THE BIOLOGY OF THE SHORE CRAB *CARCINUS MAENAS* (L.)

1. THE BACKGROUND—ANATOMY, GROWTH AND LIFE HISTORY

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Introduction

The Shore Crab, *Carcinus maenas* (L.), is one of the best known of all intertidal animals, being common, relatively large, and easily found. The readiness with which it is identified, sexed, measured or marked makes it eminently suitable for study in the field.

The mass of published work about the animal is split between specialized physiological studies on the one hand and the often superficial statements in popular accounts of the shore on the other. This paper aims at the middle position and reviews the literature in the light of current work at Dale Fort with a view to suggesting where further research might be particularly rewarding.

The life of any animal is largely determined by its anatomy, growth, and life history. The first part of this paper deals with these aspects of crab biology, whilst a later part will cover other aspects perhaps more obviously relevant to a field biologist. However, the interpretation of any field work will depend on the framework established here.

Crab anatomy

External Features

The familiar external features of the Shore Crab (Fig. 1) are those of a squat, solid animal clearly suited for walking rather than swimming (although the flattened dactylus of the last pair of walking legs show it to be a member of the family Portunidae—swimming crabs—many of which have secondarily developed powers of swimming using these legs). The head is fused with the thorax to form a cephalothorax and the greatly reduced abdomen is carried tucked underneath. The segmental nature of the cephalothorax is clear on the underside—in the relation of the sternites to the walking legs—but is hidden on the dorsal side by folds of integument, the carapace and head shield, which have grown over it. The carapace is fused to the true dorsal surface of the body only in the mid line and its lateral extensions, called branchiostegites, enclose a gill chamber on each side of the body and hide the gills from view.

The sexes are essentially similar in appearance but can usually be distinguished by the characters listed in Table 1, although crabs less than 15 mm. carapace breadth can only be reliably sexed on the number and relative development of their pleopods (Shen, 1935).

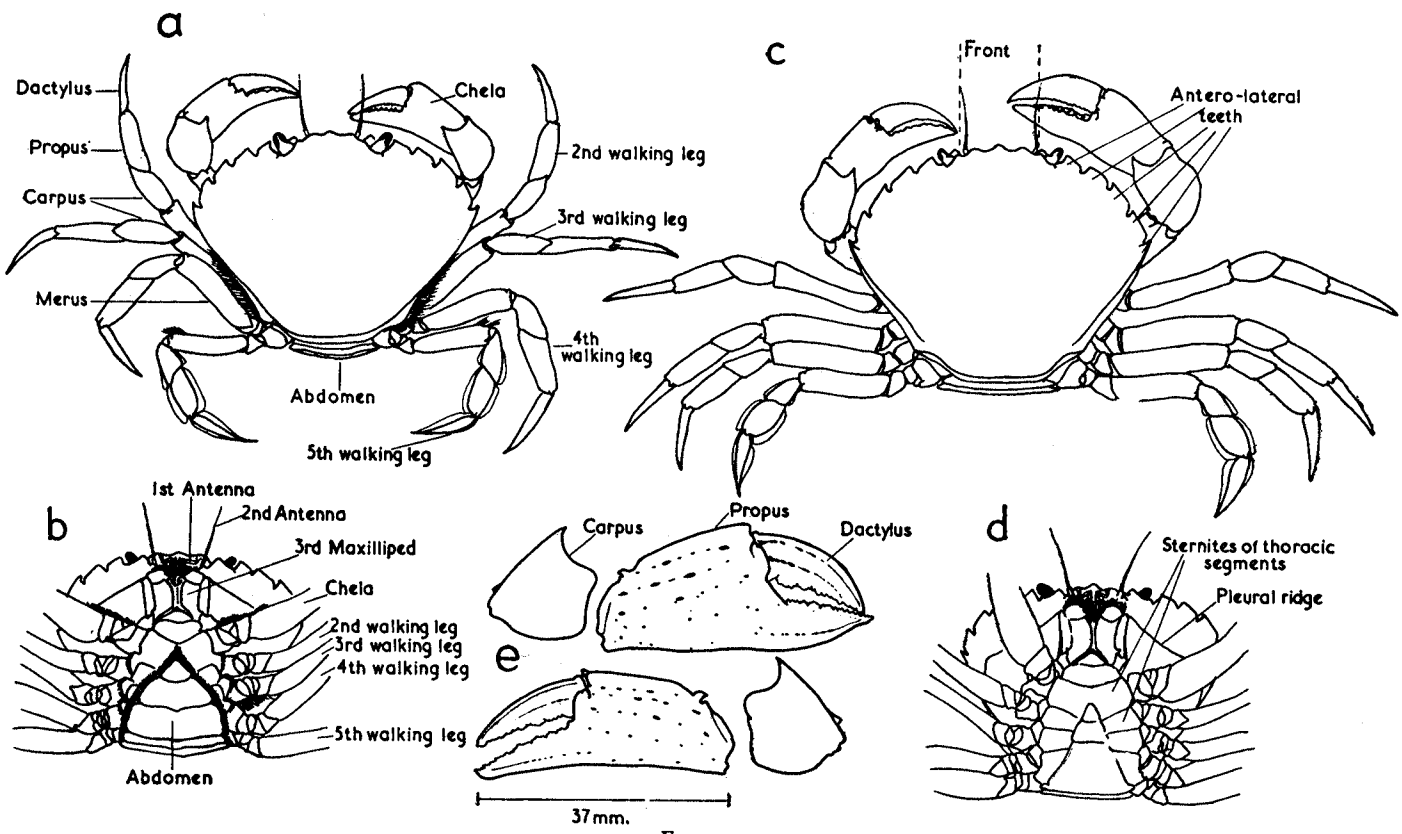


FIG. 1.

External features of *C. maenas*.

(*a*) Female, dorsal surface (*b*) Female, ventral surface (*c*) Male, dorsal surface (*d*) Male, ventral surface
(*e*) Chelae of a large male: it is impossible to see the true shape of the chelae in (*a*) or (*b*) because of the angle at which they are held.

Table 1. *Sexual characteristics of* C. maenas.

Character	Male	Female
Size	up to 86 mm. carapace breadth	up to 70 mm. carapace breadth
Shape		
—Cephalothorax	shallower	deeper
—Abdomen	triangular: apparently five segments	broad and rounded: seven segments
Appendages		
—Chelae	larger	smaller
—Legs	longer	shorter
—Pleopods	two pairs only: on segments 1 and 2: modified as copulatory styles	four pairs: on segments 2–5: long and feathery
Behaviour	aggressive when picked up usually extends all legs and chelae	less aggressive when picked up usually folds legs and chelae under body—the "Eisenchutreflex"

N.B. Males parasitized by the cirripede *Sacculina carcini* approach the female condition. Infected crabs can be recognized by the soft, yellowish non-granular mass of the parasite under the abdomen, see Crothers (in prep.).

The Integument

The hard, rigid integument of the crab represents nearly 40 per cent of its weight (Bryan, 1961) and both protects the animal from damage and provides sites for muscle attachment, being jointed in places to permit movement. Hard sections, impregnated with calcium salts, hinge on each other by "ball-and-socket" joints and are linked by pliable sections in which there has been no deposition of the salts. Surfaces for muscle attachment on the hard sections are increased by inward projections, called apodemes, which reach maximum development on the sternites of the thoracic segments forming a complex framework (the endophragmal skeleton) for support of the viscera; seen particularly well in a cast.

The integument covers all parts of the body which have arisen from the ectoderm of the embryo, and, whilst it varies in composition according to requirements, is always composed of the same four layers (epicuticle and three layers of endocuticle—pigmented layer, calcified layer, and uncalcified layer) described in detail by Dennell (1960). Only the thin epicuticle is comparable to the structure of the same name in insects. The massive endocuticle, with its outer layers often impregnated with calcium salts, is peculiar to Crustacea.

Appendages

Crustacean appendages are segmentally arranged (Table 2) with one pair to each embryonic segment. In primitive Crustacea the appendages on successive segments were similar in appearance but in the crab considerable specialization of function has resulted in no two pairs looking exactly alike.

