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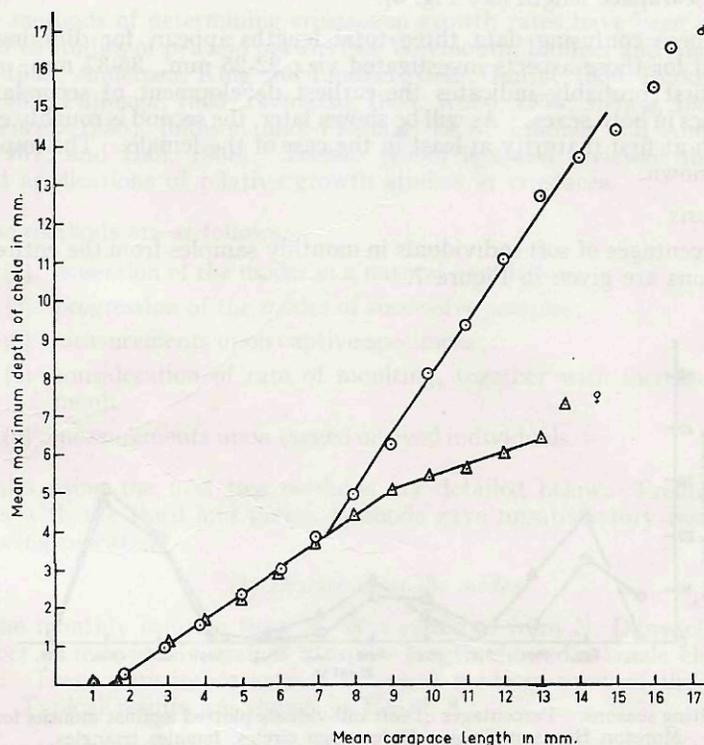
FIG. 6.—Mean maximum depths of larger chelipeds in mm., plotted against mean carapace lengths in mm. Males open circles, females triangles. The uppermost female and two uppermost male points are based on insufficient data.

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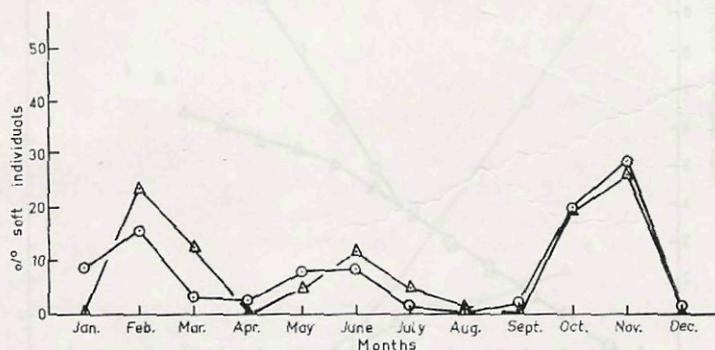
FIG. 7.—Moulting seasons. Percentages of soft individuals plotted against months for combined Moreton Bay samplings. Males open circles, females triangles.

