THE BIOLOGY OF THE BURROWING CRAB, *CORYSTES CASSIVELAUNUS*

by

R.G. HARTNOLL

Marine Biological Station, Port Erin, Isle of Man, Great Britain

ABSTRACT

Corystes cassivelaunus (Brachyura, Corystidae), a crab which burrows in clean sublittoral sand, was investigated at several inshore locations around the Isle of Man. It usually buries itself so as to leave little or no external sign of its presence. Immature crabs remain buried by day throughout the year, as also do mature crabs except during the breeding season from April to June. It is probable that *Corystes* emerges nocturnally to forage over the surface of the sand. The morphology of the respiratory system, and the respiratory behavior patterns, are both modified on account of the burrowing habit. The food consists almost entirely of burrowing invertebrates, predominantly lamellibranchs, polychaetes and amphipods. There is a puberty-moult in each sex, which is marked by morphological changes, and following which the crab becomes sexually mature. There is no post-puberty moulting. The terminal anecdysis is maintained by production of moult inhibiting hormone from the eyestalk, and consequently eyestalk removal induces pro-ecdysis and attempted ecdysis in mature crabs. Ovulation occurs in May to July, and the larvae hatch in March and April: thus incubation takes about ten months. Females breed for several successive years. Of the various organs studied all exhibited simple allometric growth except for the chelae of post-puberty males. It is postulated that this is due to their inability to achieve the very high size increments required at the puberty-moult in order to do this.

INTRODUCTION

Corystes cassivelaunus (Pennant) is the sole member of the genus *Corystes,* and the only representative of the Corystidae found in European waters. It is a boreal/warm-temperature species distributed on the eastern side of the Atlantic from 37°N on the coast of Portugal to 59°N on the west coast of Sweden. In the Baltic it penetrates only as far as the northern Kattegat, while in the Mediterranean it is recorded from the Strait of Gibraltar along the northern shores as far as the Adriatic, and from the Aegean. It is distributed generally around the British Isles, though there are no records from the northern half of Scotland. *Corystes* is restricted to substrates of clean sand and is normally sublittoral, having been found at depths down to 100 m. It is morphologically unusual in two respects: the respiratory system is extensively modified in connection with the burrowing habit, and there is an extreme sexual dimorphism of the chelae.

The present investigation was carried out around the Isle of Man on three areas of inshore sand — Port Erin Bay, Fleshwick Bay and Laxey Bay. In each of these locations the clean sand extended down to about 15 m, the majority of collections and observations being made between 5 m and 10 m in Port Erin Bay. Collecting was normally accomplished by diving, by which means live crabs could be captured, and in addition the delicate cast integuments found on the surface of the sand could be brought back intact. In situ observations on behavior were made in the same way. Other material was obtained with a 4 m beam trawl, and at Laxey Bay a number of *Corystes* were recovered from the stomachs of cod which were caught while feeding on the sandy bottom. A standard technique was developed to make a rough estimate of the abundance of unburied crabs at different times of the year. Two divers swam side by side over a set course of approximately 400 m running north east from the outer end of Port Erin breakwater: they collected or counted all of the crabs or cast integuments which they encountered.

After collection some of the crabs were kept alive in the laboratory for observations or experiments. They were maintained in tanks with a layer of sand on the bottom, provided with an open circulation of sea water at the ambient sea temperature, and fed twice weekly on mollusc muscle (usually *Pecten maximus*). They survived

well for periods of several months. The remaining material was preserved for subsequent examination: the crabs were narcotised in fresh water, fixed in 5% sea water formalin for 24 hours, and then stored in 50% ethylene glycol. Any tissues needed for histological study were dissected from freshly killed crabs and fixed in Bouin. A series of standard measurements were made on each crab or cast integument.

1. The length of the carapace, from the base of the notch in the rostrum to the middle of the posterior border.
2. The length of the chelar propodus, from the tip of the fixed finger to the articulation with the carpus.
3. The maximum width of the fifth segment of the abdomen.
4. The maximum length of the first pleopod of the male, measured in situ along the abdominal face.

BURROWING HABITS AND RESPIRATORY MODIFICATIONS

Corystes spends much of the time buried in the sand. It can burrow quickly: by digging with all four pairs of legs and using its chelae to push the sand away from its ventral surface it descends backwards into the sand. Given a sufficient depth of sand normally it will at most leave only the tips of the antennal flagellae exposed, often descending further until the tips of the flagellae are flush with the surface. In the latter event the only evidence of the crab's presence is a small opening in the sand 1—2 mm in diameter: this is difficult to spot in a tank, and proved impossible to locate whilst diving. During the breeding season males often burrow less deeply, so that portions of the chelae (the carpus, and adjacent regions of the merus and propodus) remain above the surface to reveal the location of the crab. In the laboratory, at least, some specimens burrowed so that the ends of their antennae were several cm below the surface of the sand leaving no external sign of their presence.

It is not clear exactly what proportion of its time *Corystes* spends buried in the sand. An analysis of all samples (table I) reveals that they were found abundantly above the surface only from April to June, which is the mating season of this crab (Hartnoll, 1968). They begin to appear in March, the males somewhat earlier than the females, are present in large numbers in the following three months, and a few remain in July. From August to February they are very scarce, though the single dive made in January did yield a surprisingly large sample of males. A further point of interest is that of the 151 male and 108 female crabs collected, all except three were in the final sexually mature instar. Thus on the grounds sampled immature crabs were virtually never found on the surface of the sand, while mature ones were encountered only during the mating season. Either these absent crabs had migrated elsewhere, or else they were buried and so could not be collected by the methods available. Three points argue against the first alternative:

1. The areas investigated are all discrete areas of clean sand, surrounded for considerable distances by substrates of mixed coarse gravel and muddy sand. No *Corystes* were ever found on these other quite unsuitable bottoms.
2. The cast integuments of immature crabs were found on the clean sand grounds throughout the year, so they must inhabit these grounds despite being collected so rarely.
3. Immature *Corystes* were obtained from the stomachs of cod which had been feeding on the Laxey Bay grounds, although none could be obtained by diving.

Thus it seems evident that both immature and mature crabs are present on the clean sand areas throughout the year, but that with the exception of mating individuals they remain buried. When diving various efforts were made to locate these

Table I. The mean number of live crabs and cast integuments collected per dive in each month of the year.

	No. of dives	Average no. of male crabs	Average no. of female crabs	Average total crabs	Average no. of male casts	Average no. of female casts	Average total casts
Jan.	1	10	—	10	—	—	—
Feb.	1	1	—	1	4	7	11
Mar.	5	3.8	1.4	5.2	0.6	0.2	0.8
Apr.	3	10.3	12.6	23	2	0.3	2.3
May	4	15+	11+	26+	1	1.2	2.2
Jun.	2	16+	9.5	26+	—	—	—
Jul.	2	2.5	0.5	3	2.5	0.5	3
Aug.	3	0.6	—	0.6	—	—	—
Sep.	2	—	—	—	0.5	—	0.5
Oct.	1	—	—	—	—	—	—
Nov.	2	—	—	—	—	—	—
Dec.	2	0.5	—	0.5	0.5	—	0.5

buried crabs, either by digging at what appeared to be antennal openings in the sand, or by random excavation using a small air lift, but both were unsuccessful. This was perhaps because they occur at a relatively low density: on the basis of the number observed during the time of maximum surface activity a generous estimate would be one to every 50 square metres of bottom. Garstang (1896) observed that his captive specimens remained buried by day, becoming active above the surface only by night. I likewise made some observations, and the crabs concerned did exhibit a marked nocturnal activity rhythm for several days after capture. However, this soon broke down, perhaps because of the effects of captivity, or possibly because the specimens used were of necessity caught during the mating season. In an attempt to clarify the situation a series of dives were made in Port Erin Bay by night, well outside the mating season, at a time when *Corystes* was very rarely encountered by day. None were found on these dives, although other crabs were readily seen and captured. Thus for the present the question of nocturnal surface activity is still undecided.

