

The possible over-exploitation of the species by bait collectors is shown to be very localized.

II. INTRODUCTION

Callianassid crustacea have been recorded from most of the oceans and from habitats which range from 400 fm. to between tidemarks (de Man, 1928). The genus *Callianassa* contains the greatest number of known species in the family, probably because several of its species are found on accessible intertidal mud and sand flats.

In North America callianassids are common on both the east coast (Lunz, 1937; Pearse, 1945; Pohl, 1946) and the west (Stevens, 1928, 1929; MacGinitie, 1930, 1934, 1949; Ricketts and Calvin, 1948; Barnard and Hartman, 1959), and here most of the previous ecological work has been done. They have also been reported in quantities in Africa from both the east coast (Day and Morgans, 1956; Macnae and Kalk, 1958; Broekhuysen and Taylor, 1959) and the west (Monod, 1927). In less intensive studies their abundance has been noted in the Mediterranean (Popovici, 1940; Picard, 1957), northern European coasts (Gustafson, 1936; Lutze, 1938), and New Zealand (Ralph and Yaldwyn, 1956).

Although specimens are numerous in many of these areas, when the present work commenced there were no literature records which suggested population densities approaching those observed for *Callianassa australiensis* along the Australian coasts of New South Wales and Queensland. However, recent works by Day and Morgans (1956) and by Broekhuysen and Taylor (1959) suggest similar densities in South Africa.

In eastern Australia, *Callianassa* can be obtained in quantities with relative ease by using a local invention (the "yabby pump") which will be described. Previous workers have either dug callianassids with spades (Stevens, 1928, 1929; MacGinitie, 1930, 1934, 1949; Lunz, 1937; Pearse, 1945; Pohl, 1946; Day and Morgans, 1956) or referred to specimens stranded after storms (Popovici, 1940), to migrating specimens collected in midwater (Monod, 1927), or to material obtained by bottom samplers (Barnard and Hartman, 1959).

In view of its abundance, the east Australian coast is particularly suited for studies on the biology of *Callianassa*. Only three such studies have been made in this area; that of Dakin and Colefax (1940) on planktonic stages; and the generalized accounts of Dakin, Bennett and Pope (1952) and of Stephenson (1957).

Callianassa australiensis is known in southern New South Wales as the "ghost-nipper" (Dakin, Bennett and Pope, 1952), and in northern New South Wales and Queensland as the "yabby" (a word of aboriginal origin also applied to freshwater crayfish).

The sale of yabby pumps and live yabbies for bait is an important aspect of amateur angling in southern Queensland and northern New South Wales. As bait, the species is taken readily by most demersal fish and especially by bream (*Mylio australis* Gunther), tarwhine (*Rhabdosargus sarba* Forskål) and whiting (*Sillago* spp.). Yabbies are collected in such numbers from accessible "yabby beds" in Moreton Bay for the possibility of over-exploitation to exist. Data were collected on growth and reproduction to investigate this possibility.

III. METHODS

(i) *Planktonic specimens*

Plankton was collected from Dunwich Pier (Fig. 1) with a plankton net (length 4 ft., opening diameter 15 in., c. 75 meshes/in.) towed against an ebbing tide of c. 1½ knots. Subsurface horizontal hauls of c. 30 min. duration were made at monthly intervals.

The numbers of different larval stages (see Dakin and Colefax, 1940) in each haul were recorded. Total length, carapace lengths, and maximum depths of first pereiopods of the formalin preserved material were measured (by calibrated *camera lucida*) to the nearest 0.05 mm.

(ii) *Post-planktonic specimens*

(*a*) *Collecting methods*

Shallow-burrowing juveniles were washed from sand which had been dug with spades or trowels.

The larger, deep-burrowing individuals were collected with yabby pumps.

The earlier model (Plate 1, Fig. 1) is a galvanised-iron tube (c. 4 in. diameter, c. 24 in. long) with a circular plate containing two ¼ in. thumb holes enclosing the top and with a handle of galvanised-iron tubing (c. ½ in. diameter). With thumb holes uncovered, the pump is pushed deeply into the substratum (Plate 1, Fig. 2). The thumb holes are covered, and the core of sand is extracted (Plate 1, Fig. 3), then discarded with the thumb holes uncovered (Plate 1, Fig. 4). The pump is re-inserted rapidly into the hole in the sand, and the contents removed two or three times. Yabbies are picked from the spoil of the later pumpings. This pump is cheap and robust, but is inefficient in loosely-packed sand, and fatiguing to operate.

The later model (Plate 1, Fig. 1) is a brass syringe (c. 2 in. diameter, c. 24 in. long). The plunger has a handle attached to a rubberised washer which can be adjusted with a thumb screw. The pump is pushed into the sand and the plunger simultaneously withdrawn to give slight suction (Plate 1, Fig. 5). The core of sand is removed and discarded by pushing down the handle (Plate 1, Figs. 6, 7). The tube is re-inserted into the hole, the plunger pulled out vigorously, the spoil discarded, and the process repeated. The yabbies are finally picked from the spoil. The pump can be used in about 18 in. of water, and in relatively loose sand, but is relatively costly (c. £A2/10/-) and the washers need frequent attention.

Neither pump is effective: (1) if there are too few burrows and little free liquid (two burrows per 0.1 m.^{2} represents approximately the lowest density for effective operations); (2) in substrata where most of the particle diameters are greater than c. 0.5 mm. (here either insufficient suction is obtained to dislodge the yabbies or the pumps do not penetrate).

Where these restrictions prevented collection of samples, the presence of specimens was recognized by their characteristic burrows.

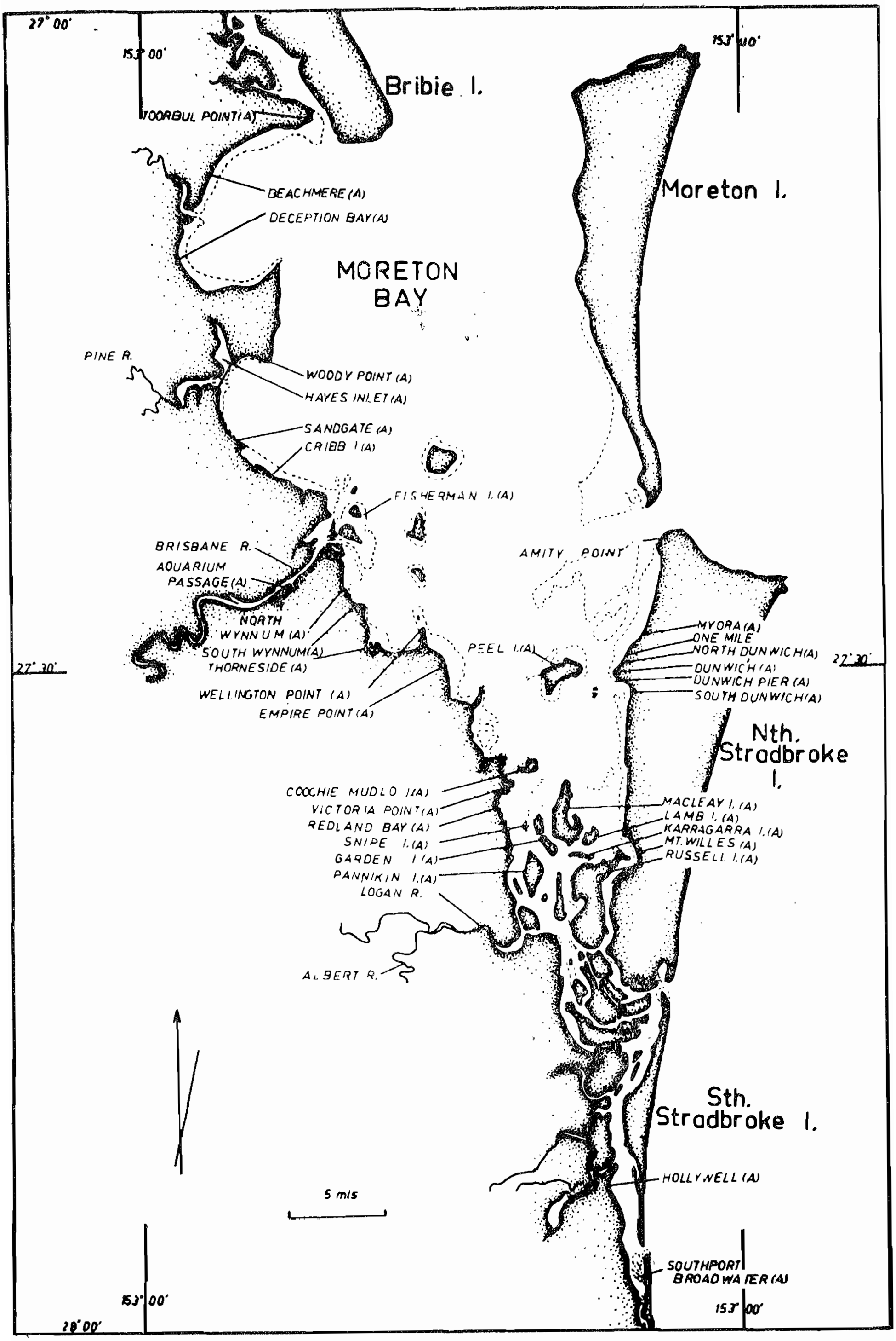

FIG. 1.—Map of Moreton Bay showing sites from which *C. australiensis* has been collected by the authors. These are indicated by "A".

