Relative Growth of the abdomen and the carapace of the Shore-Crab *Carcinus maenas.**

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With 5 Figures in the Text.

Introduction.

In 1920 the senior author undertook some experiments on shore-crabs (*Carcinus maenas*) to see whether the development of their secondary sexual characters was altered by thyroid or pituitary feeding. To carry these out, it was first necessary to find the normal relative growth-rate of these characters, and a number of measurements were undertaken for the purpose. Some further measurements were made by the senior class in Zoology at Oxford as an exercise. By then, however, it had become apparent that the interpretation of the measurements of the normal crabs offered more interesting problems than the endocrine experiments, which turned out to be wholly negative, but that more accurate methods of measurement were necessary for their solution. Accordingly the junior author undertook to devise and carry out these measurements.

The common shore-crab can be strongly recommended as material for many types of investigation. For biometric work it offers the advantage of a hard skeleton. As class-material in biometric study it is cheap and easily handled. It is good for the study of growth-problems, since it has an "unlimited" growth and since the cast moults can be measured with as great an accuracy as the whole animal. It is easily kept in captivity far from the sea. Specimens up to 1 or 2 inches' carapace-length, kept in ½ to 1 inch of sea-water in covered finger-bowls or (cheaper !) in tongue or potted-meat jars, need only to be fed and have their water changed twice a week; and larger specimens can equally well be kept if larger receptacles are provided. A few preliminary trials indicate that injections into the muscles or haemocoel can be satisfactorily made through the

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arthrodial membranes at the base of the limbs, or between thorax and abdomen. The crabs can be kept healthy on meat or still better on fish, but will accept, and thrive on, a large variety of foods. Finally, it is an abundant and easily-obtained species, and it is apparently rather variable.

All specimens with a Sacculina externa were of course rejected, since sacculinisation is known to increase the breadth of the abdomen in both sexes. Some specimens with Sacculina interna are no doubt included in the population measured ; however, the error thus introduced will not be large, partly because such individuals are not common, partly because sacculinisation will not have had time to produce much effect on the abdomen before the parasite becomes external.

In larger individuals, the measurements were made with fine callipers. This gives a slight positive error, which is, of course, relatively larger in smaller specimens. Accordingly in these (up to about 9 mm. carapace length) the size of the parts to be measured was indicated on white paper by means of a camera lucida and a dissecting microscope, measured with a ruler, and the absolute size calculated from the known magnification.

Carapace length was measured in the mid-dorsal line. Abdomen-breadth refers to the breadth at the joint between the 5th and 6th abdominal segments.

Results.

The number of crabs accurately measured was 678. Most of them came from Plymouth, at various seasons of the year. In order to obtain some specially large animals, 53 large crabs were procured from Essex : as these came from another locality, their measurements are recorded separately. The distribution of the crabs was as follows :—

Plymouth crabs : unsexable (externally), 74 ; males, 270 ; females, 281. Essex crabs : males, 22 ; females, 31. The results of the measurements are shown in the subjoined Tables I and II. The individual measurements are not given, but the means for classes according to carapace-length.

Graphic presentation of the results is given in Figures 1 and 2, where the relative abdomen breadth (percentage of carapace length) is plotted for each sex.

It was not considered worth while calculating the standard deviation for each of these means. To give some idea of the range of variability, however, the extreme variants in either direction have been given (Table II).

It will be noted that in almost every class, the range of variation shown by the females is considerably greater than that of the males ; in the one exception, they are nearly equal. This is to be expected, since slight differences in the onset of the rate of differential female abdomen-growth would make a considerable difference in the ratios.

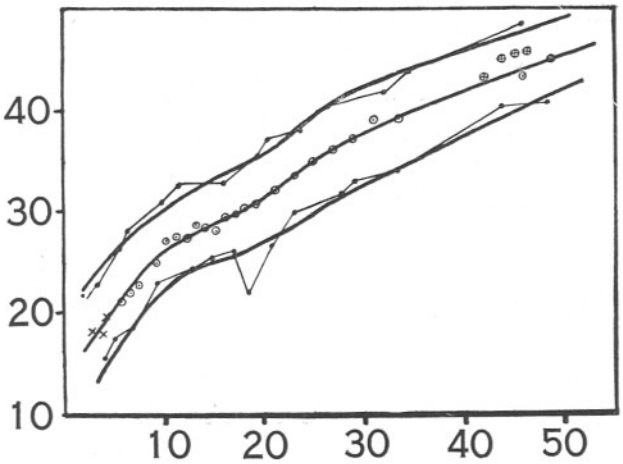

FIG. 1.