The cast integuments were usually found intact, half buried in the sand with the dorsal side uppermost, presumably in the position adopted during ecdysis. So it appears that they come to the surface to moult, where the room and freedom would be an advantage, the vulnerable post-moult crab burrowing for protection as soon as it is able. Ecdysis was not observed, probably taking place at night.

Another feature having a bearing upon the burrowing habits is the presence of epiphytic growths on the integument. These consisted of small filamentous and thalloid green algae, barnacles and naked colonial hydroids, none of which would be able to grow while the crab was buried for all or most of the time. Immature crabs or their cast integuments never bore epiphytes: as already seen they were very seldom found above the surface. The mature specimens obtained between January and April were likewise nearly all devoid of epiphytes, though there was sometimes a tuft of algae growing from the tip of the antennae which had presumably been exposed while the crab was otherwise buried. From May onwards specimens appeared with algal growths, usually

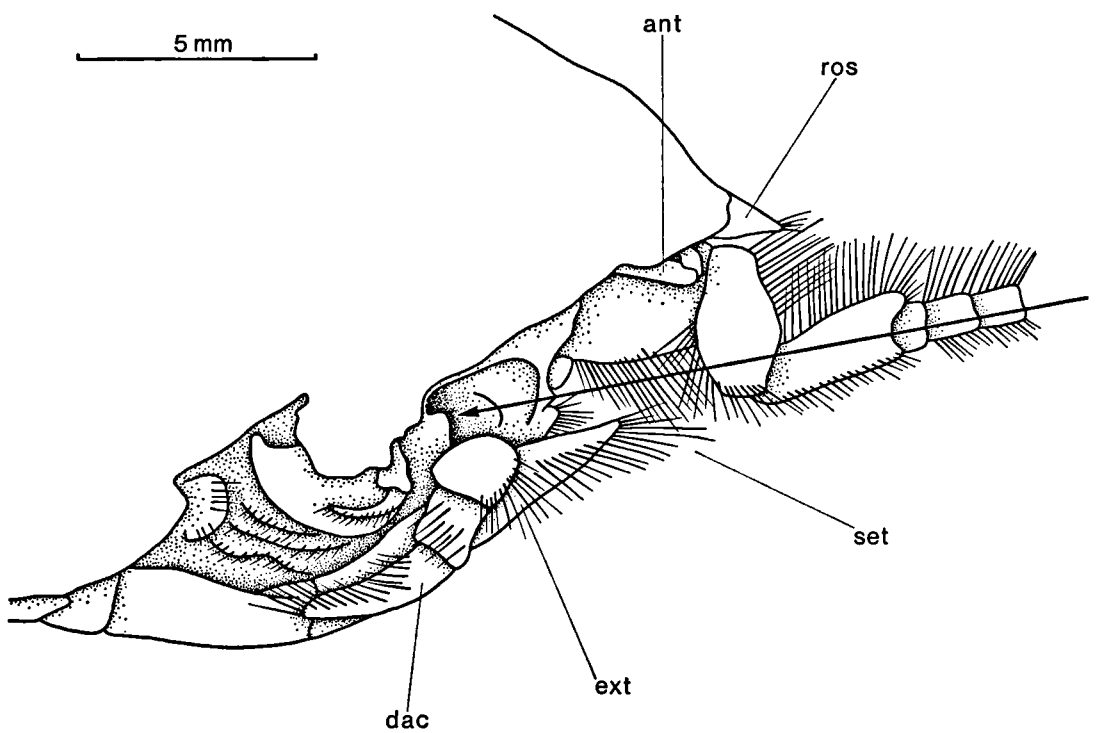

Fig. 1. Median sagittal section of the anterior region of the cephalothorax. The arrow indicates the path of inhalent water during reversed respiration. ant, antennule; dac, dactylus of maxillepede 3; ext, anterior extension of merus of maxillepede 3; ros, rostrum; set, setae forming the floor of the prostomial chamber.

on the carapace but sometimes on the chelae as well. From June onwards they bore barnacles and hydroids in addition. It is presumed that all these epiphytes had settled that year after the mature crabs began to adopt an active surface life in March. The best developed epifauna was on a male collected in July which bore specimens of *Balanus crenatus* up to 4.5 mm diameter: this size can be easily reached in two months though (Meadows, 1969), so they had obviously settled that year.

The burrowing habit naturally poses problems with regard to the respiration of the crab, which have been solved by a series of morphological adaptations. The flagellae of the antennae are elongated, and each bears two dense rows of setae. The rows are directed medially at about 90 degrees to each other, so that when the antennae are apposed they interlock with those of the other flagellum: this forms a tube from which the sand is excluded by the close-set setae, thereby creating a clear passage for the respiratory water. The third maxillepedes and the basal segments of the antennae enclose a chamber in front of the mouth through which the water passes between the antennal tube and the branchial chambers. These structures have been described by Garstang (1896) and figured by Bouvier (1940), though not in detail. Fig. 1 shows them in sagittal section, fig. 2 in ventral aspect. The antennal tube ends basally with the apposed fifth segments of the antennal peduncles, and opens into what Garstang termed the prostomial chamber. The front of this chamber is formed by the fourth segments of the antennal peduncle which are placed transversely. The sides are made up anteriorly of the fused second and third segments of the peduncle and posteriorly by an extension of the pterygostomial region of the carapace. The floor of the chamber is comprised posteriorly of a forwards extension of the merus of the third maxillepedes, and completed medially and anteriorly by a meshwork of long setae which arise from the following:

1. The fused second and third, and the fourth segments of the antennal peduncles.
2. The pterygostomial region of the carapace.
3. The merus and carpus of the third maxillepedes.

Together these form a compact sieve which excludes sand from the prostomial chamber, which at its rear communicates laterally with the branchial chambers. The antennules lie in the roof of the prostomial chamber, and are thereby well positioned to sample the water in the respiratory current.

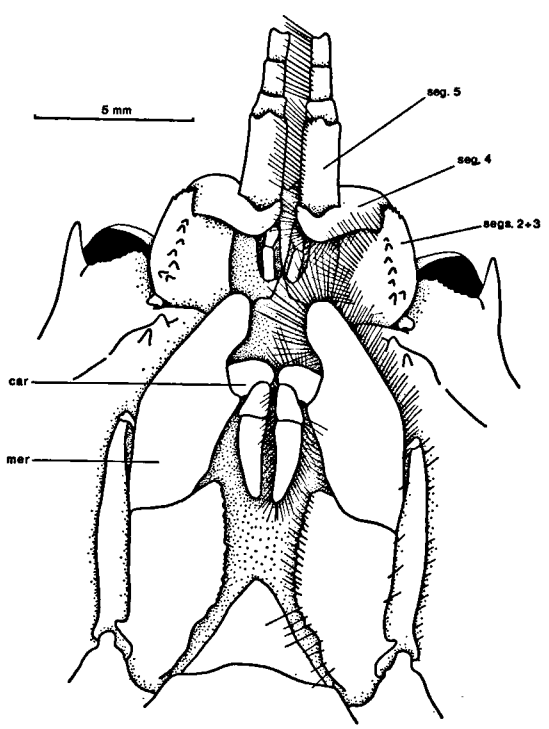

Fig. 2. Ventral view of the anterior region of the cephalothorax. car, carpus of maxillepede 3; mer, merus of maxillepede 3; segs. 2 to 5, second to fifth segments of antennal peduncle.