Many crabs will be found which have lost one or more appendages, usually

Table 2. *The segmental nature and function of the appendages in* C. maenas.

Segment	Appendage	Tagma	Function	
1	nil	Head / Cephalothorax	(embryonic)	
2	1st Antennae		Sensory: statocyst in basal section	
3	2nd Antennae		Sensory: coxopodite forms an operculum over the opening of the antennal gland	
4	Mandibles		Cut up food	
5	1st Maxillae		Hold food for the mandibles to cut	
6	2nd Maxillae		Pass food to mandibles: exopodite (scaphognathite) produces the respiratory current through the gill chambers	
7	1st Maxillipeds	Thorax / Cephalothorax	Pass food to maxillae	
8	2nd Maxillipeds		Pass food to maxillae	
9	3rd Maxillipeds		Grasp food, manipulate it, and pass it forward to the other mouth parts	
10	Chelae (1st Walking Legs)		Offence/Defence: pick up/tear off pieces of food and pass them to maxillipeds	
11	2nd Walking Legs		Walking	
12	3rd Walking Legs		Walking	
13	4th Walking Legs		Walking	
14	5th Walking Legs		Walking: burrowing: swimming	
			MALE	FEMALE
15	1st Pleopods	Abdomen	Copulatory Styles: form a tube for the passage of spermatophores	absent
16	2nd Pleopods		Copulatory Styles: form piston lying in the tube formed by 1st pair	present: used for carrying eggs
17	3rd Pleopods		absent	present: ditto
18	4th Pleopods		absent	present: ditto
19	5th Pleopods		absent	present: ditto
20	nil			

Note: all thoracic legs provide part of the gill series—see Table 3.

SYNONYMS

Antennules	=	1st Antennae	Antennae	=	2nd Antennae
Maxillules	=	1st Maxillae	Maxillae	=	2nd Maxillae
Chelipeds	=	Chelae	Pleiopods	=	Pleopods
Pereiopods	=	Walking Legs	Swimmerettes	=	Pleopods

the chelae or walking legs. These will have been cast off to enable the crab to escape from a predator, or to release it when trapped by a fallen rock, and will be regenerated (see p. 422). The appendages are cast (Bliss, 1960) at a preformed breakage plane near the base as a result of extreme flexion of a leg muscle (the autotomizer muscle). The point at which this break occurs is not the weakest part of the limb (try pulling the leg off a dead crab—it will break at a joint) but the one at which damage to the stump is minimal, for the break passes down the fold of a double membrane across the limb and the stump may be immediately sealed off from the exterior. At the moment of fracture the membrane contracts, cutting cleanly through the only structures that traverse that section of the limb—a nerve and "blood" vessels. The aperture is finally sealed by a valve on the inside, kept in place by the pressure of body fluids, and

a scab on the outside. The appendage may be cast by muscular action alone (autotomy), by muscular activity coupled with the efforts of the crab trying to escape (autospasy), or, rarely if ever in *C. maenas*, by muscular action to weaken a limb which is then pulled off by other limbs (autotilly). Under extreme stress, as when the crab is dropped into formalin, any or all the appendages may be autotomized, but under normal conditions only damaged limbs are cast—and then only if the nerve is sufficiently stimulated. This nerve does not reach the outer section (dactylus) of the limb so damage to that region will not cause autotomy. It is not unusual to find crabs showing slight damage to the outer sections of limbs patched up by the secretion of new cuticle. The repair never looks exactly normal and some bizarre abnormalities of chelae and walking legs have been described (e.g. by Bateson, 1894 and Perkins, 1924, 1925).

Respiratory System

Gaseous exchange is effected through gills. The nine pairs of *Carcinus* (Table 3) are a reduction from the theoretical thirty-two pairs of the primitive Crustacean in which there were four pairs to each thoracic segment (Kerkut, 1958) representing epipodites on the coxa and precoxa of the appendages. The precoxae of crabs are fused with the body so that the inner series of gills—pleurobranchiae—now appear to arise from the body wall. The two series of arthrobranchiae come off the basal membrane of the coxa, whilst the outer series—podobranchiae—represent half of the coxal epipodite. The other half forms a mastigobranch, not a gill but a cleaning rod which sweeps over the surface of the gills proper to keep them free of detritus.

The gill chambers are almost enclosed by the branchiostegites which fit closely against the flanks of the crab. Each chamber has six openings—a small slit at the base of each walking leg, a larger hole at the base of the chela (sometimes called the Milne-Edwards opening), and the largest in front of the mouth. Arudpragasam and Naylor (1964) studied the circulation of water within the chambers (summarized in Fig. 2). Under normal conditions the beating action of the scaphognathite draws water out of the chamber through the large anterior opening. This in turn draws water in through the other openings, predominantly through that at the base of the chela. Flow of water is thus directed anteriorly. Water is forced back to ventilate the hind end of the

Table 3. *The gill series of* C. maenas (*after Williamson*, 1903).

Gill Type	Appendage: 1 Mxp	2 Mxp	3 Mxp	Chela	2 Leg	3 Leg	4 Leg	5 Leg	(Total)
Podobranchiae	—	1	1	—	—	—	—	—	2
Anterior Arthrobranchiae	—	1	1	1	—	—	—	—	3
Posterior Arthrobranchiae	—	—	1	1	—	—	—	—	2
Pleurobranchiae	—	—	—	—	1	1	—	—	2
(Mastigobranchiae)	(1)	(1)	(1)	—	—	—	—	—	(3)
									9+3

The mastigrobranchiae of the 1st Maxillipeds lie in the epibranchial space above the gills whilst the others lie in the hypobranchial space below them.

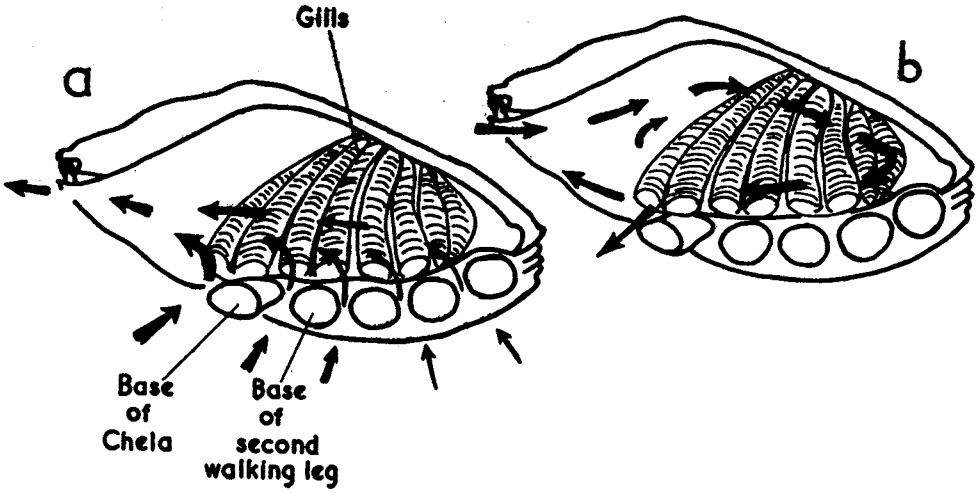


FIG. 2.

Gill ventilation of *C. maenas* (diagrammatic). Arrows show direction of water flow. (after Arudpragasam and Naylor, 1964a)

(*a*) Normal Flow
(*b*) Reversed Flow.

chamber by periodic (*c.* once a minute) reversals of flow. Earlier workers who observed these reversals interpreted them as a means of keeping the gills free of detritus—which may indeed be a useful side effect.

Flow through the chambers is rapid: 1 cc./gm. wt. of the crab/min. for large crabs and 1·5 cc./gm./min. for small ones (Arudpragasam and Naylor, 1964b): and may readily be observed if a crab is placed in a small container of water, especially if particles of carmine or indian ink are added to the water.