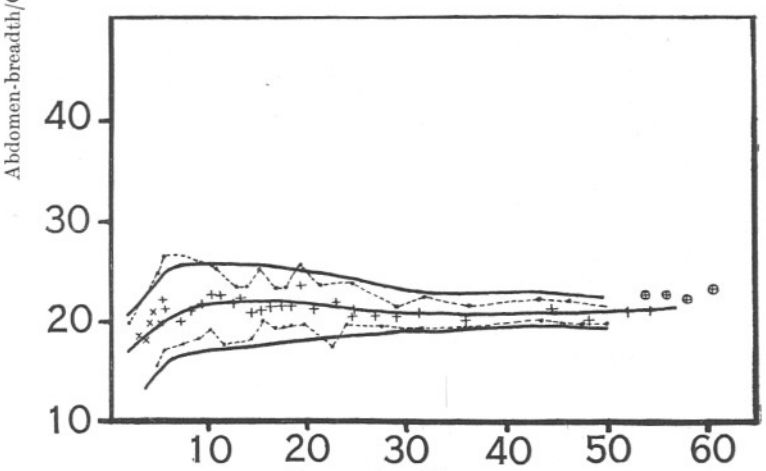

FIG. 2.

FIGS. 1 and 2.—The relative abdomen-breadth of female and male *Carcinus maenas*, against carapace-length.

× unsexable (in both figures).

⊙ Plymouth females. ⊗ Essex females.

\+ ,, males. ⊕ ,, males.

The extreme variants are also given, together with smoothed curves for the probable range of variation.

TABLE I.

ABDOMEN-BREADTH RELATIVE TO CARAPACE-LENGTH IN CARCINUS MAENAS.

(*a*) UNSEXABLE (74 specimens).

Class :— Carapace-l. (mm.)	Σ	Mean car.-l. (mm.)	Mean abd.-br. (mm.)	Mean $\frac{\text{abd.-br.}}{\text{car.-l.}}$ %
2·4–3·4	13	3·09	0·578	18·7
3·5–3·9	22	3·80	0·680	17·9
4·0–4·5	20	4·22	0·823	19·5
4·5–4·9	11	4·76	0·979	20·6
5·0–5·5	8	5·19	1·019	19·6

(*b*) MALES (292 specimens).

Plymouth crabs (270 specimens).

4·75– 6·0	11	5·50	1·238	22·5
6·0 – 7·0	6	6·37	1·224	19·2
7·0 – 8·0	16	7·51	1·48	19·7
8·0 – 9·0	14	8·41	1·75	20·8
9·0 –10·0	15	9·37	2·01	21·4
10·0 –11·0	10	10·36	2·31	22·3
11·0 –12·0	26	11·31	2·56	24·4
12·0 –13·0	12	12·63	2·72	21·5
13·0 –14·0	18	13·32	2·93	22·0
14·0 –15·0	15	14·34	2·95	20·6
15·0 –16·0	10	15·43	3·21	20·8
16·0 –17·0	14	16·35	3·47	21·2
17·0 –18·0	16	17·51	3·71	21·2
18·0 –19·0	6	18·34	3·93	21·4
19·0 –20·0	11	19·37	4·43	23·4
20·0 –22·0	13	20·73	4·56	21·0
22·0 –24·0	19	22·93	4·97	21·7
24·0 –26·0	9	24·58	4·95	20·2
26·0 –28·0	4	26·69	5·44	20·4
28·0 –30·0	3	29·03	5·93	20·4
30·0 –31·0	4	31·16	6·48	20·8
35·0 –37·0	4	35·75	7·13	19·9
43·0 –47·0	5	44·54	9·42	21·1
47·0 –51·0	4	48·35	9·63	19·9
52·0 –57·0	5	54·44	11·46	21·0

TABLE I (*continued*).

Essex crabs (22 specimens).

Class :— Carapace-l. (mm.)	Σ	Mean car.-l. (mm.)	Mean abd.-br. (mm.)	Mean $\frac{\text{abd.-br.}}{\text{car.-l.}}$ %
53·0 –55·0	9	53·98	12·09	22·4
55·0 –57·0	6	56·00	12·58	22·4
57·0 –59·0	4	57·87	12·73	22·0
60·0 –62·0	3	60·57	14·00	23·1

In plotting, the first 2 classes of the Plymouth males have been combined (Fig. 2).