The first observations on the respiration of *Corystes* were made by Robertson (1864): he noted that the antennae formed a water conduit for the buried crab, but wrongly believed that it carried the exhalent stream. Gosse (1865) studied unburied crabs, and in these correctly observed that the antennae conducted the exhalent stream. Garstang (1896) confirmed Gosse's observation that the current may flow in the normal direction in unburied specimens, though he found that it did not do so continuously. At the same time he showed that Robertson was mistaken: in buried crabs the respiratory current flowed in the reverse direction for nearly all the time, with the inhalent current passing down the antennal tube. More recently Arudpragasam & Naylor (1966) studied the respiratory currents of *Corystes* by the more sophisticated technique of recording the water pressure in the epibranchial chamber, which varies

depending upon the direction of water flow. Their records showed that in a buried crab the currents are usually reversed, with only some ten short bursts of normal flow in each hour. On the other hand when the crab is not buried there are alternate periods of normal and reversed flow of about three minutes duration. These changes of direction may have a cleansing function, but also serve to increase the efficiency of ventilation of the posterior gills.

I have some miscellaneous personal observations on respiration. In a buried crab the inhalent current entering the opening between the tips of the antennae can be demonstrated by using a little milk, and is found not to be as strong as might be expected. This is presumably because a considerable amount of interstitial water is being drawn in between the setae along the length of the antennae, which are thus acting at the same time as a snorkel and a filter. This could explain the observation that crabs may burrow so deeply that their antennae are completely covered by sand: at such times they presumably respire exclusively by filtering the interstitial water. Ovigerous females remain buried in the same way as other individuals, which raises the problem of the ventilation of the egg mass. This could be accomplished by the portion of the exhalent water which emerges adjacent to the base of the last pair of legs to flow through and around the eggs. Admittedly this water has already been deprived of part of its oxygen in passing over the gills, but presumably still contains sufficient for the eggs: thus *Carcinus* may utilise less than 25% of the oxygen in its respiratory water (Arudpragasam & Naylor, 1964).

Observations on unburied crabs revealed differences in behavior during the periods of normal and reversed respiration. During normal flow the third maxillepedes are lowered considerably to create room for the beating of the exopodites of the three pairs of maxillepedes. The flagellae of these exopodites beat for most of the time, sometimes those of both sides together, but more usually the two sides alternating in bursts of about 15 seconds each. Those flagellae which are beating throw a strong current diagonally forwards towards their own side, which carries the exhalent water well clear of the crab. At the same time they draw a current of non-respiratory water transversely across the pre-oral region, and this current flows over the extended antennules: thus the antennules are sampling untainted water, rather than that which has already passed through the branchial chamber. On the other hand, during reversed respiration, the flagellae of the maxillepedes do not beat, and the third maxillepedes are only slightly lowered. However, this slight lowering, together with a small extension of the basal segments of the antennae, results in the prostomial chamber not being closed ventrally so that water is drawn into it from all directions. The extended antennules lie in this inhalent water, and as in the case of normal flow they are bathed by water which has not passed through the gills. It is presumed that the reversed respiration of buried crabs will basically follow the same pattern, except that the prostomial chamber will be closed ventrally to exclude the sand.

FOOD AND FEEDING

The food of *Corystes* was investigated by an analysis of stomach contents, the majority being from mature specimens collected between March and June. The contents had nearly always been cut into small pieces by the mandibles, and so they were identified only as far as the major taxa, and their relative proportions then assessed by the "points" system (Hynes, 1950). Under this system 20 points are allocated to a full stomach, and proportionately fewer to a partially full one: these points are then divided pro-rata by volume among the stomach contents. The three sampling areas were analysed separately, and the results are summarised in table II.

The numbers examined were not large, but they sufficed to give a general picture of the diet. This

Table II. The food of *Corystes* as determined by an examination of stomach contents. The diet has been analysed by the "points system", and the various components are expressed as a percentage of the whole.

Area	No. of stomachs	Total points	% Amphipods	% Lamellibranchs	% Polychaetes	% Echinoids	% Algae	% Decapod egg cases
Fleshwick	20	169	53.3	34.9	2.4	0.6	3.0	5.9
Port Erin	54	563	12.6	62.5	15.8	2.1	0.9	5.3
Laxey	19	230	12.5	85.2	—	2.2	—	—

contained an insignificant proportion of algae, otherwise consisting entirely of burrowing animals, among which amphipods, lamellibranchs and polychaetes were all important. At Port Erin, and especially at Laxey, the major constituent was lamellibranchs, whereas at Fleshwick it was amphipods, though lamellibranchs still made up over a third of the food. This variation from ground to ground is doubtless in part a random one resulting from the small size of the samples, but it also probably reflects differences in the abundance of the food organisms : it is unlikely that the different populations of *Corystes* have different food preferences. The presence of empty decapod egg cases was at first puzzling, until it was realized that these were the cases of *Corystes* itself, and that they were found only in March and April, and then only in the stomachs of mature females. These females were those which had just hatched one batch of eggs, and while cleaning the pleopods in preparation for the next ovulation they had pulled off the old egg cases and eaten them.

The only previous study of the food of *Corystes* was carried out in the Plymouth area, with the following results. "The stomach contents..... show a preponderating diet of small bivalves (*Cultellus & Syndosmya* chiefly) and polychaetes (*Pectinaria, Nephthys,* etc.). Small crustaceans (*Portunus,* amphipods) are also eaten and echinoderms (*Echinocardium, Ophiura*). Only small amounts of sand or detritus occurred in the stomachs" (Hunt, 1925).

Nothing positive is known concerning the feeding behavior. Since the food consists essentially of animals burrowing in the sand, it is possible that the crab catches and consumes them while itself buried. However, in captivity the crabs did not appear to move around once buried, and the absence of sand among the stomach contents suggests that feeding more probably occurs on the surface. I have observed unburied individuals engaged in what appeared to be feeding activity : they were working their way slowly over the surface of the sand, probing it continually with the tips of the chelae and the walking legs. If in fact surface feeding is the normal pattern, then it follows that all crabs must come regularly to the surface for a fair period of time. This could certainly be during the cover of darkness, though it has already been described how efforts to demonstrate nocturnal activity have so far proved inconclusive.

GROWTH AND SEXUAL MATURITY

The basic pattern of growth is the same in both sexes. The immature crabs pass through a series of ordinary ecdyses until they reach the final immature instar. This then undergoes a special puberty-moult, which is marked in each sex by particular morphological changes, and following this moult they become sexually mature. This mature instar is, incidentally, also the final one : the crabs have entered a state of terminal anecdysis, and are incapable of further moulting.

It is clear from the cast integuments collected that moulting occurs throughout the year, apparently rather more actively between February and June. Unfortunately, though, comparatively few casts were collected, and almost no immature crabs, so it proved impossible even to estimate the rate of growth, or the age at which the puberty-moult occurs. Similarly it is not known whether the puberty-moult takes place at any special time of the year : the only conclusive evidence on this would have been provided by the collection of newly moulted post-puberty crabs, but only a very few were captured, and they were spread over the period from February to August. It is only with regard to such matters as the criteria of the puberty-moult, and those concerned with the mature instar exclusively, that adequate data become available.

In males the criteria distinguishing the puberty-moult are less clearly defined than in females, the only consistently useful feature being the form and

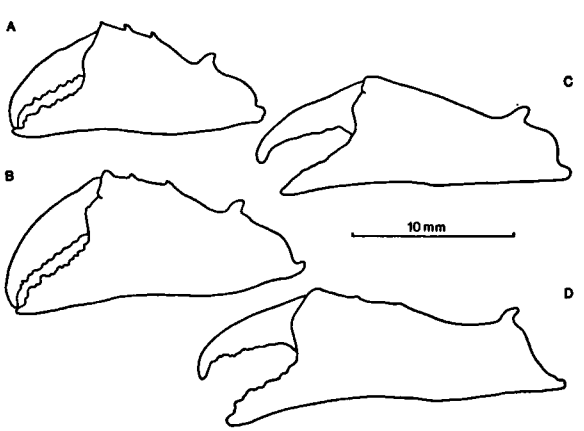

Fig. 3. Male chelae. A & B, pre-puberty specimens with carapace lengths of 27 mm and 32 mm respectively. C & D, post-puberty specimens with carapace lengths of 26 mm and 29 mm respectively.

relative size of the chelae. At puberty the chela becomes relatively narrower, while the teeth on the dactylus and propodus, and the spines on the dorsal margin of the propodus, all become less prominently developed (fig. 3). In addition the relative length of the propodus increases, most markedly at the larger sizes (fig. 8); the increase is quite noticeable even at the smallest size at which the puberty-moult occurs though, and is in nearly all instances adequate to permit the separation of immature and mature specimens. In females there is an increase in abdominal width at puberty (fig. 7), but by itself this is not always a sufficient distinction. There is additionally an increase in the length of the setae fringing the abdomen, from less than 1.5 mm to over 2.5 mm on the sixth segment, and an increase in the diameter of the vulvae from under 0.22 mm to over 0.35 mm. Taken together, these three criteria enable a ready separation of the pre- and post-puberty females.