In common with several other crabs *C. maenas* will bury itself in the sand if no other cover is available. When buried there is a danger that the inhalant openings will become blocked, despite the periodic reversals of flow. The masked crab, *Corystes cassivelaunus*, maintains a predominantly "reversed" (i.e. anterior-posterior) flow when buried (Garstang, 1896; Arudpragasam and Naylor, 1966) and sometimes *C. maenas* does the same—witness the continuous upwellings of water from the flanks of a buried crab—although normally (Arudpragasam and Naylor, 1964a) it sets up a "tidal" flow in and out of the anterior opening. In either case this opening must be kept free of sand.

Circulatory System

All the body fluid—"haemolymph"—is potentially, if not actually, in circulation for the system is "open" and the circulatory fluid (blood) is not separated from the lymphatic and interstitial fluids. When circulating the haemolymph performs most of the functions of vertebrate blood, carrying

food, dissolved gases, waste products, etc., and even contains a clotting fibrinogen and corpuscles analogous to vertebrate leucocytes (Maynard, 1960).

The respiratory pigment, haemocyanin, is a copper-containing protein that combines reversibly with oxygen; colourless in the reduced state and faintly blue when oxygenated. The oxygen capacity of decapod haemolymph is low (*c.* 1·5 ml./100 cc.), only three or four times that of sea water. Recent estimates of oxygen consumption by Arudpragasam and Naylor (1964b) gave 0·03 cc./gm. wt. of crab/hour for large crabs rising to 0·108 cc./gm./hour for small ones. The utilization of available oxygen by these crabs varied from 9 to 23 per cent.

Circulation of the haemolymph is maintained by the heart, a single-chambered sac of striated muscle lying dorsally near the centre of the cephalothorax (Fig. 3), suspended in the pericardial sinus by elastic ligaments (the alae cordis). When the muscles of the heart wall contract at systole, stretching the alae cordis, the contained haemolymph is forced anteriorly into the arteries. When they relax the alae cordis expand the heart (diastole) and haemolymph is drawn in through the ostia from the surrounding sinus (Maynard, 1960).

The arterial pressure of *C. maenas* at 13 cm. of water (Nicol, 1960) is nearly twenty times less than that of man. Non-muscular thin walled arteries carry haemolymph away from the heart and it returns in large sinuses. Circulation in the gills of decapods is often assisted by accessory hearts at the base of the gill which force haemolymph into the afferent vessels, whence it passes through the efferent vessels into the pericardial sinus.

The haemolymph is isosmotic (±1 or 2 per cent) with sea water. They both have the same concentration of ions and other osmotically active substances, but not the same composition. There cannot, therefore, be just a simple ionic equilibrium between the body fluids and the water. Instead the ionic steady

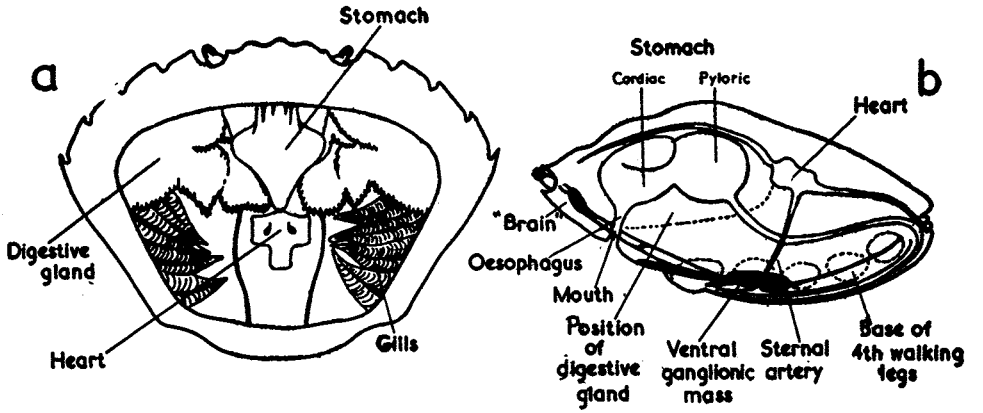


FIG. 3.
Diagrams to show approximate position of the viscera within the body of *C. maenas*
(*a*) Dorsal View
(*b*) Lateral View.

state is maintained by the active transport of ions in and out of the body. *C. maenas*, in common with other decapods, maintains a level of Na^+, K^+, and Ca^{++} above that of sea water and a lower level of Mg^{++} and SO_4^{--}, compensating for these latter with Na^+ and Cl^- (Robertson, 1960a).

The exact composition of the haemolymph varies considerably with the type and quantity of food eaten (food substances have been detected in the haemolymph—see Florkin, 1960), with the salinity of the water, and with the state of the crab's moult cycle (see Table 4) so it is not surprising that there are considerable discrepancies between some of the published figures (Robertson, 1960b).

Digestive System

The alimentary canal is short and simple, consisting of fore gut (stomodaeum), mid gut (mesenteron), and hind gut (proctodaeum). The fore and hind gut are of ectodermal origin, lined with cuticle inturned at the mouth and anus, and thus unsuited for secretion or absorption—most of which must take place in the mid gut which is of endodermal origin. In crabs the mid gut is very short, forming only the hinder (pyloric) part of the stomach, and its functional area is increased by the development of paired diverticula. One long pair arises just behind the stomach whilst a second pair, greatly modified and enlarged, forms the "digestive gland" or hepatopancreas—a large mass, orange in colour from stored carotenoids, filling most of the cephalothorax. It combines the functions of vertebrate liver, pancreas and small intestine for in addition to storing glycogen, fats, pigments, and calcium salts it is the main site of enzyme secretion, digestion and absorption of food. As Vonk (1960) stresses, it is the central control of all metabolism.

The food (Crothers, in preparation) is kneaded by the maxillae and chopped by the mandibles before being pushed into the mouth, whence it passes by peristalsis up the short oesophagus into the cardiac part of the stomach. Here it is ground up in the "gastric mill"—formed of sclerites in the cuticle of the stomach wall. It is thought (Vonk, 1960) that the gastric mill is an adaptation to a sedentary, benthic, way of life and enables the animal to make brief forays for food, swallow any food quickly, and retire into cover to chew it at leisure, in safety. This is in contrast to other Crustacea that have to chew everything in their mouthparts before swallowing it. From the cardiac stomach the food passes into the pyloric stomach which functions as a filter and pump to pass fluid and small particles into the hepatopancreas, whilst larger particles pass into the hind gut to be eliminated through the anus situated at the tip of the abdomen (Barnes, 1963; Vonk, 1960).

Excretory System

The principal waste product of nitrogen metabolism is ammonia—although amines, urea and uric acid are also produced. The amount varies with the physiological state of the crab (Parry, 1960) but an animal feeding normally may excrete an equivalent (in terms of protein) of 0·033 per cent of its body weight per day (Needham, 1957), a figure barely one-tenth of the value obtained for a copepod, which may reflect the comparatively sluggish nature of the crab (Cowey and Corner, 1963).

The excretory organs open at the base of the second antennae and are thus called "antennal organs". They consist of an internal end sac, an excretory canal and an exit duct (Parry, 1960). The end sac is a spongy mass lying in front and to both sides of the oesophagus. The excretory canal is greatly enlarged into a tripartite bladder (one arm of which is folded back over the stomach) and from it the exit duct opens at the summit of a small papilla on the base of the second antenna (Barnes, 1963). The fluid produced by these glands is called the urine, but, surprisingly, is not the principal means for elimination of nitrogenous waste.

There are three other possible excretory pathways: diffusion out through the gills, diffusion into the gut, and deposition in the cuticle to be eliminated at the next moult. Uric acid may be deposited in this way, but it is likely that ammonia is eliminated through the gills. Experiments involving blocking the gut of a crab (*Eriocheir*) give considerable weight to this view, and the gills of teleost fish are known to function in a similar manner (Parry, 1960). The hepatopancreas also has an excretory function in eliminating excessive quantities of its stored materials.

The antennal organs, unimportant in nitrogenous excretion, are concerned with the maintainance of the ionic steady state between sea water and haemolymph mentioned above (Parry, 1960).

Sense Organs

C. maenas is aware of its surroundings through the sense of touch (mechanoreception), smell/taste (chemoreception) and sight (photoreception).