(*b*) *Areas sampled*

Initial sampling was carried out on sand flats on the western side of Moreton Bay and at Dunwich (Fig. 1). The results showed differences between samples from these sites and to obtain chronologically continuous records, sampling was restricted to accessible areas at N. Wynnum (Fig. 1) and N. Dunwich (Fig. 1). After ten months the N. Wynnum collections were terminated because the grounds were nearing exhaustion but the N. Dunwich collections were continued for twenty months.

Collections from an area with a proportionally large juvenile population were then required and made from less accessible grounds at S. Dunwich (Fig. 1).

(*c*) *Sample size*

Between 100-200 individuals were collected monthly from each site.

(*d*) *Records*

Early in the work, the records for each specimen included sex, carapace length, total length, presence or absence of eggs on females, and indications of moulting. During an intermediate period total length was not measured. The later records from S. Dunwich included all of the above as well as development-stages of ovaries and eggs, and maximum depth of propodus of the large chela.

Sex was determined from the large chela (the adult male being characterized by one notably large claw), and the second pleopods which are absent in the male, but biramous and hirsute in the female (Plate 2). Ovigerous females are easily recognized.

Larger specimens were measured to the nearest 1.0 mm. with vernier calipers or ruler, and exactly intermediate readings recorded to the nearest 0.5 mm. Smaller specimens were measured to the nearest 0.1 mm. under a binocular dissecting microscope with calibrated eyepiece micrometer. Carapace length was taken as the mid-dorsal distance from distal point of the rostrum to the posterior edge of the carapace. Total length was taken as the mid-dorsal distance from the distal point of the rostrum to the distal edge of the telson. The ventral flexure and extensibility of the abdomen made total length measurements tedious and less accurate than those of the non-extensible carapace. Maximum depth of the propodus of the large chela was measured with vernier calipers (larger specimens) or calibrated eyepiece micrometer in a binocular microscope (smaller specimens).

Moulting and recently moulted specimens are soft and the exoskeleton can be dented easily.

Gonads are visible through the semi-transparent exoskeleton and the colour of the ovaries is "transparent", "white", "yellow", or "orange" (i.e., the chronological sequence seen during aquarium observation). The testes alter in size but not in colour from season to season and no records were made.

Eggs attached to the female pleopods are macroscopically recognizable as orange, yellow without eyespots, or with eyespots present.

IV. OBSERVATIONS

(i) *Distribution*

C. australiensis is distributed along the east Australian coast from Low Isles, north Queensland (lat. 16°32′S, long. 145°33′E) (Stephenson *et al.*, 1931) to Port Phillip, Victoria (lat. 38°2′S, long. 145°E) (Fulton and Grant, 1906). Sites from which specimens have been collected are shown in Figures 1 and 2.

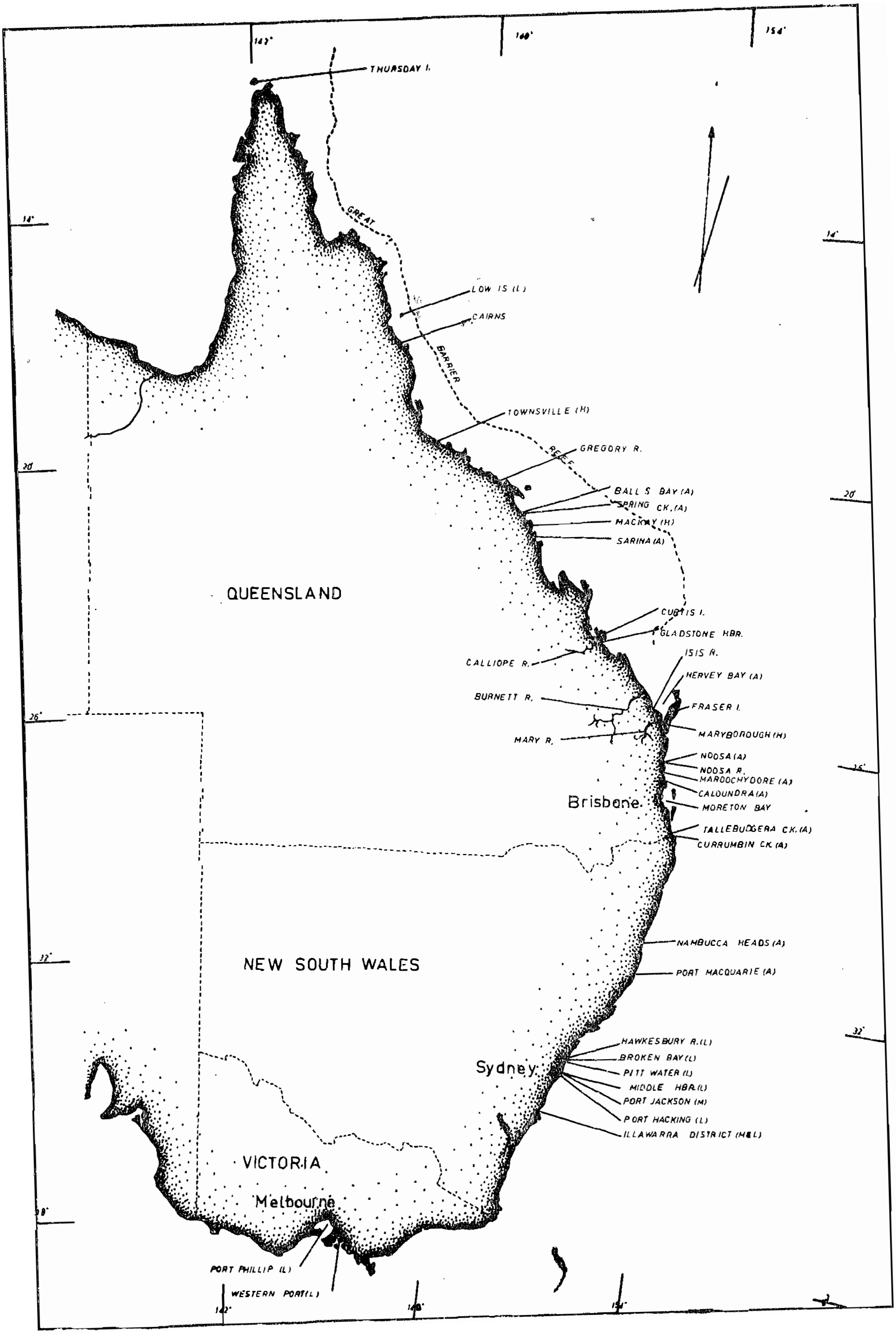

FIG. 2.—Map of East Australian Coast including sites from which *C. australiensis* has been recorded. "A" indicates collections by the present authors; "M" records based on collections in the Australian Museum; "H" specimens collected by officials of the Queensland State Department of Harbours and Marine for the authors; and "L" literature records.

(ii) *Habitat*

In Moreton Bay, the species lives in gently sloping, intertidal flats composed of fine grained sand containing a little mud (Plate 3, Fig. 1). Burrows are densest from high water to low water of neap tides, and eel grass (*Zostera capricorni* Ascherson) is commonly present.

C. australiensis also lives:

(a) in other substrata, such as firm sandy-mud (e.g., Thornside), soft sandy-mud (e.g., Wynnum), and loose gritty-mud (e.g., Wellington Point);

(b) at extreme low water of spring tides (e.g., Snipe Island, Wellington Point) and more rarely below this level (e.g., Wellington Point); and

(c) above high water of neap tides (e.g., Victoria Point), but localized in areas of drainage.

Moreton Bay consists of the estuaries of several rivers (Caboolture, Pine, Brisbane, Albert and Logan) together with an arm of the Pacific Ocean and is sheltered by Moreton and Stradbroke Islands.

Other areas resembling Moreton Bay with respect to environment and distribution of *C. australiensis* are Hervey Bay (with the Burnett, Gregory, Isis and Mary Rivers and sheltered by Fraser Island) and Gladstone Harbour (Calliope River and Curtis Island).

The remaining localities examined differ from Moreton Bay in that rivers discharge directly into the Pacific Ocean. Here *C. australiensis* is definitely an estuarine form as it decreases in abundance towards the mouths of the rivers and it is absent at and beyond the mouth where there are shifting sandbars and surf-lashed beaches.

The penetration of the species into south Queensland estuaries is related to the substratum, with extensive penetration into relatively sandy estuaries (e.g., Currumbin and Tallebudgera Creeks) but less into the more muddy (e.g., Brisbane and Albert Rivers). In the upper reaches of sandy estuaries, reduced salinity is no doubt also a limiting factor, but precise data are lacking.