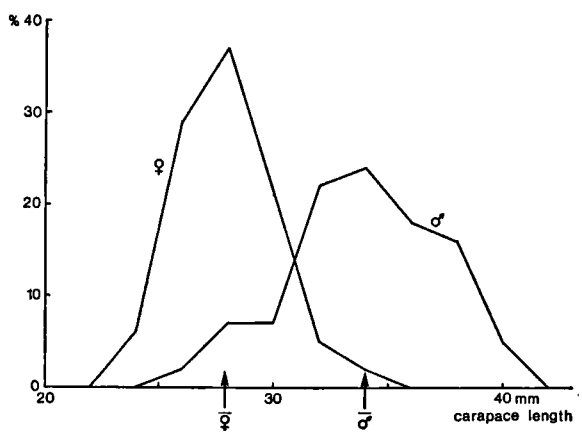

Fig. 4. Size frequency histograms of post-puberty specimens. The arrows indicate the mean post-puberty size of each sex.

The sexes differ in the size at which the puberty-moult occurs, and in the absence of any post-puberty moulting, there are consequent differences in the size-distribution of mature individuals. Thus for each sex the minimum, mean and maximum carapace lengths of the post-puberty samples were :

Males : 25 mm (34.0 mm) 40 mm
Females : 23 mm (27.9 mm) 34 mm

The males are on average larger (fig. 4), as well as being distributed over a greater size range. On the assumption of a 25% moult increment at the puberty-moult it is possible to estimate the size limits of the final pre-puberty instar:
Males : 20 mm to 32 mm carapace length
Females : 18.5 mm to 27 mm carapace length
The largest immature male collected had a carapace length of 35 mm, whilst the largest immature female had one of 26 mm : these specimens are quite close to the maximum immature sizes predicted above.

It has already been mentioned that in *Corystes* the puberty-moult is the final one, which is also true of some other crabs such as the Majidae : there is ample evidence to support the contention.

1. 40 male and 25 female cast integuments were collected, and they were all those of pre-puberty specimens.
2. Of the 250 post-puberty crabs collected none were in pro-ecdysis, nor did any of them show signs of preparation for moulting. Many of these had lost one or more peraeopods, but none had developed limb buds ; similarly a number of post-puberty crabs were caused to autotomise one of their legs, but failed to develop limb buds after being kept alive for up to five months. In both instances the breaking plane was covered by a hard calcified plaque, a characteristic of crabs in terminal anecdysis. On the other hand limb buds were nearly always found replacing any missing peraeopods in pre-puberty crabs (or their cast integuments), and any held in captivity with missing legs soon developed buds.
3. Post-puberty specimens of both sexes were held in captivity for up to a year, but neither moulted nor entered into pro-ecdysis.
4. In a succeeding section it will be described how mature females carry each batch of eggs for nearly a year, and once they have hatched lay the following batch without an intervening moult.

These observations conclusively point to the puberty-moult as the final moult. Carlisle (1957) has shown that this cessation of moulting can be the result of two different endocrinological mechanisms. One mechanism occurs in *Carcinus*, which undergoes a series of post-puberty moults but eventually enters a terminal anecdysis : this is maintained by a continued over-production of moult-inhibiting hormone by the X-organ/sinus gland complex in the eyestalk. The Y organ remains at about the size it had in the penultimate instar, and does not undergo extensive atrophy,

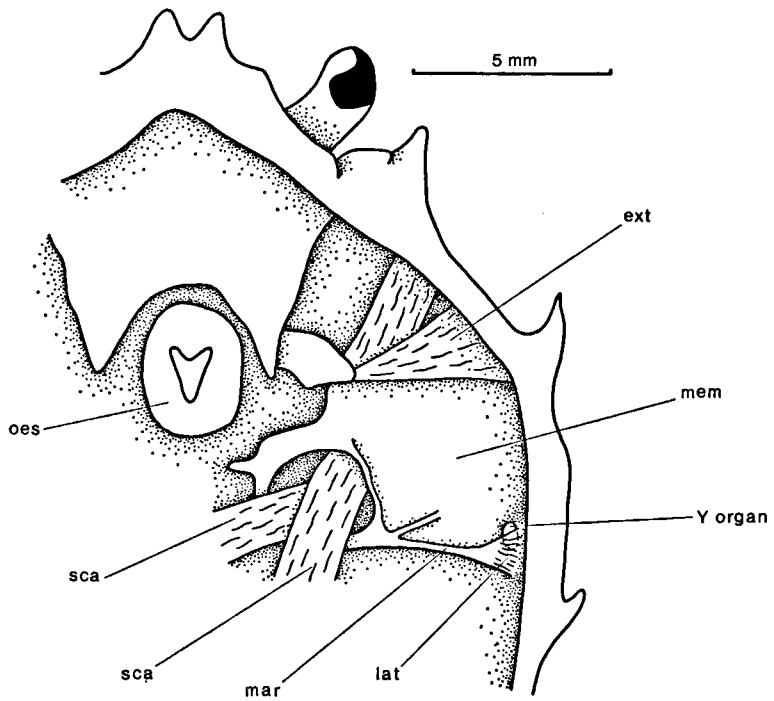

Fig. 5. Dissection of a mature female (carapace length 27 mm) from the dorsal side to display the Y-organ. The dorsal wall of the carapace has been removed, as have the gut and the ovaries. ext, external adductor muscle of mandible; lat, lateral muscle; mar, thickened posterior margin of anterior branchial chamber; mem, membranous roof of anterior branchial chamber; oes, cut oesophagus; sca, muscles of scaphognathite.

but is prevented from producing the moult-stimulating hormone by the activity of the eyestalk. If the eyestalks are removed, then the Y organ resumes activity and moulting re-commences. The second mechanism is found in *Maja,* which ceases moulting after the puberty-moult. Here there is an extensive atrophy of the Y organ, which shrinks to only a twentieth of its size in the previous instar, and does not produce moult-stimulating hormone. This atrophy is irreversible, and since moult cessation is not dependant upon secretions of the eyestalks, their removal is without effect on the terminal anecdysis.

The mechanism operative in *Corystes* was investigated morphologically and experimentally. Firstly the Y organ was examined for macroscopic or microscopic evidence of atrophy. The position of the Y organ in *Carcinus* is figured by Echalier (1959, fig. 1), and in *Corystes* it is located in a homologous position, although the relation of the parts is slightly different due to the more elongate shape of the carapace. Thus it no longer lies immediately posterior to the rear branch of the external adductor muscle of the mandible, but is located some distance posterior to this (fig. 5). It is just anterior to the thickened rear margin of the anterior branchial chamber, ventral to the small muscle which attaches this thickened margin to the carapace. This is the "musculus attractor epimeralis" of Cochran (1935), otherwise termed the "muscle latérale" by Echalier (1959). The insertion of this muscle is visible from outside the carapace, just anterior to the rearmost lateral spine and ventral to the dorso-lateral angle. The Y organ itself is a discrete oval body, pink or yellow in colour, and up to 1.0 mm by 0.5 mm in size. In post-puberty specimens it is as large as in the final immature instar (as in *Carcinus,* and in marked contrast to *Maja*), differing only by being less prominent among the surrounding tissues. Internally it is divided into irregular lobes, whose cells contain large oval nuclei measuring 6μ by 5μ. The microscopic appearance is unchanged after puberty, with no signs of degeneration. Since the Y organ does not atrophy it is likely that the mechanism of moult cessation is as in *Carcinus,* the crucial factor being a continued high production of moult-inhibiting hormone by the X-organ/

sinus-gland complex : if so, then eyestalk ablation should similarly re-initiate moulting. To test this hypothesis ten post-puberty male *Corystes* were used. Five were designated controls, and each was induced to autotomise the fifth right peraeopod. The five experimental crabs had their eyestalks removed on successive days by excision followed by cautery, and then were induced to autotomise the same leg five days later : they all survived the operations for at least three months. The ten crabs were kept under observation for eleven months. Of the five controls two died and three survived the whole period, but none of the five developed limb buds or entered into preparations for moulting. The fate of the five experimental animals was as follows :