Tactile hairs are present on various parts of the body surface. Each hair (or seta) is a rigid structure able to move only at its basal articulation, which is innervated from the central nervous system (Cohen and Dijkgraaf, 1961). Setae of this general type line the statocyst, a functionally closed cavity (formed by invagination of the body surface) lying in the basal segment of the first antenna. The statolith, formed of sand grains, and the lining of the cavity are cast and renewed at each moult although it is not clear how the sand grains are replaced. The function of the statocyst may be demonstrated best if the crab is induced to form a statolith of iron filings instead of sand (by keeping a newly moulted crab in an aquarium with iron filings as "sand") when the animal will respond to a magnet rather than to gravity.

Mechanoreceptors in the limbs, lying close to but outside the muscle blocks (Cohen and Dijkgraaf, 1961), allow the crab to detect vibrations in the water and also act as proprioceptors to inform the central nervous system of the position of the limb (Alexandrowicz and Whitear, 1957) providing another aspect of the sense of touch.

Mechanoreceptors on the antennae, especially the first pair, can detect changes in water currents and thus enable the crab to sense objects which set up a disturbance in the water. Chemoreceptors (Barber, 1961) known as aesthetascs—long sensory hairs arranged in rows along the flagellum of the first antennae—also permit detection of objects at a distance.

Barber (1961) quotes Luther's work (1930) on the ability of the crab to "taste" with its legs. The chemoreceptors involved, called funnel canals, are found on the surface of legs, chelae, and mouth parts. Their response was

demonstrated by persuading a crab to walk (out of water) over blotting paper impregnated in places with meat extract. Contact with the food substance elicited the specific grasping and searching movements shown by crabs in the presence of food (which can very easily be observed in aquaria). The receptors show little discrimination between substances and any chemical providing a big enough stimulus produces the complete response.

The eyes are the obvious photoreceptors and are built on the typical Arthropod compound eye system (Waterman, 1961). They respond best to movement, especially of shadows. On the shore at low tide a disturbed crab will strike with its chelae at an object coming into range between the eyes. One presumes that the crab responds principally to variations in light and shade but some colour perception was reported by Buddenbrock and Friedrich (1933) Chromatophores are photoreceptors and continue to show albedo (background) responses to light and shade in blinded crabs—but this is probably a local effect which does not stimulate the central nervous system.

Nervous System

The consolidated nervous system of a crab (Fig. 4) represents a contraction and fusion of the ventral ganglionic ladder seen in lower Crustacea. Its segmental nature is revealed by comparison with long-bodied decapods (prawns or lobsters) in which fusion is less advanced. Fusion of form has not brought fusion of function and the component ganglia within the ganglionic mass can still operate independently. Thus only a damaged limb is autotomized and just the one eyestalk responds to a touch on the cornea.

Crab and vertebrate nervous systems operate in very different manners—see Wiersma (1961) and related papers in Waterman (Ed.) (1961). Variable responses are rare, most stimuli produce an all-or-nothing response. There is a stimulation threshold to all actions; if weak stimuli are unable to reach it nothing happens, but any stimulus that does reach the threshold produces the complete reaction.

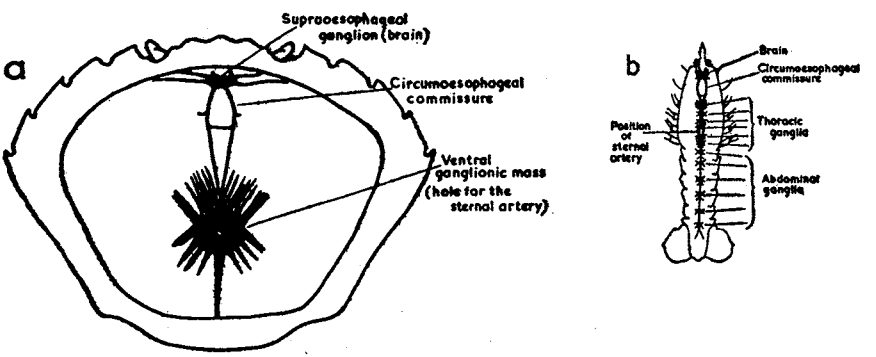


FIG. 4.

Diagram of the central nervous system of *C. maenas* compared with that of a long-bodied decapod

(*a*) *C. maenas*, dorsal view (mainly after Kerkut, 1958)
(*b*) Lobster, dorsal view (after various authors).

This does not imply an inadequate system. It permits simple and complex reflexes, apparently similar to those of vertebrates: e.g. the jaws of the chelae close if touched on the inside and the apparently complex defence reaction of raising the front of the body and extending the chelae probably arises from stimulation of a single fibre in the circumoesophageal commissure. The described complex reactions include righting, copulation, feeding, and escape. *C. maenas* is reported as showing signs of learning in a simple maze (Nicol, 1960).

Sex and the Reproductive System

Sex is genetically determined in crabs. One pair of chromosomes is involved—the sex chromosomes or heterochromosomes. In all crabs that have been examined (which does not include *Carcinus*) the female possesses a normal pair (denoted XX) whilst in the male one chromosome is incomplete (XY) or absent (XO). Genetically determined males develop an androgenic gland. Secretions from this gland cause the male sexual characteristics (see Table 1) to appear at puberty. In the absence of this hormone the female condition appears and the gonads develop as ovaries (Charniaux-Cotton, 1960). Development of the female sexual characters is promoted by an eyestalk hormone, probably inhibited in the male by the androgenic hormone (Demeusey, 1958).

The existence and significance of the androgenic gland was discovered by Hélène Charniaux-Cotton in the amphipod *Orchestia gammarella*. She later searched for, and recognized, it in other Crustacea including *C. maenas*, and published many papers on the subject. A recent review (1960) is in English and readily available.

The two androgenic glands of a male *C. maenas* lie, one attached to each vas deferens, between the muscle blocks in the coxa of the fifth walking leg. They are long thin solid strands of cells, folded back on themselves several times. The length of the strand varies with the size of the crab. One 50–60 mm. carapace breadth would have a gland extending 7 mm. along the vas deferens—implying a total length of several centimetres—continually some 30μ in diameter.

The gonads lie dorsally in the cephalothorax on top of the hepatopancreas. They unite in the mid-line and extend laterally into the angles of the carapace (Kerkut, 1958). The products are carried away in paired ducts—vas deferens, of the male: ovarian duct of the female—opening ventrally. The vas deferens, glandular distally and modified to produce spermatophores, leads into a muscular walled ejaculatory duct opening at the base of the coxa of the last leg and connecting with grooves on the copulatory styles. Fertilization is internal. The female's vagina is enlarged to receive the styles and is equipped with a pair of seminal vesicles to store spermatozoa (Barnes, 1963).

Growth

The Moult

The rigid skeleton on which the crab depends for support and protection is non-living and, once hardened, it cannot change shape. The animal grows by moulting, laying down new cuticle, cracking off the old one, blowing itself up to a much larger size (*c.* 29 per cent increase—see Table 6) and then hardening

the new cuticle. The increase in size is very rapid and hardening begins as soon as the crab has emerged from the old skeleton. Until the new cuticle is hard the animal is almost helpless, unable to feed or defend itself, and hardly able to move. Mortality amongst aquarium crabs is greatest at this stage.

Moulting has long been a favourite topic for research so that a considerable body of information and a special terminology have arisen, see Passano (1960) for references. The old concept of the moult as an interruption to the normal life of the crab has given way to the realization of a continuous growth process: in place of two phases "soft" and "hard" we now recognize a complete cycle of growth phases (Table 4).

The swelling up of the body with water provides the mechanism of moulting. During intermoult small volumes of water enter the body through the gills to balance that lost in excretion and diffusion. The very large volumes taken up at ecdysis (72–80 per cent of the pre-moult body weight—Carlisle, 1954; Robertson, 1960b) is swallowed and absorbed through the hepatopancreas. None of it enters through the new cuticle, for (*a*) osmotic uptake could not account for this volume, (*b*) the fluid is taken up complete with ions, and (*c*) removing a piece of cuticle from a crab in proecdysis does not induce swelling (Robertson, 1960b).