(iii) *Distribution of burrows*

The density of burrows varied with substratum and size of specimens. Larger individuals (c. 60 mm. total length) had a maximum density of surface openings to burrows of c. 500/m.^{2}, while smaller individuals (c. 40 mm. total length) had a maximum density of c. 1,000 openings/m.^{2} (Plate 3, Fig. 2).

Various attempts were made to determine the number of burrow openings/specimen, so that burrow density could be converted to population density. Satisfactory figures were obtained from only two of these methods.

Firstly, in sparsely colonized areas, the distribution of openings fell into one of two categories:

(1) up to six openings irregularly clustered in a c. 25 cm. square (Plate 3, Fig. 3);

(2) up to six openings in an irregular row with c. 5 cm. between openings (Plate 3, Fig. 4).

Up to two specimens were collected from each set of burrows, so that one individual corresponds to two to three openings.

Sparsely colonized areas are difficult to sample and hence the lower of the two figures is accepted.

Secondly, specimens kept in isolation in aquaria formed up to six burrows/individual, with an average of about three. This number is probably higher than under natural conditions where water turbulence silts up unoccupied burrows.

Overall, the results suggest that two to three burrow openings generally correspond with one individual. If it is assumed that there are two openings per individual, the maximum population densities observed in nature would be c. 250/m.^{2} for the larger specimens and c. 500/m.^{2} for the smaller.

(iv) *Growth*

(*a*) *Measurements related to growth*

Total and carapace lengths were measured on a fraction of the samples to determine the relationship between the two and thus allow future concentration upon the more reliably measured carapace lengths. It was suspected that the relationships may alter during post-larval life, as noted by Dall in penaeid prawns (personal communication—not mentioned in publication, Dall, 1958).

Mean carapace length of each 5 mm. total length grouping was computed for males over the range 5-80 mm., females over the range 5-75 mm., and unsexed planktonic stages up to 5 mm. exclusive.

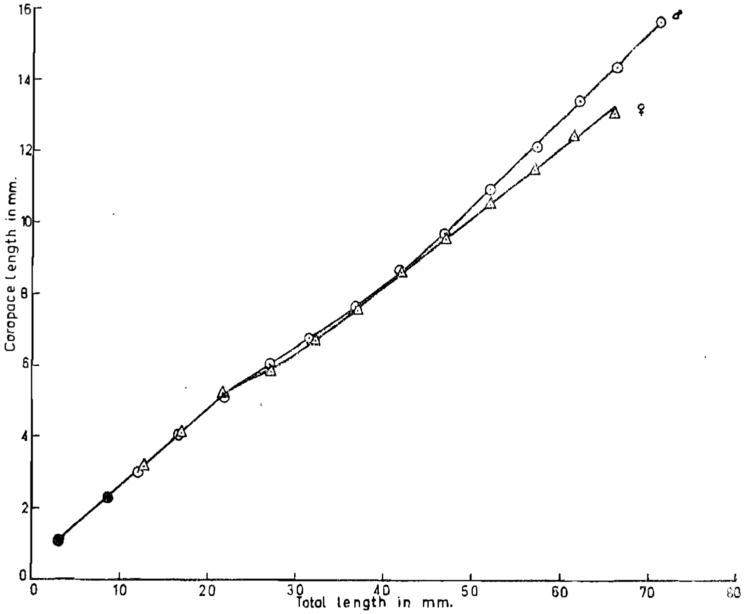

FIG. 3.—Mean carapace lengths in mm., plotted against mean total lengths, in mm., for 5 mm. class intervals of total lengths. Males open circles, females triangles, unsexed planktonic stages closed circles.

The curves of the carapace length/total length for each sex (Fig. 3) appear to consist of three portions. Below 22 mm. total length the curves for each sex appear linear and identical and can be formulated by the method of least squares as $\boldsymbol{l} = 0.216\ L + 0.458$ (where $\boldsymbol{l}$ is carapace length in mm. and L is total length in mm.).

The uppermost portions of the curves for each sex are again extremely close to straight lines which differ in slope (that of the male being greater) and in the total length at which the straight line relationship commences (male c. 47 mm., female c. 37 mm.). The formulae (calculated by the method of least squares) for the two curves over these ranges are:

Males	$\boldsymbol{l} = 0.242L - 1.686$
Females	$\boldsymbol{l} = 0.194L + 0.410$

The central portion of the graph for each sex shows a curved transition from the lower to the upper straight lines, the curvature being more abrupt in the female graph.

Formulae for these curved portions were not obtained but instead equivalent points on the two curves were compared to determine the smallest total length at which males were significantly different from females. Because the mean total length for each group of females is unlikely to be the same as that of the males, an adjustment to the female data is necessary. This was effected by (1) determining the tangent to the female curve at a given point by reference to the graph (Fig. 3), (2) from the difference between the male and female mean total lengths, calculating the equivalent difference to be expected in the female mean carapace length, and (3) adjusting the female mean carapace length accordingly.

TABLE 1

Comparison of relationship between carapace lengths and total lengths for the two sexes in the range 25-44 mm. total length. See text for details.

Class interval total length in mm.	Males				Females					Difference between male mean and adjusted female mean	Probability level of significance of difference
	Mean total length in mm.	Mean carapace length in mm.	Number of measurements	Standard error of carapace mean	Mean total length in mm.	Mean carapace length in mm.	Number of measurements	Standard error of carapace mean	Carapace mean adjusted to same total length as males		
25–29	27·14	6·06	79	0·0875	27·14	5·85	44	0·1082	—	0·21	13%
30–34	31·75	6·75	76	0·0707	32·24	6·69	62	0·0603	6·61	0·14	14%
35–39	36·96	7·65	129	0·0168	37·13	7·55	105	0·0187	7·44	0·21	<<0·1%
40–44	41·91	8·70	140	0·0535	42·07	8·64	154	0·0475	8·61	0·09	21%

The data are given in Table 1 which shows a significant difference only in the 35-39 mm. class interval. The fact that the points in the 25-29 mm. and 30-34 mm. class intervals both show the same tendency and are both only slightly below the level of significance is taken to indicate that the real point of divergence may lie at 30 mm., or possibly as low as 25 mm. (total length).

Summarizing, the above data show:

(1) that relationships between carapace length and total length are complex;

(2) conversions from carapace length to total length are more easily effected graphically than by calculation;

(3) there is a conspicuous divergence of male and female curves at a total length of c. 47 mm., above which the male carapaces are noticeably longer than the female carapaces;

(4) over the range c. 30-47 mm. total length, the male carapaces are slightly longer than the female carapaces, and this tendency may commence at a total length of c. 25 mm.;

(5) at the following approximate total lengths there appear to be changes in the form of the curve of carapace length/total length:
male 22 mm., 47 mm.; female 22 mm., 37 mm.

Since sex ratios differed between the three main collecting areas, the possibility of similar differences in carapace length/total length relationships was investigated.

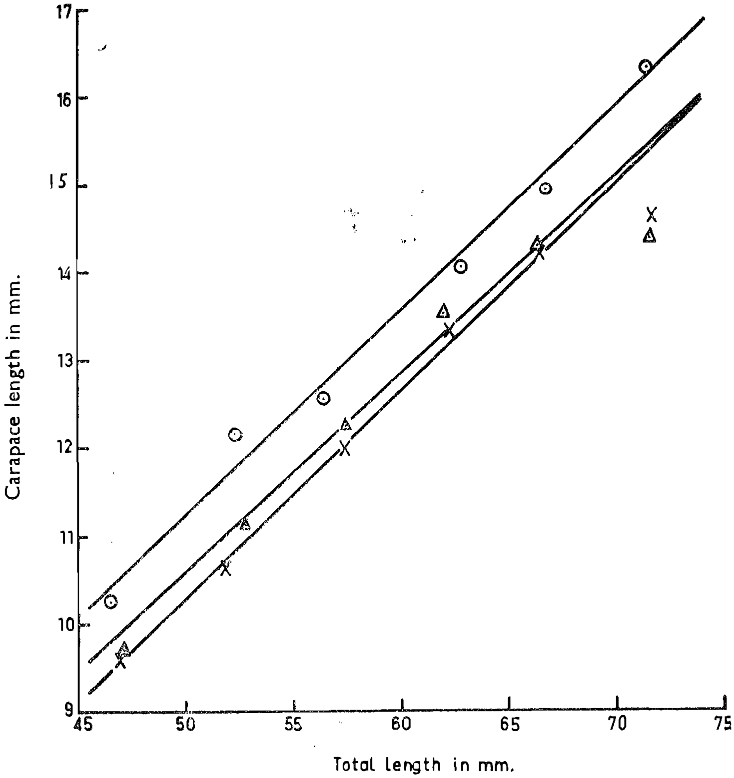

FIG. 4.—Mean carapace lengths in mm., plotted against mean total lengths in mm. (5 mm. class intervals) for males (45-74 mm. total length range) from the three main sampling sites. N. Wynnum open circles, N. Dunwich triangles, S. Dunwich crosses.