(*c*) FEMALES (312 specimens).

(by 1 mm. carapace-length classes, except that the 8 mm. and 9 mm. classes have been combined, as there was only 1 specimen in the 8 mm. class.)

Plymouth crabs (281 specimens).

Σ	Mean Carapace-length mm.	Mean Abdomen-breadth mm.	Mean $\frac{\text{Abdomen-br.}}{\text{Carapace-l.}}$ %
12	5·56	1·16	20·9
16	6·52	1·45	22·2
14	7·41	1·67	22·6
12	9·32	2·30	24·7
15	10·37	2·80	27·0
16	11·35	3·11	27·4
17	12·33	3·37	27·3
23	13·29	3·81	28·6
19	14·35	4·06	28·3
12	15·31	4·29	28·0
19	16·35	4·82	29·4
15	17·36	5·15	29·6
15	18·16	5·48	30·2
7	19·34	5·93	30·6
6	20·33	6·72	32·1
10	21·51	6·82	
12	22·40	7·54	33·6
8	23·34	7·76	
6	24·33	8·33	35·0
5	25·52	9·16	
10	26·45	9·59	35·9
6	27·65	9·79	

TABLE I (*continued*).

Σ	Mean Carapace-length mm.	Mean Abdomen-breadth mm.	Mean $\frac{\text{Abdomen-br.}}{\text{Carapace-l.}}$ %
2	28·45	10·40	37·2
3	29·30	11·03	
4	30·55	11·62	38·8
4	31·49	12·46	
3	32·37	12·75	
5	33·32	12·70	38·9
4	34·33	13·56	
1	43·50	17·50	
2	45·30	19·20	43·2
1	46·30	19·90	
1	50·20	23·70	
	Essex crabs (31 specimens).		
4	42·10	18·15	43·1
7	43·56	19·54	44·8
6	44·38	19·88	44·8
6	45·28	20·50	45·3
4	46·43	21·13	45·5
4	48·75	21·88	44·7

In plotting (Fig. 1), the Plymouth females have been combined into 2 mm. classes from carapace-length 20 to 33 mm., and the last 4 classes combined into one; and the 8 and 9 mm. classes have been combined in the table, since only one crab of the 8 mm. class was found. Of the Essex females, the 43 and 44 mm. classes, and also the 45 and 46 mm. classes, have been combined in plotting.

When the means are plotted on a double logarithmic grid (Fig. 3) further information is acquired. In general, the points lie along good approximations to straight lines, indicating that constant differential growth-ratios are maintained over long periods of the life-history. The curve for the unsexed is prolonged by that for the females up to a carapace-length of between 17 and 20 mm.; during this period the growth-coefficient of the abdomen is about 1·26. From this point onwards, the relative growth of the female abdomen increases, and remains steady at about 1·42 up to the largest specimens found.

From the moment the sexes are distinguishable, the male curve diverges from the female. It also shows two phases; the growth-coefficient for the first is about 1·07, for the second about 0·94. It is more difficult to

distinguish the exact size at which the change in growth-ratio occurs in the males than in the females, since the male points are more irregular. At any rate it takes place at approximately the same phase in the life history, certainly between 14 and 21 mm. carapace-length. If, as would seem probable on *a priori* grounds, the change occurs at sexual maturity, we should expect there to be a considerable variation in the absolute size at onset.

TABLE II.

Maxima and Minima for Abdomen : Carapace Ratio.

Maxima.				Minima.			
Class. Car.-l., mm.	Carapace-length	Abd.-br. / Car.-l. %		Class. Car.-l., mm.	Carapace-length.	Abd.-br. / Car.-l. %	
FEMALES.							
> 40	45·8	48·2		> 40	48·3	40·6	
	44·4	48·1			43·5	40·2	
30–35	31·75	41·75		30–35	33·5	34·0	
	34·5	43·5		25–30	27·5	31·8	
25–30	25·6	38·3		20–25	21·5	28·4	
	26·25	40·4			22·0	26·4	
20–25	20·25	37·0		17–20	17·0	23·6	
	23·5	37·9			18·25	21·9	
17–20	19·5	35·5		15–17	14·75	25·4	
15–17	16·0	32·8		11–13	11·0	24·4	
13–15	14·75	30·5		9–11	9·1	22·8	
11–13	13·0	30·8		5–9	5·8	20·7	
11–13	11·50	32·6					
UNSEXED.							
4·6–5·5	5·5	27·3		4·6–5·5	5·0	17·7	
4·0–4·5	4·1	26·4		4·0–4·5	4·1	15·9	
3·5–3·9	3·6	22·2		3·5–3·9	3·9	15·4	
3·0–3·4	3·4	21·6		3·0–3·4	3·1	16·1	
3·0	2·4	19·4					

Up to the size of 22 mm. carapace-length, the variation-curves for male and female overlap, the least male-type males having broader abdomens than the least female-type females.