1. Died after three months while attempting to moult. Limb bud present.
2. Died after four months while attempting to moult. No limb bud, but leg had not autotomised cleanly at the breaking plane.
3. Killed after four months for histological study. Not in pro-ecdysis, but a limb bud present.
4. Died after six months while attempting to moult. No limb bud.
5. Survived to the end of the experiment, at which time it was not in pro-ecdysis, but a limb bud was present.

Thus although none of the eyestalkless males moulted successfully, three of the five entered pro-ecdyses and attempted to moult between three and six months after the operation. Also three of the five developed limb buds, though they were abnormal in appearance : they were small, and grew out of a central aperture in a hard calcified plaque which otherwise occluded the breaking plane. These results of eyestalk ablation confirm that the mechanism of moult suppression is the same as that described in *Carcinus,* which is to some degree surprising in that the general growth pattern of *Corystes,* with moulting ceasing with the puberty-moult, resembles that of *Maja* rather than that of *Carcinus.*

The maturation of the gametes is linked to the puberty-moult, a fact only to be expected from its name. In pre-puberty males the vasa deferentia are thin and translucent, but in larger individuals at least they contain a number of sperms. In the testes spermatogenesis is taking place, with many of the lobules containing mature sperms, and while these are passing back along the vas deferens they are not being enclosed in spermatophores. The vasa deferentia of post-puberty males are swollen and opaque white, and are packed by vast numbers of sperms. In the anterior portions these are surrounded by secretions (staining blue and red with mallory) which are in the process of forming spermatophores : the posterior parts are full of oval spermatophores, ranging from those 8μ long containing a single sperm to those 30μ long containing up to 50 sperms, but mostly containing between three and ten. Thus although spermatogenesis does occur in the larger pre-puberty males the resultant sperms do not yet become enclosed in spermatophores, and such males have not been seen breeding. After the puberty-moult spermatogenesis accelerates, the vas deferens starts producing the secretions required for spermatophore formation, and the crabs are capable of mating. In pre-puberty females the ovaries are pale and contain ova of under 0.1 mm diameter. Shortly after the puberty-moult the ovaries are still pale, but the ova have increased to a maximum diameter of 0.25 mm, so the maturation of the ovaries starts at, or very shortly after, the puberty moult. The final stages of maturation are closely linked with the processes of mating and ovulation, and are better described in that context in the following section.

REPRODUCTION

The processes of courtship and mating have already been described (Hartnoll, 1968), and so they will be mentioned incidentally only in order to relate them to the overall cycle of reproduction. The males do not seem to undergo any morphological changes associated with reproduction, although they do change their behavioral habits by appearing above the surface of the sand during the mating season. Females, however, are subject to various changes affecting the gonads and accessory reproductive organs.

As the breeding season approaches the maturation of the ovaries proceeds to completion, with the ova enlarging and taking on a deep orange colour as the yolk is deposited. This maturation proceeds somewhat differently in females breeding for the first time from those in subsequent seasons, the two categories being separable by the following criteria :

1. Specimens bearing late-stage eggs or empty egg cases have obviously bred before.
2. Specimens with hard vulvar opercula (see

Table III. The maturation of the ovaries, as indicated by the mean maximum diameter of the ova in each month. Crabs in their first breeding season are treated separately from those breeding for the second or subsequent time. Measurements in mm.

	First season		Subsequent seasons	
	1967	1968	1967	1968
Mar.	—	—	—	0.33
Apr.	—	—	0.31	0.43
May	—	0.3	0.53	0.53
Jun.	0.45	0.26	0.58	0.55
Jul.	—	0.2	0.5	—

below) and not bearing eggs may have sperms in the spermathecae: these were obviously received when the crab mated the previous year.

3. Specimens without sperms in the spermathecae have not bred previously and are embarking on their first breeding season.

The ovary maturation in the two categories is summarised in table III. On average it is slower in females breeding for the first time, for the puberty-moult which initiated maturation will have occurred at various times in the past year: in those where it has taken place only recently maturation will have been late in starting. On the other hand females not breeding for the first time will have previously laid in May to July of the preceding year. During the following months the recovery of the spent ovaries has proceeded slowly, for by March the ova have attained a diameter of only 0.3 mm. Then in the next few months the final stages occur comparatively quickly, and just prior to ovulation the ova have a diameter of 0.65 mm. Once the ovaries are mature the processes of courtship, mating and ovulation follow, the three being closely linked by their common bond to the short period of twelve to twenty days during which the vulval opercula decalcify and become flexible. In this interval the male carries the female in his chelae during courtship, they mate, and the female ovulates (Hartnoll, 1968). Females with flexible opercula are first found in April, are abundant during May and June, while a few occur in July (table IV). Courtship pairing was observed between 26 May and 13 June in 1967, and 22 April and 19 June in 1968, which correlates well with the occurrence of flexible opercula. So also do the dates when ovigerous females were first collected, 2 June in 1967 and 15 May in 1968.

As the egg-laying period draws to a close in July the crabs cease to be active above the surface of the sand, reappearing in numbers only in the following April: by then the eggs have hatched, so it is not possible to observe incubation directly in natural populations except by way of the very rare berried female collected outside the breeding season. One was taken in December, bearing eggs in which eyespot pigment had yet to develop, and a second in April whose eggs were in the process of hatching. However incubation was followed successfully in captive females held at ambient sea temperature: these laid in May and June, eyespot pigment appeared in January, and the eggs hatched in March. Additional information is provided by the incidence of larvae in the plankton. At Port Erin Dr. Williamson collected first stage zoea in March and April, and second and third stage zoea in April, while Dr. Fincham obtained megalopa from the Solway Firth in June. At Plymouth the larvae occur from March to June (Lebour, 1928), and at Dale Fort from March to April (Crothers, 1966). Thus there is general agreement that the eggs hatch in March and April, and since they were laid in the preceding May and June they must have an incubation period of about ten months. This is one of the longest incubation periods in the Brachyura, comparable with that found in *Hyas coarctatus* (see Hartnoll, 1963).

It is known that females may take part in more than one breeding season, and criteria have been described above which permit those breeding for the first time to be distinguished, in most cases, from those doing so on a subsequent occasion. If these criteria are applied to all those collected in April to June of 1967 and 1968 then it appears that:

9 were definitely breeding for the first time
87 were definitely breeding for the second or subsequent time
20 were not determinable.

Table IV. The condition of the vulvar operculum, whether flexible or rigid, in female crabs collected in 1967 and 1968.

	1967		1968	
	Flexible	Rigid	Flexible	Rigid
Febr.	—	—	—	1
Mar.	—	—	—	6
Apr.	—	6	2	20
May	5	12	13	35
Jun.	2	14	5	8
Jul.	1	2	—	3
Aug.	—	—	—	1

If these specimens were a random sample of the population it follows that only a small proportion of the post-puberty female population is replaced each year by recruitment, and that most females breed for several years. The maximum rate of annual recruitment would be $\frac{9+20}{116} = 25\%$, implying a minimum survival rate of 75%. This compares favourably with maximum annual survival rates of from 15% to 70% calculated for the post-puberty females of various spider crabs (Hartnoll, 1963).