The analysis was restricted to the upper portions of the male curves with total lengths above 45 mm. and the relevant data are plotted on Figure 4. The formulae of the best fitting lines (calculated by the method of least squares) for each sampling area are:

N. Wynnum	$l = 0.2352\,L - 0.5154$
N. Dunwich	$l = 0.2273\,L - 0.7839$
S. Dunwich	$l = 0.2377\,L - 1.5974$

A test for significance of differences between N. Dunwich and S. Dunwich values was made. Mean values of carapace length were calculated and a correction factor (based upon the slope of the curves) was applied to bring each to a common total length suitable for comparison.

The difference between the corrected values was highly significant (less than 0.001 level, t. test). Thus the males from N. Dunwich and S. Dunwich in the 45-74 mm. total length range constitute different populations with respect to the carapace length/total length relationship.

Since the best fitting straight line to the N. Wynnum data is situated further from either of the Dunwich lines than they are from each other, the N. Wynnum data indicate that another separate population is there present.

The S. Dunwich males are closest to females with respect to carapace length/total length ratios.

(*b*) *Development of secondary sexual characteristics*

The change in the carapace length/total length relationships which becomes obvious in males at a total length of c. 47 mm. might be a secondary sexual characteristic. The enlarged cheliped of the males is a much more obvious sexual feature and its development was studied as a possible indicator of sexual maturity.

One of the easiest measures of cheliped size is the maximum depth of the deepest segment, the propodus (see Plate 2, Fig. 3). From the combined Moreton Bay data, mean depths of this segment and mean total lengths of the body were computed for 5 mm. total length groupings of both sexes. These data are plotted on Figure 5.

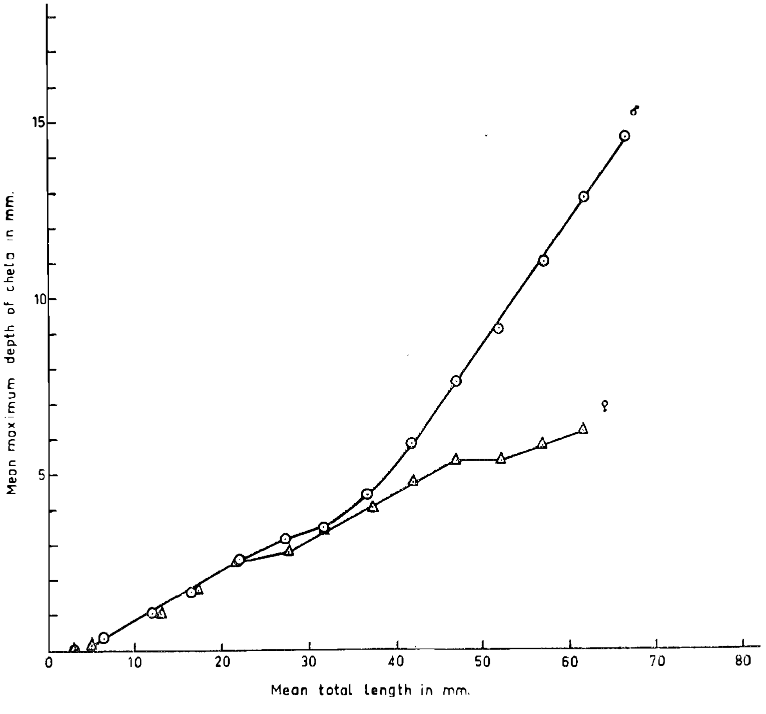

FIG. 5.—Mean maximum depths of the larger chelipeds in mm., plotted against mean total lengths in mm. (5 mm. class intervals). Males open circles, females triangles.

Each graph approximates to a series of straight lines with abrupt inflections between them. Up to a total length of c. 22 mm. the two sexes follow the same curve, but thereafter differ. In the female curve three straight line portions are recognizable, these being roughly parallel to each other, and with two marked inflections in the total length ranges between c. 22-27 mm. and c. 47-52 mm. In the male curve two straight line portions are recognizable, the upper having a greater slope than the lower. The transition from one line to the other covers a broad range (c. 27-37 mm. total length).

It is difficult to interpret these curves and understand why female body length should increase from 47-52 mm. while the chela depth remains unchanged. Possibly, the points of inflections indicate critical moults in the life cycle. They are much more clearly distinguishable in the chela depth/total length curve (Fig. 5) than in the carapace length/total length curve (Fig. 3). Unfortunately the two figures do not give identical critical points, the only overall agreement being at a total length of 22-25 mm. in both sexes.

It is possible that the increasing weight of the male chela affects the size of the supporting thoracic region, therefore relationships between chela depth and carapace depth were investigated.

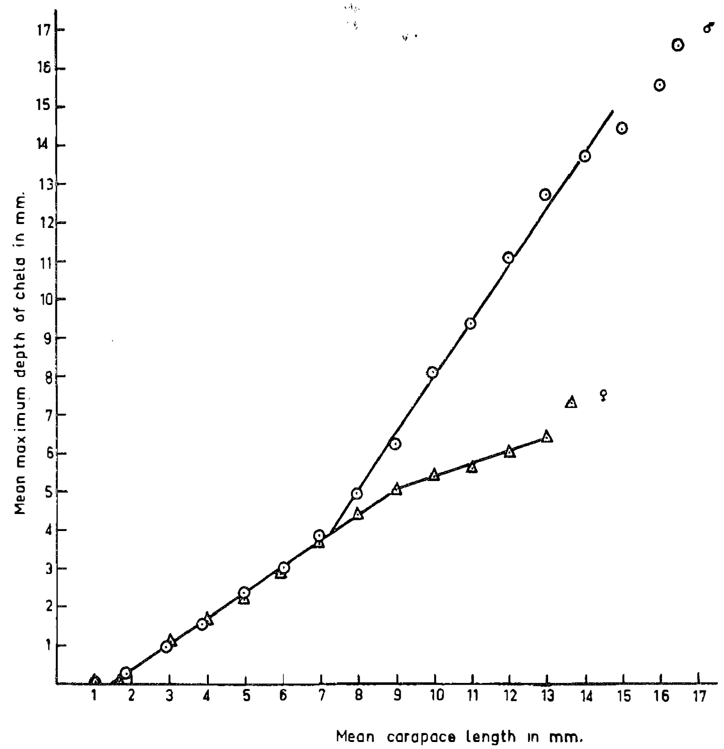

FIG. 6.—Mean maximum depths of larger chelipeds in mm., plotted against mean carapace lengths in mm. Males open circles, females triangles. The uppermost female and two uppermost male points are based on insufficient data.

Data from all Moreton Bay samplings for both sexes are given in Figure 6. The male curve is either curvilinear or more probably, two approximately straight lines intersecting at c. 7 mm. carapace length (equivalent to c. 36 mm. total length). The female curve, which diverges from the male at c. 7 mm. carapace length, is a straight line to c. 9-10 mm. carapace length (equivalent to c. 45-50 mm. total length) and then becomes a second straight line (neglecting the last point which is based on too few data).

Summarizing all data upon relative proportions of parts, the following appear to be the likeliest common factors:

(a) Up to a total length of 22-25 mm. the sexes are similarly proportioned as regards size of chela and carapace length in relation to total length.

(b) Between the above total length and c. 35 mm. the same straight line relationship between size of chela and carapace length apparently holds for both sexes. However, over this range the relationship of either measurement to total length is a far from simple one in the two sexes.

(c) At total lengths above c. 35 mm. the male chela increases proportionally faster than the carapace length.

(d) At total lengths above c. 45-50 mm. the female chela increases proportionally slower than the carapace length.

(e) At total lengths in excess of c. 37 mm. in the females and c. 47 mm. in the males straight line relationships exist between total length and carapace length (see Fig. 3).

From these confusing data three total lengths appear, for differing reasons, to be critical for those aspects investigated viz., 22-25 mm., 35-37 mm., and 45-50 mm. The first probably indicates the earliest development of secondary sexual characteristics in both sexes. As will be shown later, the second is roughly equivalent to the length at first maturity at least in the case of the female. The import of the third is unknown.

(c) *Ecdysis*

The percentages of soft individuals in monthly samples from the entire Moreton Bay collections are given in Figure 7.

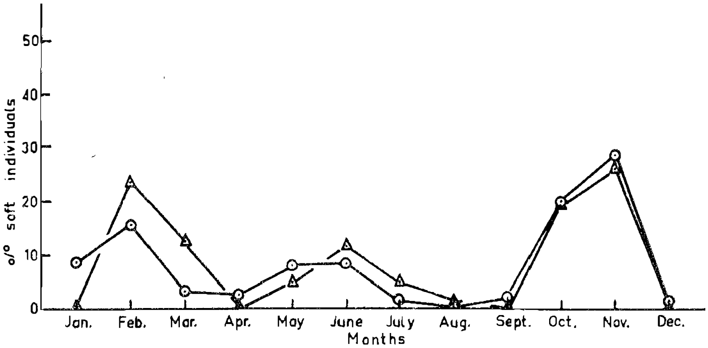

FIG. 7.—Moulting seasons. Percentages of soft individuals plotted against months for combined Moreton Bay samplings. Males open circles, females triangles.