It is of considerable interest to find the growth-ratio during the earliest (unsexed) phase apparently identical with that of the first female phase.

It would seem difficult to escape the conclusion that the growth-ratios of the male abdomen change not once but twice, the first time at carapace-length about 5 mm., whereas that of the female only changes once. It

would however be desirable to check this result by measurement of specimens unsexable externally, followed by sexing by means of dissection.

After a large number of measurements had been taken, it was realised that perhaps carapace-breadth would have been a better means of absolute

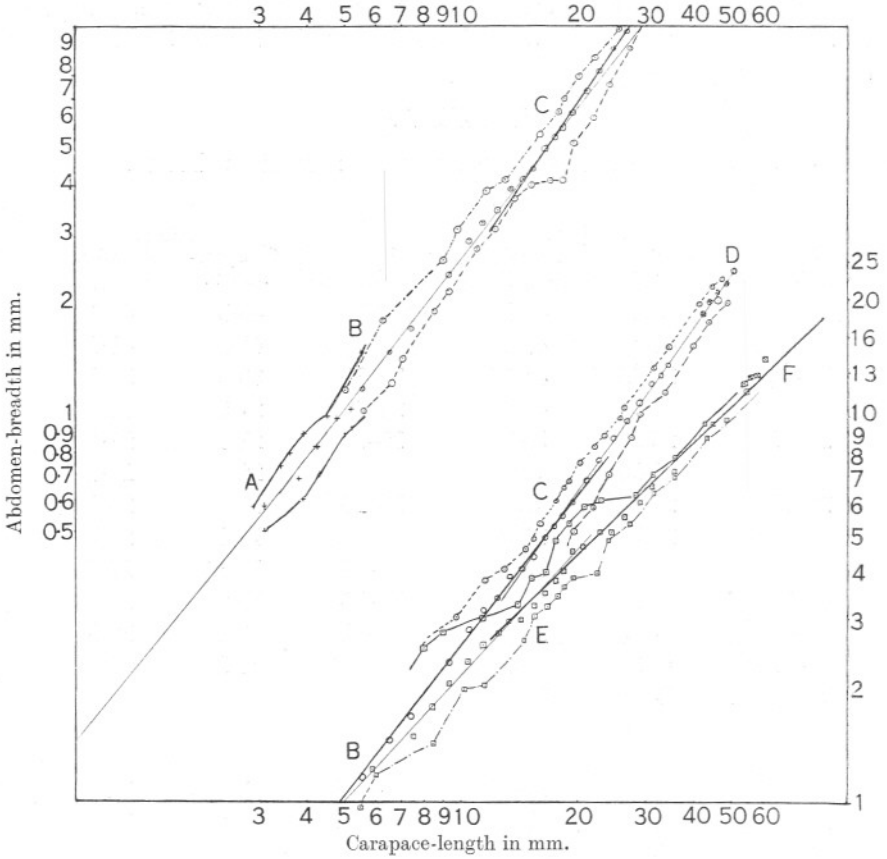

FIG. 3.—Double logarithmic plot of abdomen-breadth against carapace-length in *Carcinus maenas*. Above (abdomen-breadthscale to left) the curve for unsexable crabs (+) and the first part of that for females (⊙). Below (abdomen-breadth scale to right) the curves for females (⊙) and males (⊡).

A–B, unsexable period.
B–C, 1st female period.
C–D, 2nd female period.
B–E, 1st male period.
E–F, 2nd male period.

In addition to the means, the extreme variants are also given.

size than carapace-length, since in that case one would be comparing two breadths, instead of a breadth with a length. Accordingly, in the case of the last 201 animals measured, the greatest carapace-breadth was taken in addition to the other two measurements. The following results were found.

TABLE III.