RELATIVE GROWTH

The length of the carapace was taken as an index of body size, and growth of several organs relative to this was investigated. This was done partly for the practical reason that it showed the changes which occurred in these organs at the puberty-moult, enabling it to be more easily recognized. Also to provide some insight into the way in which relative growth rates vary between organs, between the sexes, and between immature and mature individuals. The dimensions investigated were the length of the chelar propodus and the width of the fifth abdominal segment of both sexes, and the length of the first pleopod of the male. In each case the pre- and post-puberty crabs were treated separately, the measurements of the variable were averaged for 1 mm or 2 mm size classes of the carapace length, and the results plotted on double logarithmic axes. Previous studies have shown that relative growth in the Brachyura nearly always conforms to the allometric growth equation, $y = B x^a$, a relationship which produces a straight line when plotted logarithmically. In the present study nearly all the data did closely approximate to a straight line, in which case a regression line was fitted. The only exception was the chelae of post-puberty males, the peculiarities of whose growth are discussed in some detail below.

The first pleopod (table V, fig. 6)

In pre-puberty specimens the first pleopod exhibits slight negative allometry (a = 0.91). At the puberty-moult there is a small increase in relative size, but the post-puberty specimens show an intensified negative allometry (a = 0.74). Marked negative allometry of a sexual character is unusual

Table V. The length of the first pleopod of the male, averaged for each 1 mm carapace length group. Pre-puberty and post-puberty specimens have been treated separately. All measurements in mm.

	PRE-PUBERTY		POST-PUBERTY	
Carapace length	n	Pleopod length	n	Pleopod length
16.5	1	3.0		
18.5	1	3.5		
19.5	4	3.9		
20.5	2	3.9		
21.5	3	4.0		
22.5	3	4.2		
23.5	5	4.4		
24.5	5	4.6		
25.5	7	4.9	1	5.4
26.5	4	5.1	2	5.2
27.5	3	5.3	3	5.8
28.5	3	5.4	2	5.9
29.5	4	5.4	1	6.3
30.5			4	6.1
31.5			7	6.5
32.5	1	6.0	8	6.5
33.5	1	6.0	11	6.6
34.5			10	7.0
35.5			9	6.9
36.5			10	7.0
37.5			10	7.3
38.5			2	7.4
39.5			3	7.5
40.5			1	7.4

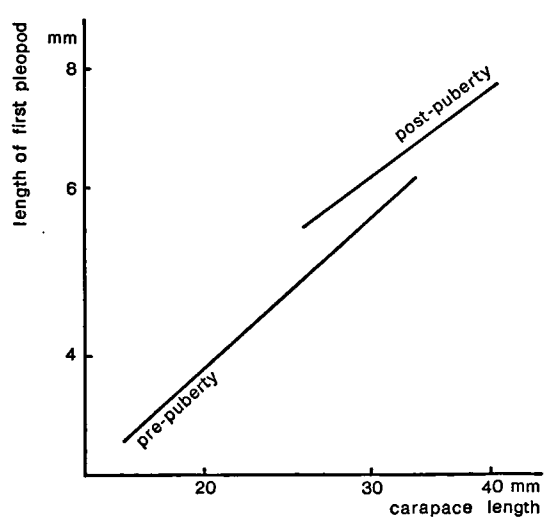

Fig. 6. Regression lines for the log. length of the first male pleopod plotted against the log. carapace length. pre-puberty specimens : a = 0.91, B = 0.254. post-puberty specimens: a = 0.74, B = 0.499.

among mature crabs, but in the case of the first pleopod is capable of explanation. Its effect will be to restrict the variation in size of the pleopod which would otherwise occur between mature males of different carapace lengths. This move towards the standardisation of the accessory male copulatory appendages could facilitate a greater overall sexual compatability between the populations of the two sexes. The relative growth of the first pleopod has been studied in two other crabs, and in both of these it showed negative allometry: 0.96 in *Aratus pisoni* (cf. Hartnoll, 1965) and 0.95 in *Eriocheir sinensis* (cf. Hoestlandt, 1948). This is not as marked as in *Corystes*, but is indicative of a general trend.

The abdomen (table VI, fig. 7)

The abdomen is broader in females than in males. In males the relative growth rate is 1.05 before puberty, there is then a small size increase at the puberty-moult, following which growth is once again nearly isometric (a = 0.95). In females growth is positively allometric in the pre-puberty phase (a = 1.35), there is a marked size increase at the puberty-moult, and in the post-puberty phase growth is isometric (a = 1.00). This pattern

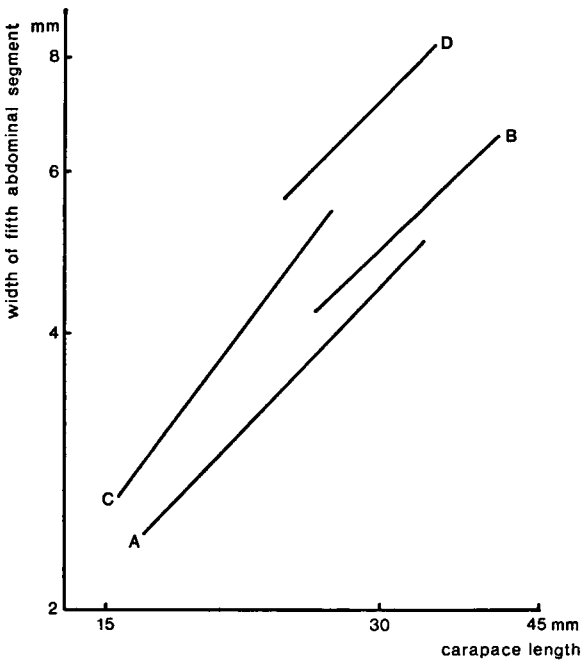

Fig. 7. Regression lines for the log. abdomen width plotted against the log. carapace length.
A. Pre-puberty males, a = 1.05, B = 0.128.
B. Post-puberty males, a = 0.95, B = 0.196.
C. Pre-puberty females, a = 1.35, B = 0.0653.
D. Post-puberty females, a = 1.00, B = 0.263.

Table VI. The maximum width of the fifth abdominal segment averaged for 1 mm carapace length groups. All measurements in mm.

	MALES				FEMALES			
	PRE-PUBERTY		POST-PUBERTY		PRE-PUBERTY		POST-PUBERTY	
Carapace length	n	Abdomen width	n	Abdomen width	n	Abdomen width	n	Abdomen width
15.5					1	2.7		
16.5	1	2.3						
18.5	1	2.6			1	3.4		
19.5	4	2.9						
20.5	3	3.0			4	3.8		
21.5	3	3.1			4	4.1		
22.5	3	3.3			1	4.4		
23.5	4	3.4			7	4.6	3	5.5
24.5	5	3.6			3	4.9	3	5.6
25.5	6	4.0	1	4.2	3	5.2	13	6.1
26.5	4	4.0	1	4.5	2	5.5	14	6.3
27.5	3	4.1	3	4.5			20	6.5
28.5	3	4.3	2	4.8			21	6.8
29.5	4	4.3	1	5.1			18	7.0
30.5			4	4.9			7	7.4
31.5			8	5.2			5	7.6
32.5	1	4.9	8	5.3			2	8.0
33.5	1	5.1	12	5.4			2	8.1
34.5			10	5.7			1	7.9
35.5			9	5.8				
36.5			9	6.0				
37.5			10	6.1				
38.5			2	6.4				
39.5			3	6.5				
40.5			1	6.4				

of growth has a clear functional basis. Both the high pre-puberty growth level and the large size increase at the puberty-moult serve to bring the abdomen to its full size in order to perform its function of carrying and protecting the incubating eggs, without, however, encumbering all of the earlier instars with an unnecessarily large abdomen. At maturity the abdomen enters into a functional relationship with the sternum, and the isometric post-puberty growth enables this relationship to be maintained throughout the post-puberty size range.