Three peaks of moulting activity occurred in February, June and October-November respectively.

The data are barely adequate for distinguishing between the moulting seasons of the sexes, but there is an indication in the February and June peaks that the males precede the females. This might be expected if hardened males are copulating with soft females.

Aquarium observations showed that the exoskeletons of moulted individuals harden in about six days. From this it is possible to calculate the percentages of the population which moult at a particular season as shown in the following example.

The February mode of the female curve can be dissected visually from its neighbours, and its area determined graphically. This area is equivalent to 12.8 per cent soft individuals throughout the entire period of about three months, which in turn is equivalent to c. 180 per cent of soft individuals over a period of six days.

Analysed in this manner, the equivalent percentage of soft individuals over a six day period for the three peaks from each sex is:

February	c. 129% (males);	c. 180% (females)
June	c. 112% (males);	c. 106% (females)
October-November ..	c. 258% (males);	c. 252% (females)

From this it seems probable that each individual moults twice during the October-November period and once during the June period. Most individuals appear to moult once in February, but some females appear to moult twice.

(*d*) *Growth rates*

Five methods of determining crustacean growth rates have been suggested for or applied to studies of penaeid prawns (see Weymouth, Lindner and Anderson, 1933; Pearson, 1939; Anderson, King and Lindner, 1949; Gunter, 1950; Burkenroad, 1951; Menon, 1952; Fujinaga, 1955; Ikematsu, 1955; Kubo, 1955; Menon, 1955; Williams, 1955; Menzel, 1955; Johnson and Fielding, 1956; Lindner and Anderson, 1956; Racek, 1957; and Dall, 1958). Teissier (1960) has also reviewed the theoretical basis and applications of relative growth studies in crustacea.

These methods are as follows:

(1) dissection of the modes in a natural population;
(2) progression of the modes of successive samples;
(3) measurements upon captive specimens;
(4) consideration of rate of moulting, together with increase in size per moult;
(5) measurements upon tagged or dyed individuals.

Results using the first two methods are detailed below. Preliminary determinations with the third and fourth methods gave unsatisfactory results, and the work is being repeated.

(1) *Dissection of the modes*

In the monthly samples from N. Wynnum and from N. Dunwich, the curves for number of individuals against carapace length showed a single clear mode for each sex. There were indications of a second mode in some of the N. Dunwich samples. Typical results are shown in Figure 8.

Curves for the monthly samples at S. Dunwich were more irregular and therefore data were lumped seasonally viz., summer (December, January, February), autumn (March, April, May), winter (June, July, August) and spring (September, October, November).

In general, the resultant curves (Fig. 9) are bimodal with a suggestion of an intermediate mode nearer the second mode than the first. The distance between the main modes decreases progressively from spring through summer and autumn to winter, because the main second mode is not progressing. The method is obviously inapplicable.

(2) *Progression of the modes*

In the results from N. Wynnum and N. Dunwich the single mode did not progress, but merely oscillated from 14 mm. to 16 mm. (♂) and 12.5 mm. to 13 mm. (♀) at the former collecting area and from 12 mm. to 14 mm. (♂) and 10 mm. to 12 mm. (♀) at the latter.

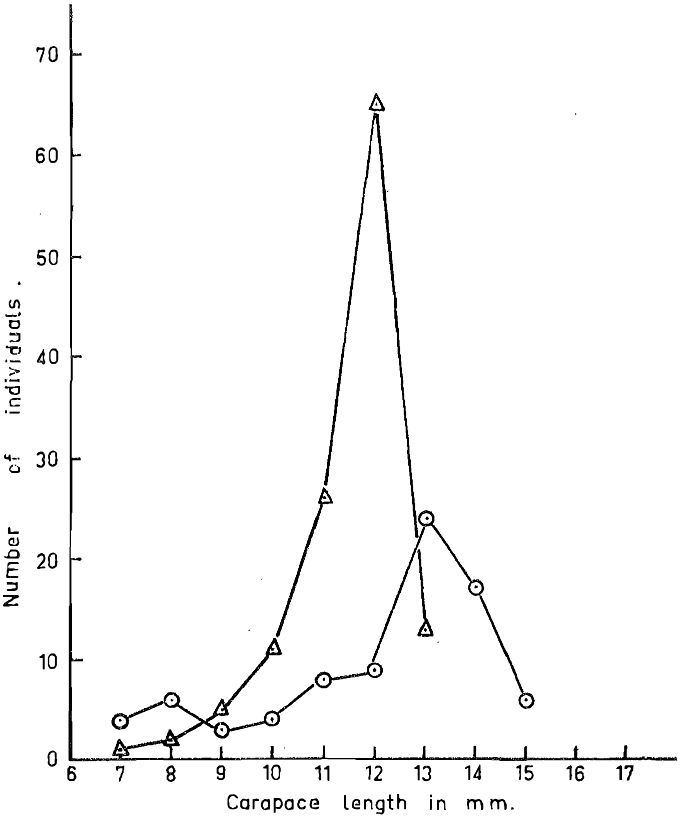

FIG. 8.—Typical modal results from a monthly sample (N. Dunwich, June, 1958). Number of individuals plotted against carapace lengths in mm. Males open circles, females triangles.

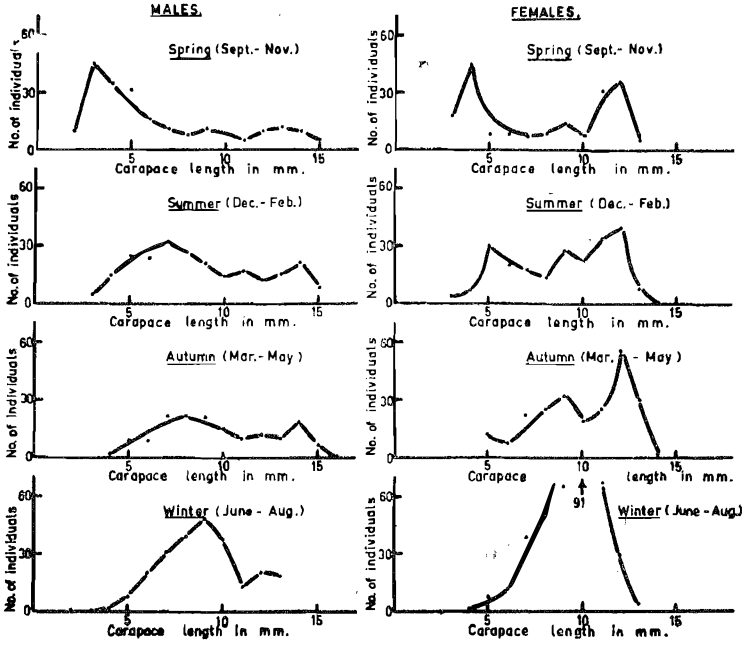

FIG. 9.—Seasonal modal results for S. Dunwich samplings. Number of individuals plotted against carapace lengths in mm. for each season.

In the results from S. Dunwich, as already indicated the second mode was stationary, but the first one progressed by the values below (expressed as carapace lengths in mm.):

Spring results: ♂ 3, ♀ 4
Summer results: ♂ 4, ♀ 1
Autumn results: ♂ 1, ♀ 4
Winter results: ♂ 1, ♀ 1

The overall mean gives an annual growth rate of c. 9.5 mm.

Some confirmation is obtained by extrapolating the growth curve to determine the season of origin of the modal population. This lies between autumn and winter i.e., slightly after the main season of egg bearing in April.

The absence of progression of most of the modes is noteworthy, and compares with a similar stability noted by Dall (1958) in *Metapenaeus mastersii* (Haswell). It suggests continual recruitment to and loss from the population.

(v) *Breeding activity*

(*a*) *Size at first maturity* (*females*)

Data on the smallest ovigerous females collected are shown in Table 2.

TABLE 2

Smallest ovigerous females from Moreton Bay collecting sites.

Site	Carapace length (mm.) of smallest ovigerous female	Numbers of this size collected during breeding season	
		Ovigerous	Total
N. Wynnum	9	1	3
N. Dunwich	8	1	17
S. Dunwich	9	6	22

At Ball's Bay, N. of Mackay, the smallest ovigerous females in a small collection were 7 mm. carapace length whereas Moreton Bay specimens mature at 8-9 mm. carapace length.

(*b*) *Breeding seasons*

Breeding was investigated via the percentages of ovigerous females in each collection, neglecting specimens smaller than the size at first maturity (i.e., 9 mm.).

Summated results for all Moreton Bay specimens (Fig. 10) show a major breeding peak in April, and a minor one in August-September with some mergence between the two.

Since collections from the three main areas differed in other respects their breeding seasons were compared. The results (Fig. 11) show that at N. Wynnum, breeding was more pronounced and much more continuous than elsewhere.

The most noteworthy characteristic of the N. Wynnum samples was the large size of the individuals and so the effect of size upon breeding season was investigated on the summated data from all Moreton Bay collections. The following carapace length groups were separated: 9-10 mm., 11-12 mm., and 13-15 mm. (intermediates were taken to the adjacent groups). The results (Fig. 12) show:

(1) a bimodal curve for each size group;
(2) the larger the specimens the greater the percentage ovigerous at any time during the "breeding season";
(3) the larger the specimen, the more continuous the breeding activity.