THE RELATION OF CARAPACE-LENGTH TO CARAPACE-BREADTH IN 201 SPECIMENS FROM 2 TO 52 MM. CARAPACE-LENGTH.

Class; car.-l., mm.	Σ	car.-l.	car.-br.	car.-br. / car.-l. % mean	range.	Σ	car.-l.	car.-br.	car.-br. / car.-l. % mean	range.
	Unsexed (50 specimens).									
2–4	18	3·54	4·13	116·7	(103–136)					
4–6	32	4·69	5·56	118·5	(110–125)					
	Males ♂ (66 specimens).					Females ♀ (85 specimens).				
5–10	24	7·35	8·88	121·0	(112–127)	37	6·88	8·37	121·6	(116–132)
10–15	12	13·80	17·19	124·6	(121–130)	10	12·80	15·97	124·8	(120–130)
15–20	12	17·13	21·96	128·2	(126–130)	21	17·90	23·37	130·0	(125–135)
20–25	8	22·40	29·33	130·5	(128–133)	9	22·19	28·98	130·6	(129–132)
25–30	5	26·60	34·34	129·8	(128–133)	3	26·77	35·07	131·0	(130–133)
30–35	1	31·6	41·1	130·1		3	32·0	31·3	129·1	(127–133)
35–40	2	36·4	48·2	132·5		—	—	—	—	
45–55	2	49·7	66·8	134·5		2	51·7	67·8	131·1	

These results have been plotted in two ways: (*a*), (Fig. 4) the relative carapace-length against absolute carapace-length; (*b*) absolute carapace-breadth against absolute length, on a double logarithmic grid. The mean percentage (relative) carapace-breadth increases from 116·7 to nearly 135, an increase of about 15%. The means for the females are at first slightly above those for the males, but much greater numbers would be needed to establish this point significantly. (The numbers for the last points, from class 25–30 mm. onwards, are too certainly small to warrant attaching any importance to sexual differences.)

The range of variation in percentage carapace-breadth is considerable,

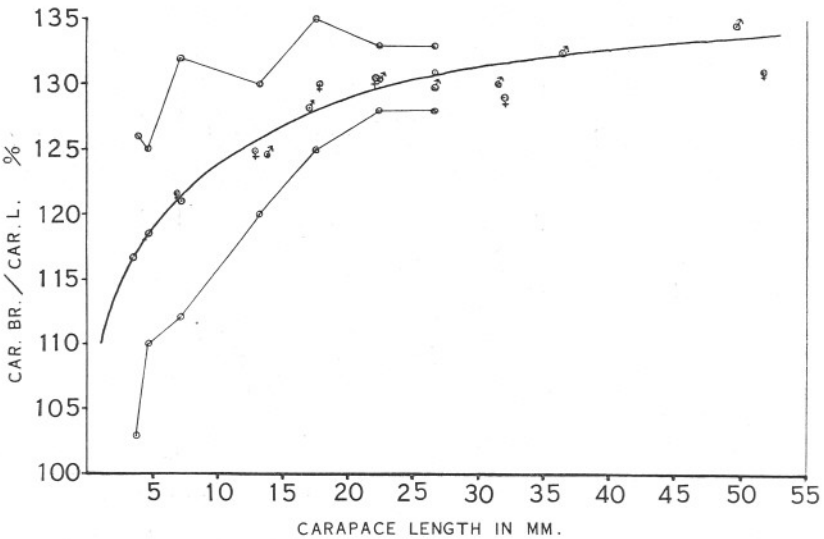

FIG. 4.—The alteration in relative carapace-breadth with absolute size. The mean values are given for unsexed, ⊙; females, ♀; and males, ♂. In addition the extreme variants, irrespective of sex, are given up to 28 mm. carapace-length.

being 23 for the smallest specimens, and diminishing to 10, in spite of increased numbers, by the 15–20 mm. class.

On the double logarithmic plot (not reproduced) the points fall on to a very close approximation to a straight line, whose inclination gives a value of 1·06 or just below, for the growth-coefficient of carapace-breadth relative to carapace-length. The points for the last three classes fall slightly below the line, giving a growth-coefficient of unity or slightly over; but they comprise too few specimens to enable us to say for certain that there is any real change in the growth-ratio. Extrapolation of the curve downwards enables us to say that at carapace-length 1 mm., the carapace-breadth should be 1·1. This is indicated on the graph for percentage values.