The presence of this excess water within the skeleton permits subsequent tissue growth by displacement. When all the water has been displaced the crab must moult again, for the rigid skeleton can allow no expansion or compression of the tissues.

Broekhuysen (1936) quotes crabs taking 1 hour 57 minutes and 3 hours 16 minutes from the appearance of a rupture in the branchiostegite (D_4) until the animal was completely free of the old skeleton (E). Subsequently the rate of hardening varies with the size of the crab, temperature, pH, and Ca^{++} ion concentration of the water. Broekhuysen's figures range from 3–4 days (a crab of 17 mm. carapace at 16° C.) to 16 days (adult at 10–11° C.).

Control

The growth of body tissues and increasing food reserves, perhaps coupled with favourable external conditions of temperature and light, stimulate the crab to moult. It may be (Passano, 1960) that the enlargement of the hepatopancreas imposes a strain on the epidermis which stimulates the central nervous system through strategically placed strain receptors. Crabs with low food reserves, as a result of parasitization, starvation or gonad maturation or under certain conditions of cold and reduced salinity, may be inhibited from moulting.

The moult sequence is: stimulation of the central nervous system from the hepatopancreas; changes in hormonal secretion; physiological changes in epidermis and haemolymph—increased Ca^{++} ion level, etc. Many hormones may be involved but three or four are relatively well known, emanating from the brain, the Y-organ (a mass of secretory cells in the maxilla) and the X-organ/Sinus Gland complex (in the eyestalk).

The Y-organ continuously secretes a moult-promoting hormone, but proecdysis is not initiated until the inhibition from other hormones is lowered or removed. During anecdysis this inhibition is due to an eye-stalk hormone

(Carlisle, 1957). Removal of the eyestalks removes the source (or store) of the hormone and the crab will moult. Inhibition during diecdysis is from a brain hormone, so removal of the eyestalk has no effect then on moulting (Carlisle, 1957). Failure to recognize the two intermoult states leads to direct contradictions in published work (e.g. Carlisle, 1954 v. Passano, 1953).

Later in the moult sequence uptake of water is inhibited by another (?) eye-stalk hormone which restricts increase in size. Crabs without eye-stalks may increase in volume by 180 per cent as compared with the normal 80 per cent (Carlisle, 1955; Carlisle and Knowles, 1959). One could imagine that local light conditions might affect the secretion of an eye-stalk hormone, and, since this hormone controls the timing of ecdysis, there might exist a means of correlating the timing with environmental conditions.

Growth

When a crab moults it usually (but not always—see Williamson, 1903) increases in size, volume, and linear dimensions. The linear dimensions may not all increase in the same proportion, some parts of the body growing faster than others. The growth of any body dimension y may be expressed in relation to a reference dimension x by:

$$y = bx^a \qquad (1$$

where a and b are constants. The expression is commonly used in the form:

$$\log y = a \log x + \log b \qquad (2$$

which is a straight line of gradient a and thus a measure of the growth of y with respect to x. When $a = 1$ growth of the two dimensions is parallel, or isometric. When a differs from 1, growth is allometric. Biometricians recognize two types of allometry—of growth and size. Allometry of growth refers to specimens (e.g. cask skeletons) belonging to successive stages in the same developmental series. Allometry of size refers to specimens at the same developmental stage. Thus the relative enlargement of the male's right chela at successive moults is allometry of growth, but its size in comparison to the left chela at any stage is allometry of size.

For analytical purposes the expression (2) assumes y to be a measure of a small part of the body, and x that of a large part. Too many people compare dimensions (e.g. length and breadth of the carapace) where x and y are of equal standing. Too often the choice of a reference dimension has simply been one of convenience, but it would obviously be better to define a reference parameter that involves simultaneously all the possible dimensions of the body (Teissier, 1960).

Assuming that a suitable parameter for x has been established, an almost infinite number of graphs could be drawn to represent the growth of all the possible dimensions of the crab. In practice it is usual to concentrate on a few easily measured dimensions.

Occasionally it may be possible to represent the growth of y by a single straight line, but usually two or more lines are required. The growth of a crab is divided naturally into distinct phases, each of several moults, separated by more or less violent changes. During each phase (represented graphically by a straight line) the various components of the body grow, relative to each other,

Table 4 *The moult cycle of* C. maenas.

(Data from: Bliss, 1960; Carlisle, 1954, 1955, 1957; Dennell, 1960; Drach, 1939; Florkin, 1960a; Passano, 1960; Nicol, 1960; Robertson, 1960b; Scheer, 1959; and Williamson, 1903).

Stage	Symbol	Description	Activity: Feeding	Activity: Mobility	Ca++ ion concentration as % sea water conc.	Water as % total weight	Other changes in haemolymph composition	Duration as % of total cycle
PROECDYSIS	D	The period of preparation for the moult	normal	normal	126% increasing to 146% (max. 188%)	steady at 60%	food substances increasing——→ Na^+, Mg^{++}, and Cl^- increasing ——→ fibrinogen decreasing to——minimum	10+
	D_0	The tissues under the integument become activated to begin absorbing material from the old cuticle and to begin laying down the new. Changes in haemolymph composition are detectable before there is any visible structural change						5
	D_1	The outer layers of the new cuticle are laid down under the old. New cuticle first visible in the setae on the mastigobranch of the first maxilliped		reduced				5
	D_2	All tissues of the new integument (except the uncalcified layer) now complete—folded into complex corrugations to fit the available space	reduced	none		rising		3
Peeler	D_3	Rapid resorption of materials from the old cuticle, to leave principally waste products and calcium carbonate by the end of D_4. Absorption lines appear on the surface and an area at the base of the chela becomes completely decalcified	slight					1
About to moult	D_4	Crab begins to swell and cracks old cuticle along prepared lines of weakness. Cracks first appear along the pleural ridges on the branchiostegite						

Ecdysis		E	The act of casting the old integument As the animal swells with water the rupture in the branchiostegite spreads back along the pleural ridge, crosses the base of the abdomen just behind the carapace, and then tears forwards to the orbits. The old carapace hinges up on the integument between the eyes, allowing the crab to withdraw from the old skeleton and escape backwards. The old carapace finally drops back into place on the empty skeleton	slight	none	falling rapidly	rising rapidly	Food substances low — — — increasing — — falling to normal Na+, Mg++, and Cl⁻ returning to normal Fibrinogen minimal — — rising — — to normal	0·5
Metecdysis		A/B	The period of recovery from the moult	increasing		falls below 126% within 24 hr. and thereafter drops below 100%	rising		
	Newly Moulted	A1	The crab continues to swell and thus increases markedly in size (often 30% increase) before the new cuticle hardens. Calcification begins almost immediately, starting at the tips of the appendages and working inwards						0·5
	Soft	A2	Uptake of water stops: visible growth stops: hardening continues				86		1·5
	Paper Shell	B1	The new uncalcified layer is laid down under the rest of the integument. Hardening continues—in all half the calcium for the new integument comes from stores within the body, and half is taken up from the sea				85		3
		B2	All layers of new integument complete: hardening continues—appendages now hard: tissue growth begins	to normal	begins		83		5
Diecdysis	Hard	C	A brief period between the end of one Metecdysis and the beginning of the next Proecdysis		normal	rises to 126%	78	normal	15
		C1:2	Period of main tissue growth						
		C3	Integument complete				68		15
		C4	The main intermoult period: accumulation of food reserves in the hepatopancreas				61		30+
Anecdysis			A longer period between Metecdysis and Proecdysis during which moulting temporarily stops. Endocrine control distinct from diecdysis—but no outward differences			126%		normal normal normal	
	Terminal Anecdysis	C4T	Moulting finally ceases: the last stage in the life cycle				60		until death

according to the rules of allometry. The changes occur when the rules governing the allometry change, often without corresponding changes in size or weight of the animal, and these new rules operate throughout the ensuing phase (a different straight line on the graph). *C. maenas* provides many examples of this type of growth and is indeed an eminently suitable animal for biometric study. The most obvious examples are those concerning the development of sexual characters, with the graphical discontinuities at the moult of puberty.