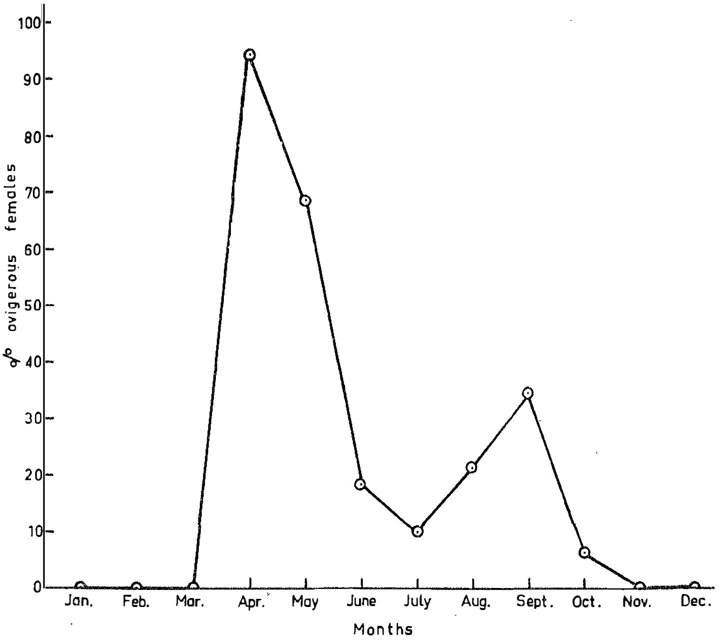

FIG. 10.—Percentages of ovigerous, mature females plotted against months for combined Moreton Bay samplings.

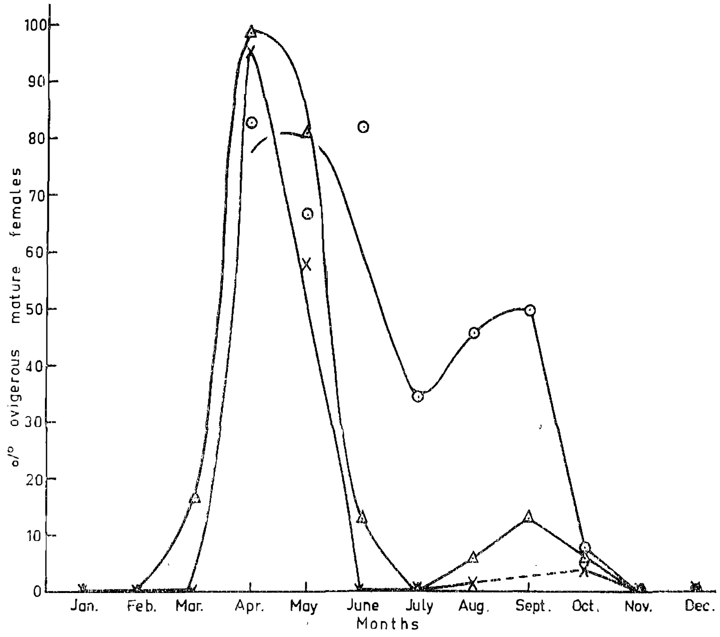

FIG. 11.—Percentages of ovigerous, mature females plotted against months for the three main sampling sites. N. Wynnum open circles, N. Dunwich triangles, S. Dunwich crosses. All curves smoothed visually.

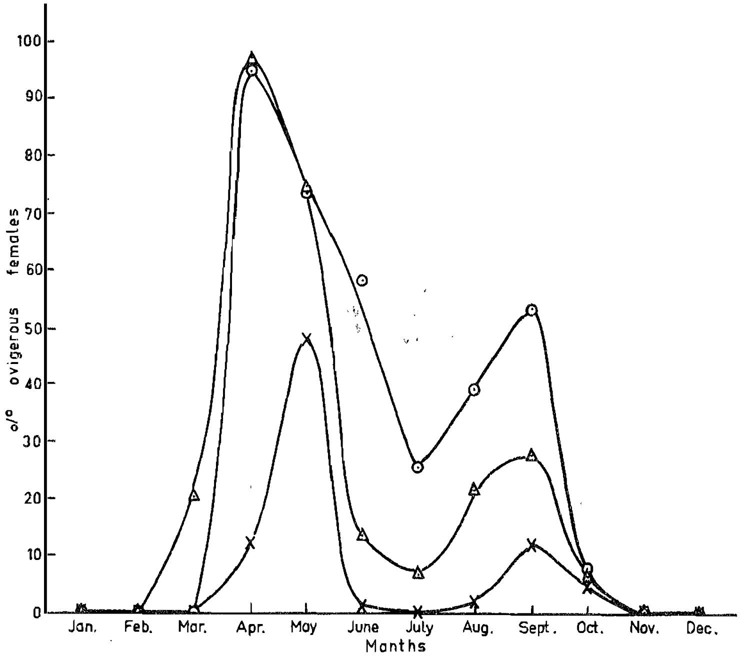

FIG. 12.—Effects of size upon breeding seasons. Percentages of mature, ovigerous females (grouped by carapace lengths) plotted against months for combined Moreton Bay samplings: 9-10 mm. carapace length crosses, 11-12 mm. carapace length triangles, and 13-15 mm. carapace length open circles.

The differences between the N. Wynnum and remaining populations can be explained to a large extent in terms of size of the individuals. This leaves unexplained why the individuals from this area should be noteworthily large.

The "breeding seasons" as considered above include all stages in the chronological sequence from the attachment of newly laid eggs to the pleopods up to the time of hatching. The macroscopically visible stages of this sequence, as observed on aquarium specimens, are as follows: newly laid eggs are bright orange, colour then changes to yellow, then to khaki, and finally eyespots are visible shortly before hatching. Field observations confirmed the extremes of this sequence, the first ovigerous females of the year bearing preponderantly bright orange eggs, and the last bearing khaki coloured eggs with eyespots visible.

Aquarium observations showed that eggs are carried for at least six weeks during September-October. The effect of lumping together these phases is to extend the apparent breeding peaks by about six weeks during the first breeding peak, and possibly by about seven weeks during the second.

Adjustments to the breeding seasons to allow for this were effected by: (1) resolving the bimodal curve into two separate unimodal curves (see Fig. 13) and (2) compressing the time scales by six weeks and seven weeks respectively, towards the earliest points of the curves.

These adjusted curves indicate the approximate times of egg laying, but give erroneously high values of the percentages of females laying them at a given time. The adjusted curves show clearly that there are two discrete breeding seasons with comparatively little overlap.

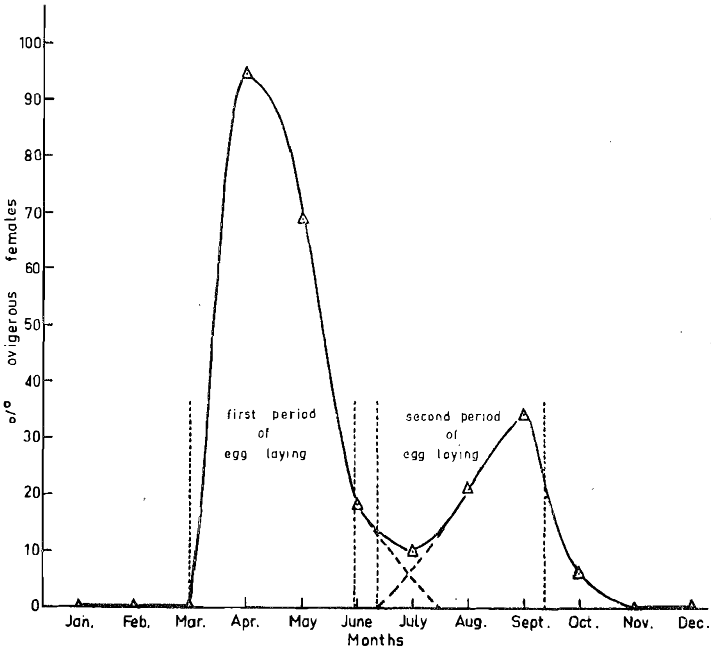

FIG. 13.—Breeding seasons adjusted to show periods of egg laying. Percentages of mature, ovigerous females plotted against months for combined Moreton Bay samplings.

Towards the end of the investigations, more detailed studies were made upon breeding, using the S. Dunwich population. In these the macroscopic appearance of the ovaries prior to egg laying was divided into three categories: (1) transparent, white or cream; (2) yellow; and (3) orange. The percentages of females in each category (excluding specimens smaller than 9 mm.) are shown in Figure 14. Three categories of ovigerous females were also distinguished in which the ova were respectively, orange, yellow, and with eyes. Results are plotted in Figure 15. Figure 14 shows that in this population the ovaries pass from their transparent, white or cream stage at about November, the yellow stage about January, and the orange stage about March. Immediately the percentage with orange gonads declines, ovigerous females appear (Fig. 15). Surprisingly, small numbers of specimens with well developed eggs appeared amongst the first ovigerous females, suggesting either that they had reached this stage in less than a month or, and less likely, that ovigerous females produced earlier on adjacent grounds had migrated into the sampling area.