By using the ratios thus obtained as a correction coefficient, it was possible to prepare a graph (not here reproduced) of the relation between abdomen-breadth and carapace-breadth. As was to be expected from the regularity of the relation between carapace-breadth and carapace-length, this graph was essentially similar to those constructed with carapace-length as the standard.

Discussion.

Extended discussion of these results need not be undertaken here, as the theoretical bearings have been discussed elsewhere (Huxley 1927, etc.).

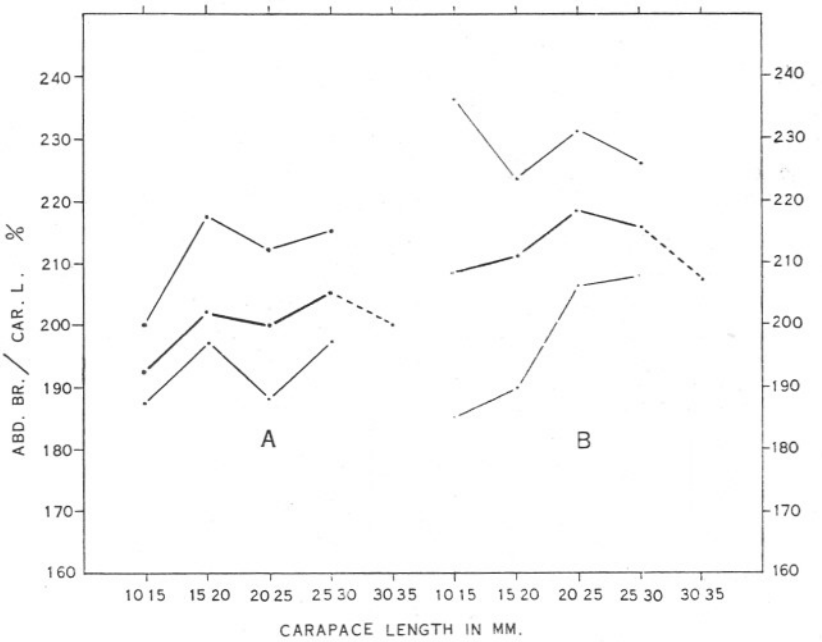

Fig. 5.—Seasonal variation in abdominal-breadth. Relative abdomen-breadth of male crabs from Plymouth (mean and range), A, in June, on left; B, in October, on right.

We need only stress the fact that in regard both to abdomen-breadth and carapace proportions, Carcinus has no fixed proportions in either sex, although the changes are more obvious in regard to the female abdomen. Since these animals show unlimited growth, there is not even any set of proportions which we can regard as adult or in any sense definitive. All that is fixed about the proportions of the shore-crab is their rate of change, as given by the growth-coefficients of the various organs.

One point deserves mention. In the Fiddler crab, Uca, the female abdomen grows heterogonically through all the early periods of life,

but after a certain time approaches the isogonic type (Morgan, 1923, and Huxley, 1924). The difference between this species and Carcinus is presumably correlated with the fact that in Uca the abdomen of the large females touches the bases of the legs on either side, whereas in Carcinus in the largest specimens I have seen there is still a considerable gap between lateral margin of abdomen and leg-bases—but by what means the abdomen growth is slowed down at the correct moment we do not know.

The matter is complicated, however, by the fact that in Pinnotheres, the pea-crab, the female abdomen continues to increase in relative size throughout life, even though it comes to overlap the bases of the legs very considerably (see the illustrations in Atkins, 1926 ; and Huxley, 1931).

A minor point is the apparent seasonal variation in the relative size of the male abdomen. The following table gives the results for 73 of the male crabs measured late in the investigation, all of which were taken at Plymouth, but 23 in early June, 50 in October.

The results are set forth in Table IV and Figure 5.

It will be seen that the October males have a consistently higher relative abdomen-breadth. As possible explanation of this, it may be suggested that after the breeding season a non-breeding phase sets in in which the male characteristics tend somewhat in the direction of the female ; this is known to occur in regard to certain species of Inachus as regards the male chela (G. W. Smith, 1906, and Shaw, 1928).

TABLE IV.

Relative abdomen br. $\left(\frac{\text{abd. br.}}{\text{car-l.}}\right)$ %, males.