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.
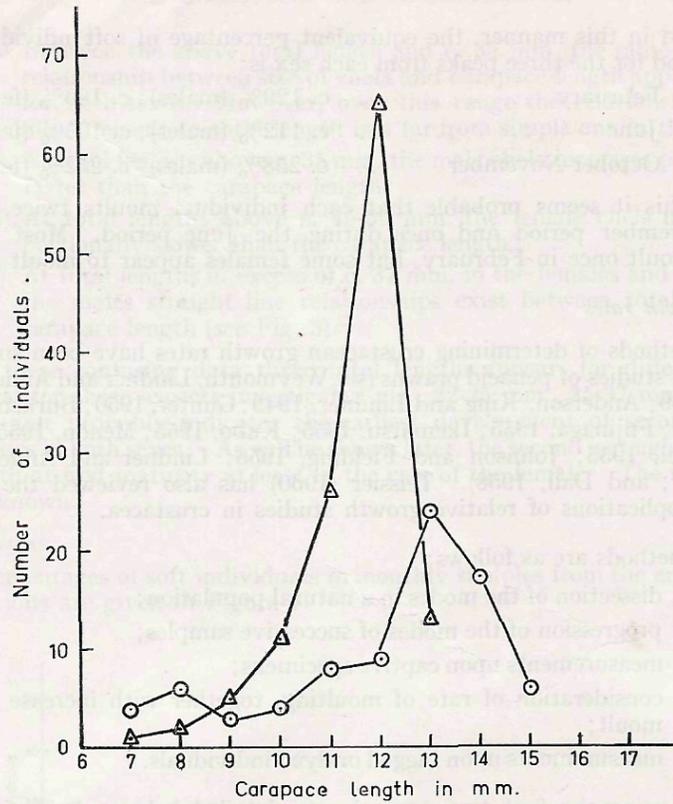
Fig. 8.—Typical modal results from a monthly sample (N. Dunwich, June, 1958). Number of individuals plotted against carapace lengths in mm. Males open circles, females triangles.
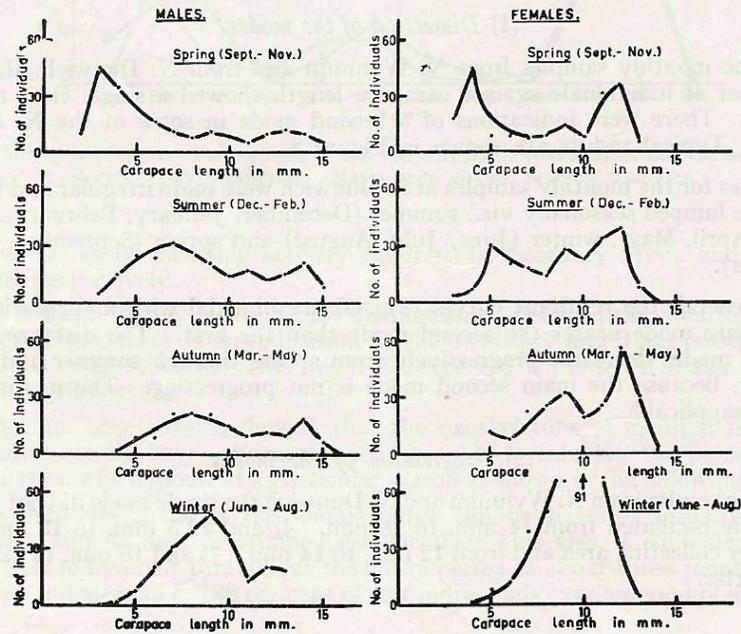
Fig. 9.—Seasonal modal results for S. Dunwich samplings. Number of individuals plotted against carapace lengths in mm. for each season.

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.):

<div style="margin-left:2em">

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

</div>

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:

<div style="margin-left:2em">

(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.