Shore animals lacking a pelagic larva (e.g. *Nucella lapillus*, *Littorina saxatilis* and *L. littoralis*) are frequently isolated by habitat factors into small communities, usually distinct in colour and/or form. It would be surprising if *C. maenas*—which does have a pelagic larva (see below)—formed biometrically distinct communities but Weldon (1894; 1898) and Williams and Needham (1941) give data showing small differences when comparing the ratio of frontal width: carapace length in young males of a given size. In the course of his work Weldon noticed that this ratio was decreasing in successive years (when considering crabs of the same size). Williams and Needham (1941) confirm this observation but not Weldon's explanation of it (Natural Selection producing crabs with a narrow front and hence a narrower aperture to the gill chambers in response to progressive silting up of their habitat). This ratio cannot decline indefinitely. If it continued at the rate Weldon described it would reach zero in 650 years—and there would have been noticeable changes over the last hundred years. This latter is in fact not so, and since the data of Williams and Needham overlap numerically those of Weldon forty years earlier they suggest that periods of increase must offset these periods of decrease.

Regeneration

Regeneration of lost or damaged limbs provides the only example of visible growth during diecdysis. The speed of regeneration varies with the nature of the damage, availability of food, temperature and the stage of the moult cycle. It is most rapid following a break at the preformed breakage plane (see above) (Bliss, 1960).

The new limb begins to grow immediately and within a few days a tiny limb bud has appeared on the stump, pushing away the scab. The limb bud grows quickly (basal growth) until it reaches a certain size at which it waits until the crab enters proecdysis. Basal growth includes all tissue differentiation and has produced a new leg, bent over twice, in a soft extensible protective sac. During proecdysis the limb bud grows rapidly again (pre-moult growth) and the crab moults to reveal a fully formed limb (Bliss, 1960). In first-year crabs the regenerate limb is of normal size, although very light in colour, but when a larger crab regenerates a limb it appears rather smaller than expected and then grows allometrically to normal size in subsequent moults. When the master chela is lost, subsequent moults may transform the left chela into the master, and the regenerate develops the form of a normal left chela.

Damage at a site other than the pre-formed breakage plane follows a different sequence (Bliss, 1960). Damage to the distal joint of a leg (dactylus) is either patched up or the regenerate develops inside the penultimate joint (propus),

where it is invisible and protected from bruising and emerges more or less complete at the next moult.

Damage to the limb base is more serious for there is then no mechanism for stopping bleeding. If the crab survives it must regenerate a limb base before producing a replacement limb. The sequence becomes damage; regenerate base; moult; regenerate limb; moult; functional limb appears.

Autotomy and regeneration are commonly performed by small crabs but with the approach of sexual maturity the frequency decreases (Bauchau, 1961) until it stops altogether when the crab enters terminal anecdysis. Obviously regeneration of this type is impossible without moulting and the threshold for the autotomizing reflex is raised very high in old crabs—although it never disappears entirely in *C. maenas* (Carlisle, 1957).

A number of abnormalities may occur as a result of faulty regeneration. For example the production of extra projections—especially bifid chelae (Perkins, 1924; 1925), heteromorphosis—development of an inappropriate appendage, or tridactyly which results in three exopodites in the place of one (apparently three legs from one stump). A crab showing this latter condition was found recently at Dale (Crothers, 1966). It results from a peculiar type of injury leaving two wound surfaces. The three "legs" are the original and two regenerates (Bliss, 1960). The Dale specimen unfortunately died before moulting, for it would be interesting to know if these malformations are maintained.

Life history

The Stages

Male *C. maenas* attain sexual maturity at a carapace width of 25–30 mm.: females between 15 and 31 mm. depending on the season of the year (Broekhuysen, 1936; Demeusey, 1963b: Williams and Needham, 1937). The adult male can probably copulate whenever his skeleton is hard, but the female is receptive only immediately after moulting, whilst her integument is still soft (Broekhuysen, 1936).

The male selects his mate a few days before she is due to moult and carries her around with him, clasped beneath his body. Initially (pre-copula) she is carried ventral side downwards, but on moulting the male turns her over and carries her ventral side upwards (in copula) until she hardens. Selection by the male must be very efficient as nearly all adult females are fertilized (Broekhuysen, 1936) and it seems that the male will attempt copulation with any crab that responds passively to his touch—and this usually means a receptive female (Broekhuysen, 1937). Whilst carrying his mate the male behaves as normally as possible, remaining on the shore at low tide and apparently even foraging for food—pairs have been taken from crab traps at Dale.

Some time after copulation the female lays her eggs. They are not released into the sea but become attached to the long setae on her pleopods until they hatch. To attach the eggs (all 185,000 of them) the female must bury herself in the sand and form a large enclosed cavity beneath her body. Each egg must be pushed between the setae with sufficient force to rupture the outer membrane before it will adhere, and only by forming this large cavity can the female exert enough force without scattering her eggs (Broekhuysen, 1936). A female

deprived of sand cannot attach her eggs successfully. Females carrying eggs are said to be "ovigerous", "berried" or "in berry": whilst the mass of eggs is called the "egg plug".

The egg plug is carried for several months, periodically cleaned and prodded by the mother's legs and ventilated by a fanning motion of her abdomen. The newly laid plug is bright orange but changes colour slowly through a dull brown to a dirty grey (Williamson, 1903) or black (Broekhuysen, 1936) before the eggs hatch into free swimming planktonic larvae.

C. maenas has six larval instars representing three stages: protozoea (= prezoea), zoea, and megalopa (see Fig. 5; Lebour, 1928 and Williamson, 1903). The egg hatches into the protozoea which is best considered as the first zoea enclosed in a thin embryonic membrane. Long spines are borne on the telson and on both pairs of antennae but not on the carapace. The abdomen is unjointed. The only visible appendages are the first and second maxillipeds with which it swims. It moults within a few hours into the first of four zoeae.

The zoeal carapace bears two long (rostral and dorsal) spines, the abdomen is jointed, and all the head appendages are functional. The larva still swims with the first two pairs of maxillipeds but the other appendages, complete with gills, gradually develop and are visible (though not functional) in the fourth zoea. The long carapace spines presumably maintain direction and balance whilst the animal swims, increase the surface area and hence buoyancy, and hinder would-be predators (Lebour, 1928; Hardy, 1956). As the zoeae grow and increase in weight they must expend more energy to keep station in the water. This is reflected in the increasing efficiency of the maxillipeds—those of the first zoea each have four swimming setae, the second six, the third usually eight, and the fourth ten (Lebour, 1928; Williamson, 1903).

Carcinus zoeae are typical members of the temporary plankton (see Hardy, 1956) rising to the surface each evening to feed on smaller organisms (Lebour, 1928 gives a list) and sinking lower by day. The zoea is attracted to a weak light source but is repelled by strong light and/or high pressure. Vertical migration can be explained as follows (Hardy and Bainbridge, 1951; Rice, 1964): an increase in pressure above a given threshold stimulates the larva to swim towards the light (i.e. normally upwards) and it rises to the surface of the sea as the light fades in the evening. In the morning, with increasing light, they move down to an optimum depth where the inhibitions from strong light and high pressure balance each other.

The fourth zoea moults into the megalopa, which looks more like a crab and whose appendages are all functional. Gaseous exchange may now take place through the gills as the hind four pairs are complete. The megalopa walks on its thoracic legs and swims with well developed pleopods on abdominal segments 2–6. Some observers (e.g. Williamson, 1903) state that it always carries its abdomen outstretched but Atkins (1954) noted that sometimes the abdomen was tucked up when walking. Perhaps it is a habit that develops with age. When swimming the legs are tucked out of the way in a characteristic attitude, assumed as the megalopa jumps off the bottom—Fig. 5 (Atkins, 1954).