Classes (mm. car. l.)	June. No.	Mean.	Max.	Min.	October. No.	Mean.	Max.	Min.
10–15	6	19·4	20·0	18·8	21	20·8	23·6	18·6
15–20	6	20·2	21·7	19·7	13	21·0	22·3	19·0
20–25	5	20·0	21·2	18·9	11	21·8	23·2	20·6
25–30	5	20·6	21·5	19·7	4	21·6	22·6	20·8
30–35	1	20·1			1	20·7		

Feeding Experiments.

With regard to the feeding experiments, mentioned in the introduction, a few comments may be made in spite of the results being wholly negative.

Table V gives the percentage increases at the moults for the three classes of the thyroid-fed, the pituitary-fed, and the control animals.

At first sight it may seem surprising that crabs fed exclusively for periods of 6 to 12 months and over on fresh ox-thyroid or ox-pituitary should exhibit no changes in growth or other characteristics as compared with controls fed on fresh fish. As regards the thyroid, however, the work of

Romeis (1925) has since shown that we should not expect any results of an endocrine nature to be obtained from feeding experiments with crustacea. He found that in the crayfish the active principle of the thyroid hormone was destroyed by the digestive enzymes, instead of being absorbed unchanged as in vertebrates, and we may presume that the same holds true for other Decapoda. Any experiments on the effect of thyroid upon crustacea should therefore be made by means of injection of extracts.

TABLE V.

GROWTH MADE BY CRABS FED ON FRESH FISH, FRESH OX-THYROID AND FRESH OX-PITUITARY, OVER PERIODS OF 1 OR 2 MOULTS.

		Initial carapace-length. mm.	1st moult, % increase.	2nd moult, % increase.
CONTROL		9·0	23·4	27·0
		10·9	20·2	19·8
		11·6	24·4	25·2
		14·1	26·2	23·6
		15·2	22·9	21·3
		14·0	18·6	—
	Mean		22·6	23·4
THYROID		9·1	27·6	24·1
		14·4	21·5	20·6
		15·5	25·8	23·6
		16·2	27·6	10·6
		17·2	26·8	17·0
		14·1	20·6	
		15·7	20·4	
		16·1	26·1	
		18·5	18·8	
		19·2	18·7	
	Mean		23·4	19·2
PITUITARY		13·7	23·5	25·4
		15·0	23·4	20·6
		15·4	25·4	21·2
		18·4	23·4	20·7
		13·8	24·4	
		14·6	24·4	
		15·0	25·3	
		16·9	23·6	
		17·9	24·6	
	Mean		24·2	22·0

The mean increase in carapace-length for all first moults is 23·5%; for all second moults, 21·5%; for all moults taken together, 22·8%.

Przibram has contended that arthropods in general tend to double in weight (bulk) at each moult. For an animal remaining constant in all its proportions, the percentage increase in a linear dimension needed to fulfil this condition is almost exactly 26%: ($\sqrt[3]{2}$=1·26). In Carcinus, we have already seen that carapace-breadth is increasing a little faster than carapace-length; it is also certain from analogy with other crustacea that the growth of at least the larger limbs will be at a slightly higher rate than that of the carapace. The increase of carapace-length at each moult needed to give a doubling in weight should therefore be slightly less than 26%. The figures actually found thus support Przibram's contention.

SUMMARY.

1. In regard to relative abdomen-breadth and relative carapace-breadth, the common shore-crab *Carcinus maenas* in both sexes exhibits a continuous change of proportions throughout life, from small animals of 2 mm. carapace-length to the largest obtainable (over 50 mm. carapace-length).

2. The parts measured exhibit constant differential growth-ratios (growth-coefficients) relative to carapace-length taken as standard, over long periods of the life-history.

3. The approximate growth-coefficients are as follows, relative to carapace-length:

Carapace-breadth, 1·06. This appears to be constant throughout the range of size measured, with a possible decline to nearly unity at large sizes.

Abdomen-breadth.

Crabs unsexable externally (2–6 mm. carapace-length), 1·26.
Females: early phase, 1·26; late phase, 1·42.
Males: early phase, 1·07; late phase, 0·94.

The early phase begins as soon as the sexes can be distinguished. The onset of the late phase may be presumed to be correlated with sexual maturity. In females it occurs certainly between 17 and 20 mm. carapace-length, in males between 14 and 29 mm.

4. There are indications of seasonal and local differences in relative abdomen size.

5. Feeding crabs of 9 to 22 mm. carapace-length solely on fresh ox-thyroid or fresh ox-pituitary for periods up to a year produces no change in growth-rate or in secondary sexual characters as against controls fed on fresh fish.

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