</div>
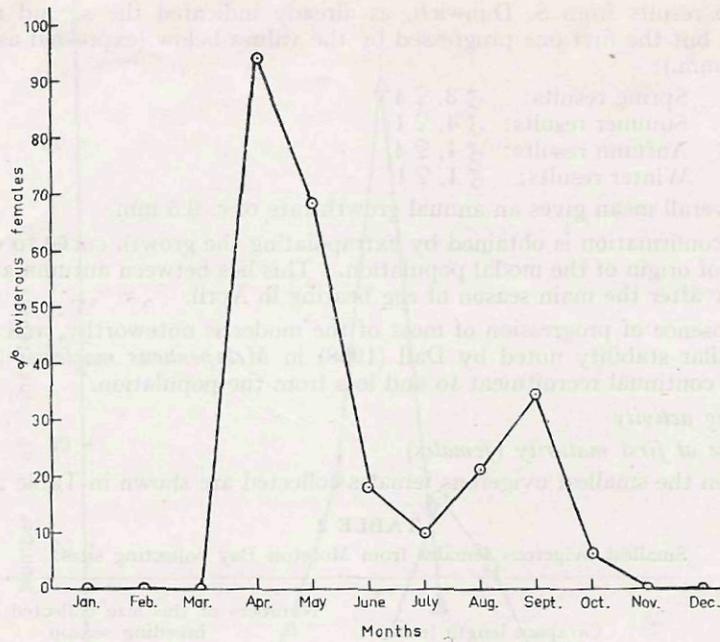
FIG. 10.—Percentages of ovigerous, mature females plotted against months for combined Moreton Bay samplings.
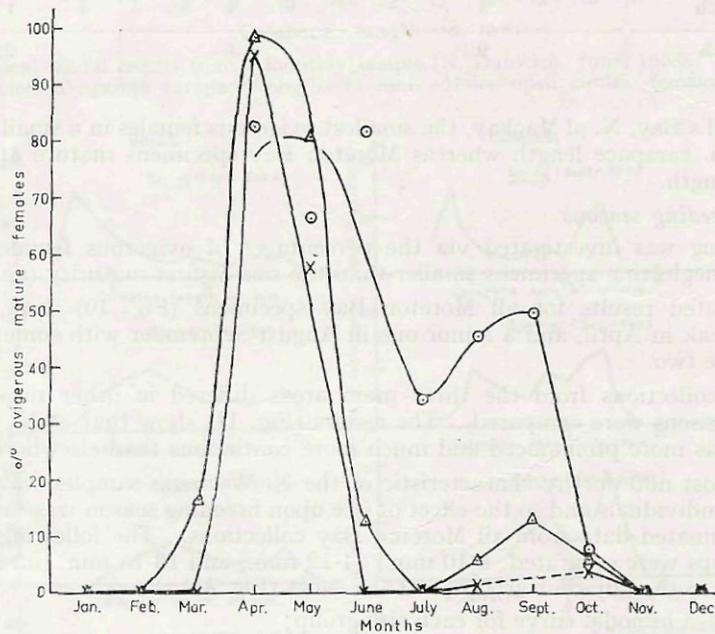
FIG. 11.—Percentages of ovigerous, mature females plotted against months for the three main sampling sites. N. Wynnum open circles, N. Dunwich triangles, S. Dunwich crosses. All curves smoothed visually.
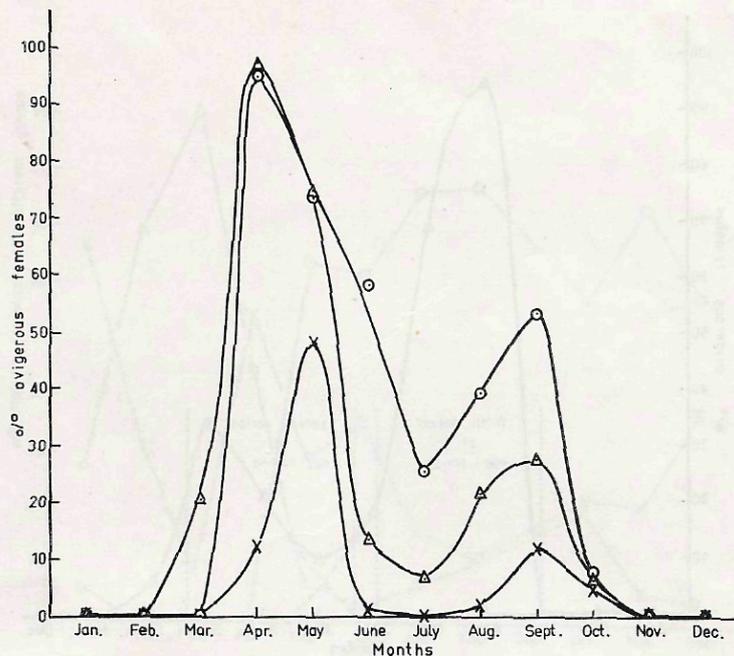
FIG. 12.—Effects of size upon breeding seasons. Percentages of mature, ovigerous females (*grouped by carapace lengths*) *plotted against months for combined Moreton Bay samplings:* 9-10 mm. carapace length crosses, 11-12 mm. carapace length triangles, and 13-15 mm. carapace length open circles.