The chelae (table VII, fig. 8)

Growth is isometric in pre-puberty females (a = 1.00). At the puberty moult there is little change in relative size, but growth becomes positively allometric in the post-puberty phase (a = 1.27). The relative growth of the chelae of males is, by comparison, both more pronounced and more complex. In pre-puberty males there is a high level of positive allometry (a = 1.49), the highest which has been recorded for the length of the pre-puberty chelar propodus: the next highest is 1.41 in *Pisa tetraodon* (cf. Vernet-Cornubert, 1958). It would not be justified by the evidence to continue the regression line beyond the point where it intersects that for pre-puberty females at a carapace length of about 20 mm. Only two males smaller than this size were collected, but further material would probably show that there was a change at this size to a lower level of allometry: this would be a moult of pre-puberty, such as has already been recorded for a number of species at the size where sexual dimorphism of the chelae first becomes apparent.

In the case of post-puberty males there was very great variation in chelar propodus length between individuals of the same carapace length, and with the number available it was necessary to average the data for 2 mm carapace length groups in order to override this variation: the average for each of these groups is plotted in fig. 8. They indicate firstly that there is a great increase in relative chelar length at the puberty-

Table VII. The length of the chelar propodus, averaged for 2 mm carapace length groups in post-puberty males, and 1 mm length groups in all others. All measurements in mm.

	MALES				FEMALES			
	PRE-PUBERTY		POST-PUBERTY		PRE-PUBERTY		POST-PUBERTY	
Carapace length	n	Chelar length	n	Chelar length	n	Chelar length	n	Chelar length
15.5					1	7.3		
16.5	1	8.0						
18.5	1	8.8			1	9.1		
19.5	4	10.0						
20.5	3	10.6			4	10.0		
21.5	5	10.6			5	10.6		
22.5	3	11.7			2	10.9		
23.5	7	12.6			7	11.4	3	11.8
24.5	7	13.2			3	12.3	2	12.0
25.5	7	14.1			3	12.8	13	13.1
26.5	4	15.3			1	11.5	13	13.5
27.5	4	16.5					20	14.1
28.8	3	16.6					21	14.8
29.5	4	17.9					19	15.4
30.5							6	16.2
31.5							5	16.7
32.5	1	20.1					2	16.7
33.5	1	22.1					2	17.9
34.5							1	20.1
26.0			3	18.5				
28.0			4	22.5				
30.0			7	29.3				
32.0			25	34.4				
34.0			20	38.8				
36.0			13	41.8				
38.0			15	45.6				
40.0			3	48.2				

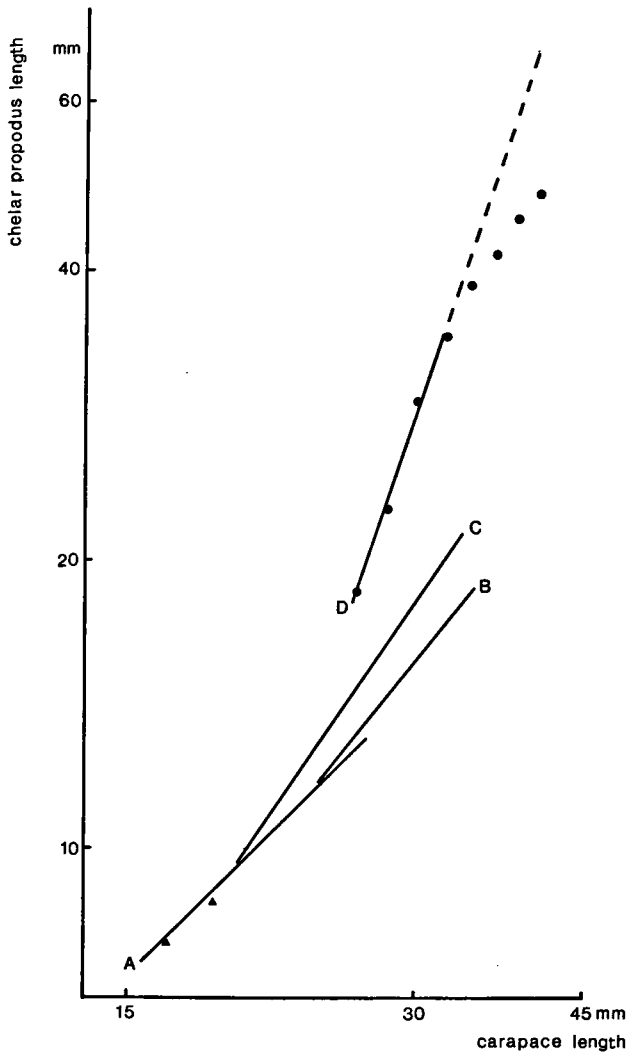

Fig. 8. Regression lines for the log. chelar length plotted against the log. carapace length.
A. Pre-puberty females, a = 1.00, B = 0.488.
B. Post-puberty females, a = 1.27, B = 0.285.
C. Pre-puberty males, a = 1.49, B = 0.115 (▲ = small individuals).
D. Post-puberty males (● = average for each 2 mm carapace-length group).

moult, and secondly that the chelae of post-puberty specimens do not even approximate to a single level of allometry. From 25 mm to 33 mm carapace length there is a reasonable fit to the extremely high level of positive allometry of 3.1, but at larger sizes there is an increasing shortfall from the extrapolation of this growth line. This is unusual, for the growth of the chelae has been studied widely in the Brachyura, and in almost all instances there is good agreement with the allometric growth rule throughout the size range. Perhaps the very high growth level of 3.1 exhibited by the smaller post-puberty males of *Corystes* is responsible for the anomalous growth of the larger specimens: the highest chelar growth level recorded elsewhere in the Brachyura is 1.90 for the post-puberty males of *Maja squinado* (cf. Teissier, 1935). It seems possible that if the larger specimens were to attain the proportions necessary to lie on the extrapolation of the growth line of the smaller post-puberty males, then this would entail an impossibly large increase in chelar length at the puberty-moult. This possibility is investigated in table VIII, which assumes that there is a 25% increment in carapace length at the puberty-moult, and which does lend support to the hypothesis. Over the size range which conforms to the growth rate of 3.1 the increase in chelar propodus length at the puberty-moult rises from 83% to 139%, but in the larger specimens which exhibit a shortfall from this growth rate the increase is pegged to about 145%. In order to conform to the allometry level set by the smaller specimens the largest individuals would have required an increase of 243%, and if the maximum increase observed of 150% is in fact the maximum possible, then here is a possible explanation of the anomalous chelar size of large male *Corystes*. As one test of this hypothesis the situation in various other crabs was examined: the only ones appropriate are those in which the puberty-moult occurs over a wide size range, and in which it is the final moult, which restricts consideration to the Majidae. Again assuming a 25% size-increment at the puberty-moult the following maximum increases in chelar propodus length have been calculated:

55%	*Inachus phalangium*	— Hartnoll, 1963
67%	*Macropodia rostrata*	— Hartnoll, 1963
70%	*Macropodia longirostris*	— Hartnoll, 1963
80%	*Eurynome aspera*	— Hartnoll, 1963
84%	*Hyas coarctatus*	— Hartnoll, 1963
88%	*Maja squinado*	— Teissier, 1935
92%	*Pisa gibbsi*	— Hartnoll, 1963
109%	*Pisa tetraodon*	— Vernet-Cornubert, 1958
111%	*Inachus leptochirus*	— Hartnoll, 1963

None of these even approach the 150% increase which occurs in *Corystes*, and in none of these is the allometric relationship of the post-puberty chelae distorted by an inability to achieve the required chelar increments at the puberty-moult. It lends some support to the idea that 150%

Table VIII. The changes in chelar propodus length occurring at the puberty-moult, compared with those required to maintain a simple allometric relationship in all post-puberty males.