Hardy (1956) implies two megalopa instars when he writes that the larva "passes through a young megalopa stage to a late megalopa stage in which the spines get shorter (and) the carapace and limbs more crab like". Lebour (1928)

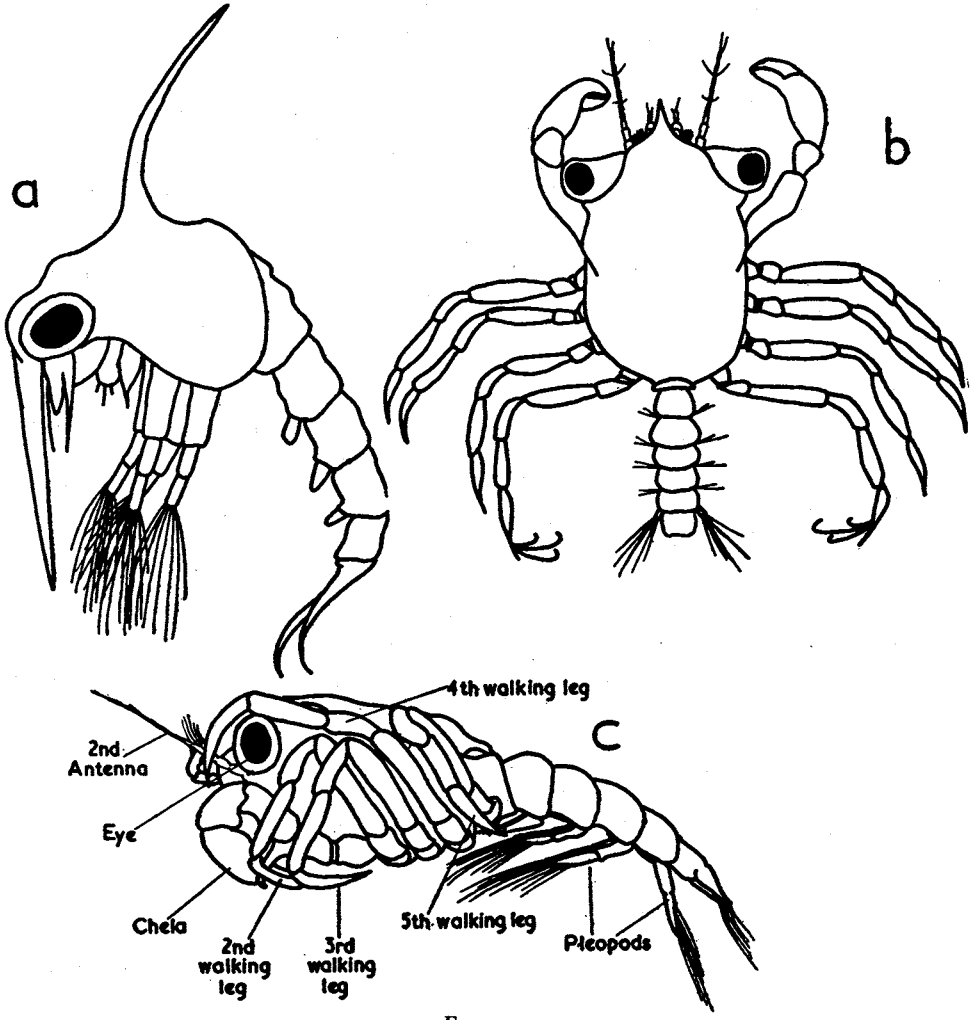


FIG. 5.
Larval stages of *C. maenas*
(*a*) Zoea (3rd zoeal stage, after various authors)
(*b*) Megalopa (after various authors)
(*c*) Megalopa swimming (after Atkins, 1954).

is definite that there is only one megalopa, although it certainly changes shape with age.

The megalopa is still planktonic and still shows vertical migrations—e.g. Colman and Segrove (1955) townetted few over Stoupe Beck Sands by day but thousands by night. The mechanism of the migration is different as the

megalopa has a fully developed statocyst and now responds to increases in pressure by swimming upwards regardless of the direction of any light (Rice, 1964).

The old megalopa sinks to the bottom, chooses a suitable substrate (e.g. fine mud—Southward, 1953) and metamorphoses into the first young crab stage. The young crab (Lebour, 1928; Shen, 1935; Williamson, 1903) has lost the carapace spines and the last pair of pleopods. The other pleopods are no longer used for swimming. The front of the carapace is minutely tri-lobed and the anterolateral teeth are present, but the carapace itself is nearly circular—not until the fifth stage does the familiar shape appear.

The sexual characteristics develop progressively in successive stages (Demeusey, 1958; Shen, 1935) and are complete by the moult of puberty—although they may become further accentuated later. They appear at the second crab stage (Shen, 1935) when a pair of pleopods develop on the first abdominal segment of the male, but not of the female. In later stages the posterior pleopods degenerate (male) or elongate (female). The distinctive form of the male abdomen appears at about the fifth stage although the sutures between segments 3 : 4 and 4 : 5 become indistinct after the third stage when the characteristic ridges on the anterior segments also appear. Females reach puberty after 11–12 moults (Demeusey, 1958) at 16–23 mm. carapace breadth in spring, but at 23–31 mm. in summer (Demeusey, 1963b).

The young crab grows rapidly, with females outgrowing the males over the first nine stages (Shen, 1935). Some individuals reach puberty in the autumn of their first year but late settlers do not attain this size until the following spring (Broekhuysen, 1936). Some aquarium raised crabs have grown even slower (Table 7b) but perhaps their food supply was unsuitable or inadequate.

Broekhuysen (1936) found the growth of Dutch crabs slowed down after puberty, so that by the end of the first year all young crabs were approximately the same size regardless of the time that they settled and thereafter they moulted only once a year (in summer) until they entered terminal anecdysis in the third or fourth year. In Britain (Carlisle, 1957; Naylor, 1962) and in France (Demeusey, 1963a) adults may moult more than once a year, although they usually show a period of anecdysis during the three coldest months (January to March) when moulting almost ceases. Terminal anecdysis is approached through successively longer winter anecdyses (Carlisle, 1957). British crabs also grow appreciably larger than Dutch specimens (Table 7a). Broekhuysen suggested (1936) that the British data (which at that time came entirely from aquarium specimens) showed an abnormal rate of growth correlated with artifically warmed water. However, it could equally be argued that it is the Dutch crabs that are inhibited from moulting for a longer period of the year by the cold and estuarine conditions.

The data in Tables 5 and 7, somewhat confusing because of the differing experimental conditions, suggest (to me) that the life cycle of *C. maenas* is limited to some eighteen moults after the first crab stage. The aquarium raised crabs (e.g. Meek, 1902; Williamson, 1903) grew very slowly in the first year (Table 7b) so if we ignore their data for the moment (and the equivalent data in Table 5) we may postulate that most crabs require some ten moults to reach a carapace breadth ±20 mm., five or six more to reach ±60 mm. and seven

or eight more to reach maximum size (86 mm.) (Carlisle, 1957). In fact very few crabs reach this size as terminal anecdysis may halt growth any time after ±60 mm. (Carlisle, 1957). Turning again to the slower growing crabs it will be noted that eighteen moults is not exceeded, although they enter anecdysis at a smaller size.

Table 5. *Changes in size over a number of moults in aquarium* C. maenas.

References: 1—British Museum (Nat. Hist.) (1927); 2—Carlisle (1957); 3—Crothers (unpublished); 4—Demeusey (1958; 63); 5—Lebour (1928); 6—Shen (1935); 7—Williamson (1903).

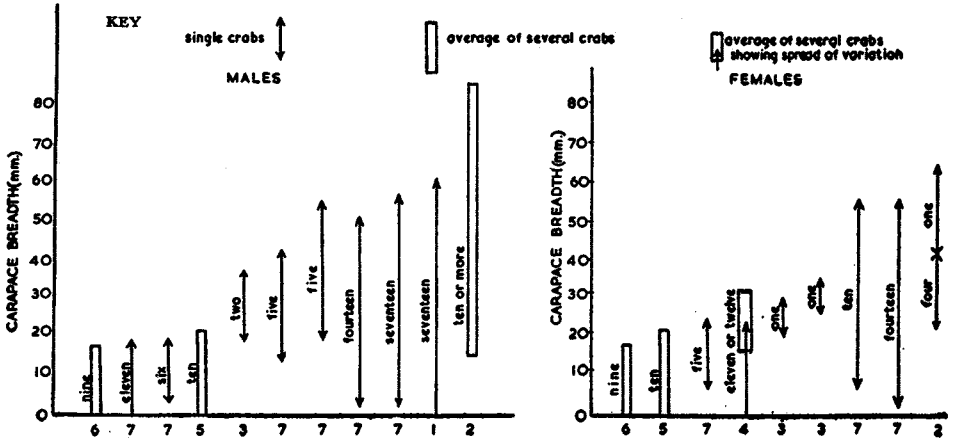


Table 6. *Increase in size (carapace breadth in millimetres) of* C. maenas *on moulting expressed as a percentage of the initial size.*

Data from: Broekhuysen (1936), Crothers (unpublished), Shen (1935) and Williamson (1903).