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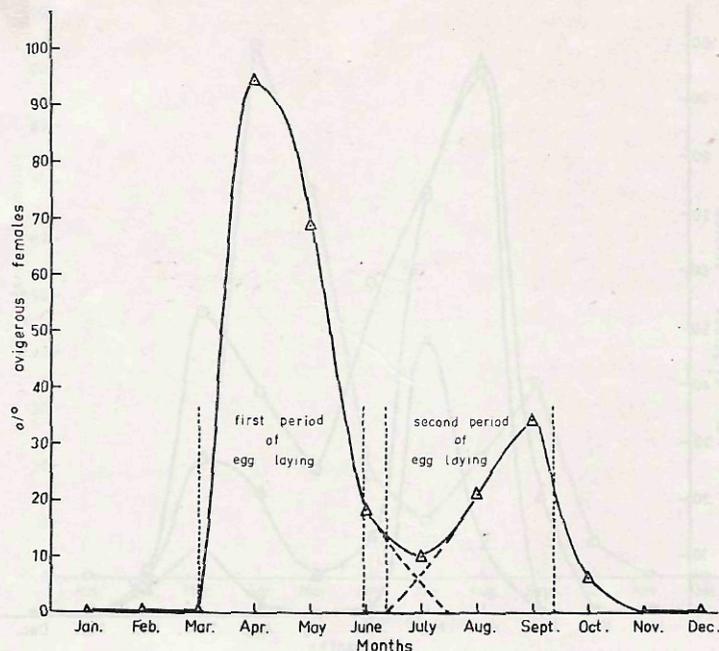
Fig. 13.—Breeding seasons adjusted to show periods of egg laying. Percentages of mature, ovigerous females plotted against months for combined Moreton Bay samplings.

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.
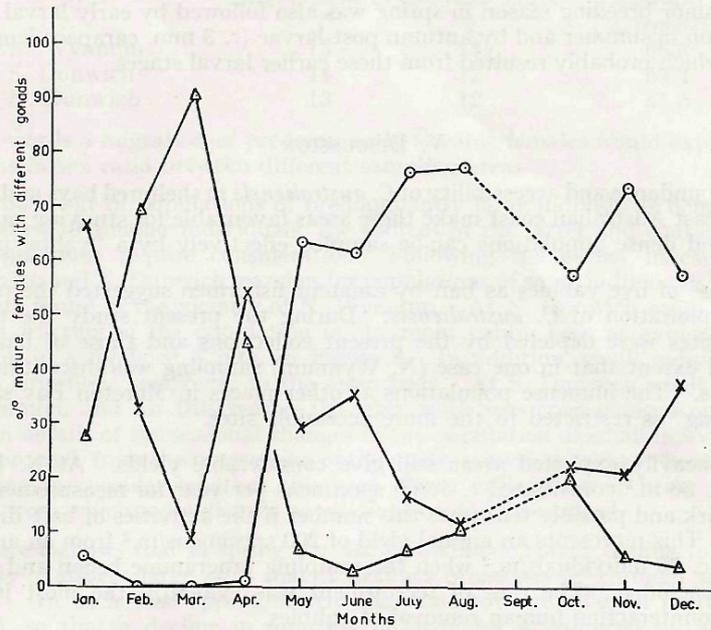
FIG. 14.—Percentages of mature females with gonads at different stages plotted against months for S. Dunwich samplings.   Ovaries transparent, white or cream—open circles; ovaries yellow—crosses; ovaries orange—triangles.
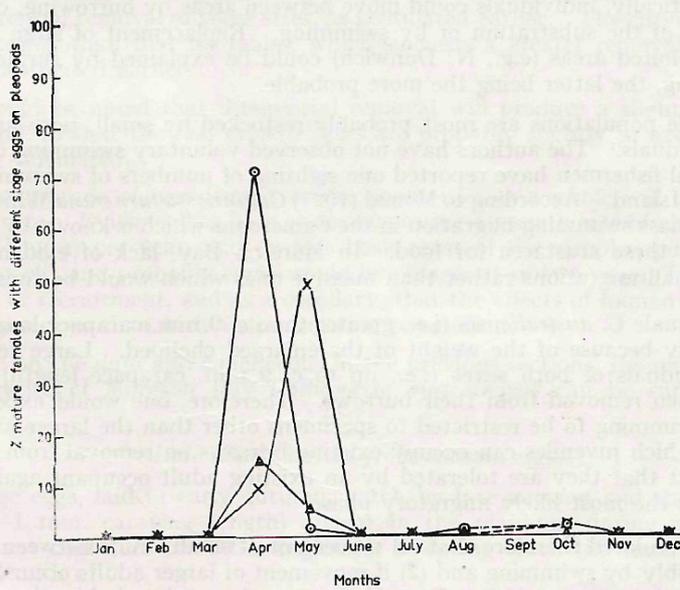
FIG. 15.—Percentages of mature, ovigerous females with eggs at different stages on the pleopods plotted against months for S. Dunwich samplings.   Orange eggs—open circles; yellow eggs—triangles; yellow eggs with eyespots—crosses.

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