(c) *Planktonic stages*

Dakin and Colefax (1940) described six larval planktonic stages, each of which has been recognized during the present work.

The first larval stages (c. 1 mm. carapace length) appeared in the plankton about one month after the major breeding season and later stages were collected throughout the winter. The sixth larval stages (c. 3 mm. carapace length) were collected during early spring, and later in spring early post-larval stages (c. 4 mm. carapace length) also appeared in the plankton. These latter presumably settle to the adult environment by the beginning of summer, as post-larvae (c. 6 mm. carapace length) have been collected at S. Dunwich during this period.

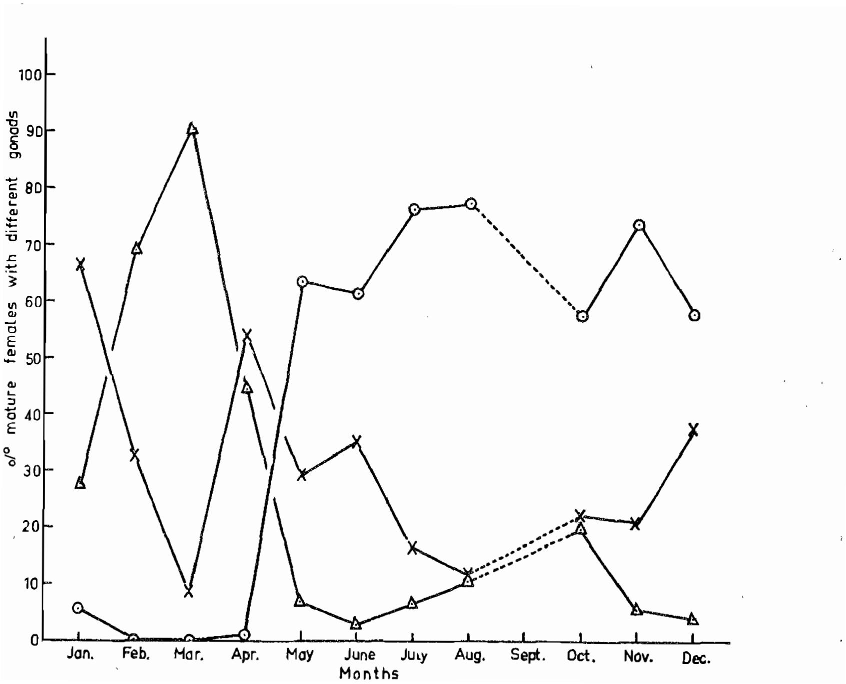

Fig. 14.—Percentages of mature females with gonads at different stages plotted against months for S. Dunwich samplings. Ovaries transparent, white or cream—open circles; ovaries yellow—crosses; ovaries orange—triangles.

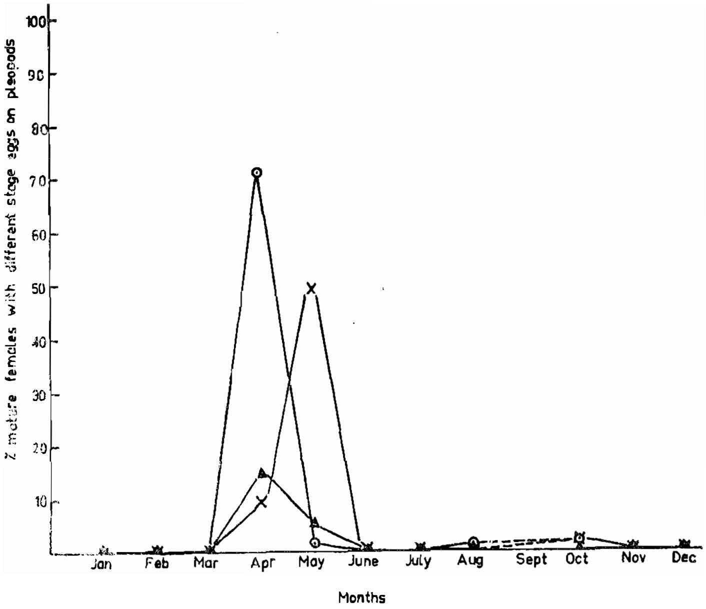

Fig. 15.—Percentages of mature, ovigerous females with eggs at different stages on the pleopods plotted against months for S. Dunwich samplings. Orange eggs—open circles; yellow eggs—triangles; yellow eggs with eyespots—crosses.

The minor breeding season in spring was also followed by early larval stages in the plankton in summer and by autumn post-larvae (c. 3 mm. carapace length) were collected which probably resulted from these earlier larval stages.

V. Discussion

The abundance and accessibility of *C. australiensis* in sheltered bays and estuaries along the east Australian coast make these areas favourable for studying callianassid ecology, and dense populations can be sampled effectively by a "yabby pump".

The use of live yabbies as bait by amateur fishermen suggested the possibility of over-exploitation of *C. australiensis*. During the present study the two main sampling sites were depleted by the present collections and those of bait diggers to such an extent that in one case (N. Wynnum) sampling was discontinued after ten months. The immense populations at other places in Moreton Bay show that "over-fishing" is restricted to the more accessible sites.

Most heavily exploited areas still give considerable yields. At N. Dunwich, one area c. 50 m.^{2} contributed c. 1,000 specimens per year for measurements in the present work and possibly ten times this number if the activities of bait diggers are included. This represents an annual yield of 200 specimens/m.^{2} from an area which contained c. 50 individuals/m.^{2} when the sampling programme began and c. 10/m.^{2} when it concluded. The rate of recruitment was evidently the most important influence counteracting human removal of yabbies.

The lack of progression of most modes in the data is also relevant to this concept of mobility of the species. A non-progressing mode implies negligible growth rate (which is unlikely) or balanced recruitment and loss in populations.

Theoretically, individuals could move between areas by burrowing, crawling on the surface of the substratum or by swimming. Replacement of large individuals in over-exploited areas (e.g., N. Dunwich) could be explained by surface crawling or burrowing, the latter being the more probable.

Sizeable populations are most probably restocked by small, post-larval, swimming individuals. The authors have not observed voluntary swimming of this type though local fishermen have reported one sighting of numbers of swimming yabbies near Bribie Island. According to Monod (1927) *Callianassa turnerana* White performs an annual mass swimming migration in the Cameroons which is known to the natives who collect these crustacea for food. In Moreton Bay, lack of evidence favours frequent small migrations rather than massive ones which would be conspicuous.

Large male *C. australiensis* (i.e., greater than c. 9 mm. carapace length) do not swim readily because of the weight of the enlarged cheliped. Large females and small individuals of both sexes (i.e., up to c. 9 mm. carapace length) can swim actively when removed from their burrows. Therefore, one would expect recruitment by swimming to be restricted to specimens other than the larger males. The ease with which juveniles can occupy existing burrows on removal from their own, and the fact that they are tolerated by an existing adult occupant again point to juveniles as the most likely migratory phase.

It is postulated therefore that (1) movement of small adults between areas may occur, possibly by swimming and (2) if movement of larger adults occurs, it is most likely to be a movement of females. If the second postulate holds, then the larger the individuals forming a population the greater the percentage of females to be expected. This expectation is fulfilled, as shown by the following data.

Area	*Largest mode of carapace length*		*sex ratio*
	♂	♀	(*% females*)
N. Wynnum	15	13	66.5
S. Dunwich	14	12	53.4
N. Dunwich	13	12	51.5

In other words a migration of predominantly sizeable females would explain in part variations in sex ratio between different sampling areas.

In the event of populations of predominantly large individuals being recruited by migration of smaller individuals, the sources of the latter and characteristics of their populations require consideration. Following the earlier investigations at N. Wynnum and N. Dunwich searches for populations of small individuals were made. None were found in the vicinity of N. Wynnum. At N. Dunwich small individuals formed a fraction of the population in the main yabby beds as evidenced by the suggestion of a mode at 8 mm. in Figure 8. In addition, small individuals were found in situations peripheral to the main beds. At S. Dunwich small individuals were common, and for this reason the later work was concentrated on this area. The main details of the seasonal changes in the population of small individuals have been given, and, from the progression of the mode, growth rates have been computed. It remains to consider whether this area shows indications of being a "nursery ground" from which more distant populations could be recruited.

Figure 9 shows that in spring the size of the mode corresponding to small individuals is relatively large, and that it declines progressively through summer and autumn. (In each case approximately the same total number of individuals was collected, so that a decline in numbers of juveniles is balanced by an increased proportion of larger specimens.) The only feasible explanation is that smaller specimens of both sexes move out of the sampled population at all seasons.

There are indications of the frequency/length curves for the juveniles being skewed in autumn as their modes approach the range 9-10 mm. This suggests some differential removal of these sizes, as postulated earlier. The curve for females is more skewed than that for males, which suggests a greater removal of females, again as postulated earlier.