PRE-PUBERTY DIMENSIONS		POST-PUBERTY DIMENSIONS				
			Chelar propodus length		Chelar propodus percentage increment	
Carapace length	Chelar propodus length	Carapace length	Actual	Required	Actual	Required
20.8	10.1	26.0	18.5		83	
22.4	11.7	28.0	22.5		96	
24.0	13.0	30.0	29.3		125	
25.6	14.4	32.0	34.4		139	
27.2	15.6	34.0	38.8	41.5	149	166
28.8	16.9	36.0	41.8	49.5	144	193
30.4	18.4	38.0	45.6	58.0	149	215
32.0	19.8	40.0	48.8	68.0	143	243

could be the maximum length increment attainable at a single moult.

There are interesting contrasts in the growth patterns of the three organs studied, and these can be related to the functional relationships of the organs. Thus the first pleopod of the male is functionally linked to the genitalia of the female, and exhibits negative allometry to restrict size variation between males: this will enhance the overall compatability of the populations of the two sexes. The female abdomen is functionally related to the female sternum, and so it exhibits isometric growth in the post-puberty phase. The male chelae are organs of combat, display and courtship, acting as virtually independent effectors. Thus they are freed from restraint and exhibit an untrammelled positive allometry, which in the larger specimens would seem to be the maximum obtainable at the puberty-moult.

HERMAPHRODITE SPECIMENS

About 250 specimens of *Corystes* were examined, and these included two hermaphrodites. Since hermaphoditism is comparatively rare in the Brachyura, and as these specimens displayed an unusually complete type, they are described and discussed.

Specimen 1. Collected in Port Erin Bay in June 1967. This is externally abnormal in respect of the sternum and the abdomen. There are paired vulvae on the sixth abdominal sternite, occluded by rigid opercula with a diameter of 0.32 mm, which is smaller than the 0.4 mm normal for a mature female of that size. In addition penes of normal size protude from foramina in the coxae of the fifth peraeopods. The sternum has the male rather than the female pattern of setation. In the abdomen the third to fifth segments are fused as in the male, and only normal first and second male pleopods are present. However the fringing setation, 2 mm long, exceeds the normal 1.2 mm of a male. Internally there are paired ovaries which are bright orange and contain ova of about 0.4 mm diameter. Posteriorly each ovary abuts against the dorsal surface of one of a pair of

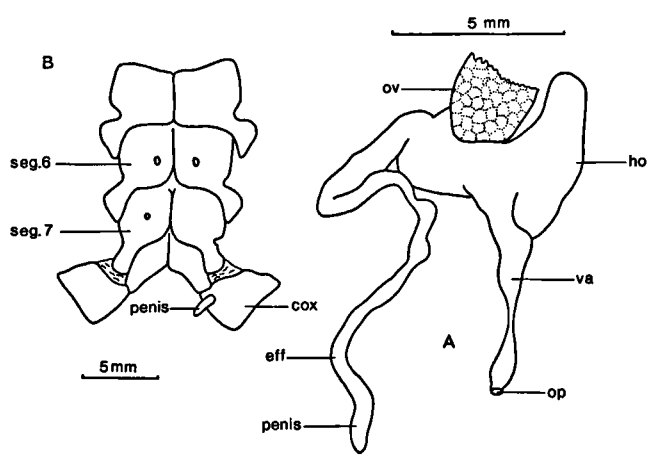

Fig. 9. A. Hermaphrodite specimen 1, reproductive organs of the left side in median view. eff, efferent duct; ho, hermaphrodite organ; op, vulval operculum; ov, ovary; va, vagina. B. Hermaphrodite specimen 2, sternum and the coxae of the fifth peraeopods. cox, coxae of fifth peraeopods; seg. 6 & 7, sixth and seventh thoracic sternites.

complex hermaphrodite organs (fig. 9A). Each is an irregular whitish body giving rise anteriorly to the vagina which runs ventrally to the vulva, and posteriorly to the coiled vas deferens which continues as the ejaculatory duct through the musculature of the last leg to the penis. The hermaphrodite body is composed of loose parenchyma, with the cells flattened in the outer regions; between it and the ovary lie convoluted strands of columnar oviduct tissue. There are two apparently unconnected cavities. The anterior one is empty, and leads to the vagina which has a normal columnar wall and extracellular chitinous lining. The posterior one is continuous with the vas deferens, whose wall is composed of a single layer of columnar epithelium, and contains inclusions which stain blue and red with Mallory; there are, however, no sperms or stages in spermatogenesis. The vas deferens leads into the ejaculatory duct, alongside which is a strand of androgenic tissue about 400 microns by 50 microns, which is smaller than in a normal male.

Specimen 2. Collected in Port Erin Bay in March 1970. On the sixth thoracic sternite are paired vulvae with rigid opercula, which with a diameter of 0.48 mm are a little smaller than in a normal female. On the seventh thoracic sternite there is an unpaired vulva on the right side, with a rigid operculum of a diameter of 0.44 mm. A single penis protudes from a foramen on the coxa of the left fifth peraeopod (fig. 9B). The setation of the sternum is intermediate between the male and the female condition, while all of the abdominal segments are free in the female manner. The first pleopods are of the normal type, as are the second, except that they are slightly longer and bear enlarged distal setae. The third pleopods are uniramous and slightly shorter than the second, while the fourth and fifth pairs are of normal biramous female type. The setae fringing the sixth abdominal segment are 2.5 mm long. There are paired ovaries, pale orange and containing ova 0.25 mm in diameter. The vulvae on the sixth sternite each lead to a normal vagina and spermatheca, the latter being empty and very loosely attached to the ovaries. The vulva on the seventh sternite leads to a reduced vagina and spermatheca lying entirely within the leg muscles, and not protuding into the body cavity. This spermatheca consists mostly of parenchyma, with no sign of oviduct tissue, and a reduced lumen without any contents. Attached to the rear of the right ovary is a small body of tissue similar in type to the spermathecal parenchyma; between it and the ovary are traces of oviduct tissue, and it contains a small lumen. At the rear of the left ovary is a short region of empty convoluted tube with a wall of simple columnar epithelium, and this is presumably homologous with the vas deferens: its lumen is perhaps continuous with that of the ovary, and at the junction of the two there appear to be patches of oviduct tissue. From the vas deferens an efferent duct, also with simple columnar walls and containing blue and red staining inclusions, runs to the penis. There are patches of androgenic tissue alongside it.

Neither of the above specimens showed any sign of past or present parasitic infection, so it is assumed that the hermaphroditism is a developmental abnormality. They are both bilateral hermaphrodites with both internal and external modifications, a form which is comparatively rare in the Brachyura (Hartnoll, 1960). Both contain maturing ovaries, and at the same time have normal male first pleopods and at least one efferent duct

Table IX. The dimensions of the hermaphrodite specimens compared with those of normal individuals.

	CHELAR PROPODUS LENGTH			ABDOMEN LENGTH				PLEOPOD 1 LENGTH		
CARAPACE LENGTH	Hermaphrodite	Immature male	Mature female	Hermaphrodite	Mature male	Immature female	Mature female	Hermaphrodite	Immature male	Mature male
26.5	13.6	14.5	12.7	4.6	4.4	5.4	6.3	5.2	4.9	5.6
37.5	27.1	25.2	20.7	7.4	5.9	8.2	8.6	7.3	6.8	7.3

with its accompanying androgenic gland. In table IX the dimensions of some secondary sexual characters are compared in the hermaphrodite and normal specimens. The results are rather inconsistent, for whereas the larger hermaphrodite has a greater overall feminisation, it displays a stronger masculinisation of the chelae and the first pleopod. The control of the development of the sexual characters in crabs has been discussed in detail with reference to the phenomenon of parasitic castration (Hartnoll, 1967). A possible explanation of the hermaphroditism of these specimens is that there has been an incomplete development of the androgenic gland and an under-production of the androgenic hormones. Sufficient could be produced to mediate the production of certain male organs presumably requiring a low titre of hormone — the first and second pleopods and the penes. Other organs such as the ovaries, however, have developed under the control of the female genotype which has not been fully suppressed.

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Received: 8 November 1971