It should be noted that differential removal will produce a slight retardation of the mode, so that the real growth rates are probably slightly in excess of those previously calculated.

The magnitude of recruitment to the population as a whole will depend upon the death rate. Evidence has been given suggesting a growth rate of about 9.5 mm. (carapace length) per year, and on this basis most of the sampled population are over a year old, and probably some would live longer than two years. This implies a rapid rate of recruitment, and as a corollary, that the effects of human exploitation will be less serious than with a slow growing population.

Based on the data and conclusions in the previous sections, the main events in the life cycles of Moreton Bay *Callianassa australiensis* can be summarized as follows:

Individuals derived from autumn eggs

Orange eggs, laid in early autumn, hatch by late autumn and the first larval stages (c. 1 mm. carapace length) appear in the plankton during early winter. Development continues until the beginning of spring when the sixth stage has a carapace length of c. 3 mm.

Early post-larvae (c. 4 mm. carapace length) also occur in the plankton in spring. In early summer (at a carapace length of 6 mm.) some can be collected in established yabby beds (e.g., S. Dunwich) while others establish new populations. About this time there is a change in the relationships of carapace length to total length which is possibly indicative of the onset of sexual maturity.

A moult in late summer, followed by growth to c. 8 mm. carapace length, precedes further changes in body proportions and development of gonads. This moult is probably of a precopulatory nature because the colour of the ovaries becomes orange soon afterwards and eggs are laid in the major breeding season (autumn) at a minimal carapace length of c. 8-9 mm.

Another moult for both sexes in early winter, after breeding activity, is followed by slight growth (carapace length 9-10 mm.). A third change in body proportions occurs at this stage and is more marked in the male where the increasing size of one cheliped is accompanied by an increase in carapace size.

A minor breeding season occurs in early spring and in late spring another moult is followed by growth (carapace length: males c. 13 mm., females c. 12 mm.).

The next event is the precopulatory moult (late summer) which leads to growth to the maximum size (carapace length: males 15-16 mm., females 14-15 mm.) and is followed by breeding activity in the major breeding season (autumn).

The onset of winter probably results in the death of these larger adults as the largest modes in carapace length now drop from 14 mm. (males) and 12 mm. (females) in autumn, to 12mm. (males) and 10 mm. (females) in winter.

The above then suggests a life span of two years from the time of hatching.

Individuals derived from spring eggs

The minor breeding season in spring gives rise to fewer ovigerous females than that during autumn and is followed by early larval stages in the plankton in summer. A few post-larvae (carapace length c. 3 mm.) occur in the plankton during autumn. Small numbers of juveniles (c. 3-5 mm. carapace length) appear in yabby beds in winter.

Further evidence of the development of these individuals is fragmentary. In the seasonal frequencies of each carapace length there are suggestions of modes in summer and autumn between the major modes. Based on the life cycle of individuals from autumn eggs, these "smaller modes" would certainly fit the expected growth of individuals developing from spring eggs. It is postulated therefore that these individuals undergo roughly the same type of developments as those derived from autumn eggs excepting for the time difference.

The "spring" individuals would attain a carapace length of c. 12 mm. during the autumn in which the second major breeding season of "autumn" individuals occurs. The winter following this autumn was suggested (because of the sudden change of modes) as the time of death of those specimens from autumn eggs. It is possible that some, if not all, of the "spring" individuals survive this winter, as evidenced by the rather large adults (carapace length: males c. 16 mm., females c. 15 mm.) which were collected occasionally.

The original suggestion of a life span of approximately two years is still considered to apply to "spring" individuals for only very rarely have "soft" very large specimens been seen.

VI. ACKNOWLEDGMENTS

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PLATE 1

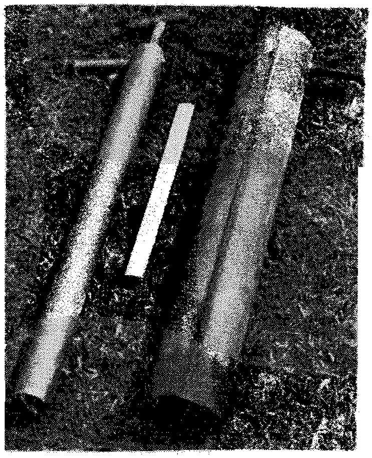

Fig. 1

Fig. 4

Fig. 2

Fig. 3

Fig. 5

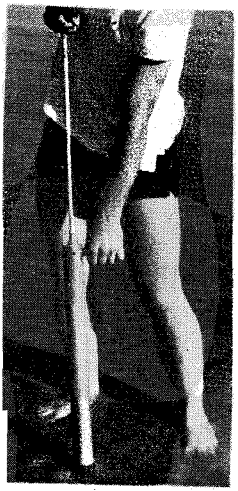

Fig. 6

Fig. 7

PLATE 1

FIG. 1.—The two models of "yabby pumps" sold commercially. Earlier model on right and later model on left. The scale is a one foot rule.

FIG. 2.—Earlier model "yabby pump" being pushed into substratum with thumb holes uncovered.

FIG. 3.—Thumb holes covered and pump being extracted.

FIG. 4.—Pump fully extracted, thumb holes uncovered and core of sand with yabbies to the left. The hole, filled with water, is seen to the right of the pump.

FIG. 5.—Later model "yabby pump" being pushed into substratum as the plunger is extracted.

FIG. 6.—Pump being extracted with plunger fully out.

FIG. 7.—Pump completely removed from hole (lower centre) and core of sand discarded (lower right) by pushing plunger down.

PLATE 2

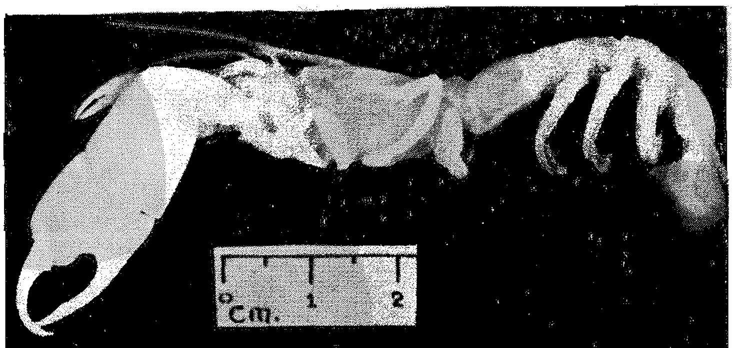

Fig. 1

Fig. 2

Fig. 3

PLATE 2

FIG. 1.—Adult male *C. australiensis* showing the male features of one enlarged cheliped, unbranched first pleopods and absence of second pair of pleopods.

FIG. 2.—Adult female *C. australiensis* showing the female features of less enlarged cheliped and biramous, hirsute pleopods of the first and second abdominal segments.

FIG. 3.—A series of typical larger chelipeds of *C. australiensis*. Those on the left are from males, those on the right from females. The lowermost pair are from immature specimens, the central pair from young adults, and the upper pair from fully mature adults.

PLATE 3

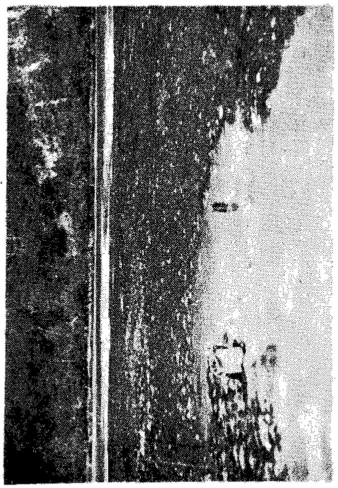

Fig.1

Fig.2

Fig.3

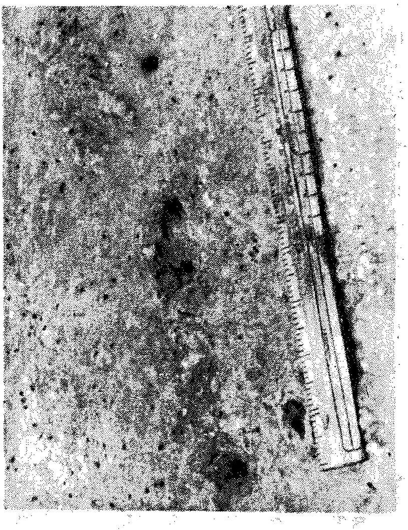

Fig.4

PLATE 3

Fig. 1.—A typical yabby bed at S. Dunwich. The darker area (centre) consists of *Zostera*-covered sand and the larger lighter areas "yabby circles" cleared of *Zostera*. The small light patches amongst the *Zostera* are mounds of sand excavated by yabbies. Mangroves colonise the upper levels of the sand flat (background). (Photograph taken at low tide from approximately mean tide level.)

Fig. 2.—Typical distribution of surface openings to burrows in a densely colonised yabby bed. The scale is a one foot rule in this and the following figures.

Fig. 3.—An isolated group of burrow openings in a sparsely colonised yabby bed.

Fig. 4.—An irregular row of burrow openings in a sparsely colonised yabby bed.