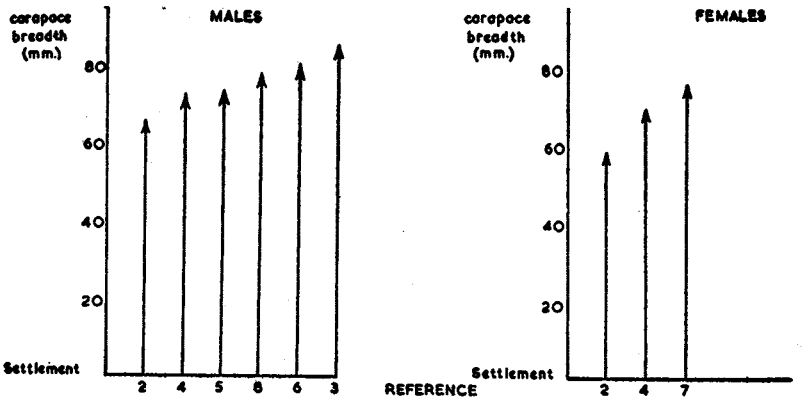
Initial size	all crabs		males only		females only	
	mean	(spread)	mean	(spread)	mean	(spread)
– 3	33	(14–77)	29	(14–50)	33	(20–59)
4– 6	26	(0·8–45)	23	(0·8–45)	29	(20–40)
7– 9	27	(0·7–38)	26	(0·7–33)	27	(15–34)
10–12	29	(17–40)	30	(24–35)	29	(21–40)
13–15	32	(20–47)	30	(20–40)	32	(27–40)
16–18	29	(17–38)	27	(24–33)	31	
19–21	33	(17–48)	37	(29–45)	34	(29–36)
22–24	26	(24–30)	27	(25–30)	26	(24–28)
25–27	30	(25–35)	33		26	(25–27)
28–30	25	(17–34)	28	(24–34)	23	(23–24)
31–40	25	(20–37)	26	(20–30)	25	(22–37)
41–50	19	(10–33)	15	(10–20)	17	(14–23)

The data for crabs larger than 50 mm. are too sparse to be worth including but Williamson (1903) quotes one crab—62 mm.—which moulted without increasing in size.
So average percentage increase 29 (with a spread of 0–77).

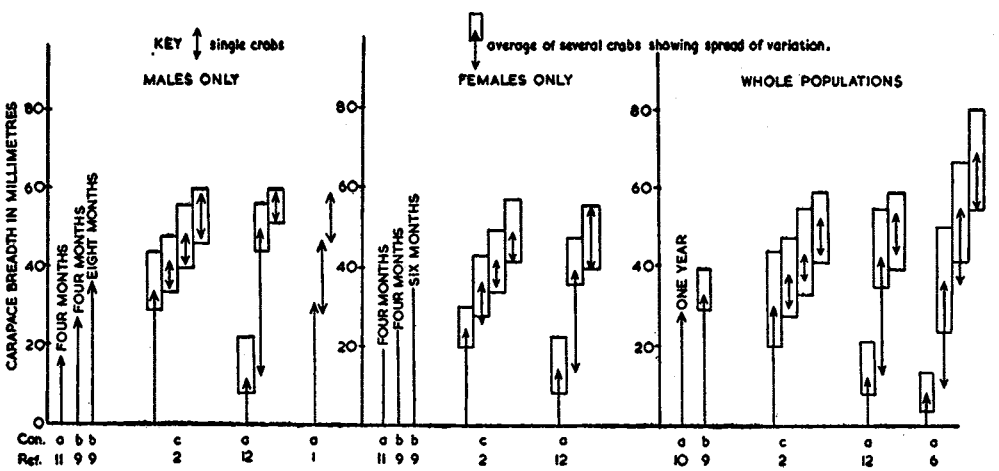
Table 7. *The age and size of* C. maenas.

References: 1—British Museum (Nat. Hist.) (1927); 2—Broekhuysen (1936); 3—Carlisle (1957); 4—Crothers (unpublished); 5—Edwards (1958); 6—Meek (1902); 7, 8—Naylor (1962; 65); 9—Orton (1936); 10—Rothschild (1940); 11—Shen (1935); 12—Williamson (1903).

a. *The size range in natural populations.*



b. *Annual increments in size (carapace breadth) of* C. maenas.



Conditions: (*a*) laboratory aquaria; (*b*) cages in the sea; (*c*) estimates from natural population. Annual increments are unlabelled: series of increments represent growth over the first, second, third year, etc.

C. maenas has a closed growth cycle. On completion of a number of moults (and I suggest ±18) it remains in permanent anecdysis. This has the dual effect of increasing life expectancy amongst young adults—for any reduction in the number of moults decreases their chance of being eaten whilst soft—and at the same time removing the senile, since a crab's time is limited once it enters terminal anecdysis: perhaps this is because it can no longer dispose of waste products deposited in the cuticle, or as a result of the ageing of glandular tissue. But *C. maenas* artificially made to moult again not only grows larger, but lives longer than normal.

Physical Limits to Breeding

Salinity and temperature may both affect the breeding cycle. The adult crab is essentially an estuarine animal, tolerating salinities ranging from normal sea water at 33‰ NaCl down to 10‰ or even 4‰ without harm. The eggs, however, can develop normally at 10° C. only in salinities above 26‰ and at lower temperatures even higher salinities are required. Even short drops in temperature will kill high proportions of the eggs (Broekhuysen, 1936).

Naylor (1965) has described an upper temperature barrier. In the continuously warm water (14–26° C.) of Swansea Docks *C. maenas* could not breed, although the population appeared healthy in other respects. When, subsequently, the water cooled to 6–18° C. breeding became possible.

The Breeding Season

C. maenas pairs when the female moults in summer (see Table 8). The egg plug appears some months later, earliest in the older females. Table 8 shows considerable variations amongst published data for the seasons at which berried females and subsequent larval stages appear. When considering the berried females we are dealing with two variables: the crabs and the chance of finding them. Most berried females move offshore into fully saline surroundings and do not expose themselves to the rigours of shore life. The few that do not move offshore form a small percentage of the crabs found on the shore at low tide. In winter, when adult *C. maenas* are rare on the shore (Naylor, 1962; Crothers, in preparation), one is most unlikely to find a female in berry. The chance of man finding such females is greatest in summer, even though most authors agree that maximum numbers occur in winter.

The data (in Table 8) are obviously inadequate and can lead to no certain conclusions. But, assuming no errors of identification, there are two possible explanations:

(1) The crab breeds continuously, throughout the year: the Plymouth data alone approach completeness: workers in other areas have only recorded the maximum occurrence of eggs or larvae.

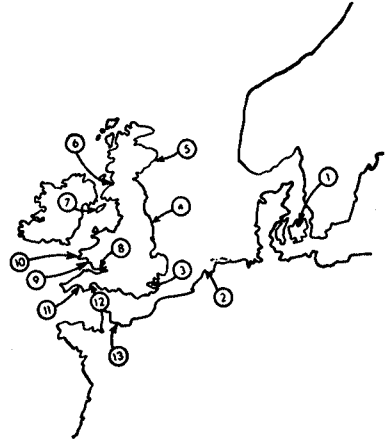
(2) The crab has one or two well-marked breeding seasons in all localities mentioned, but they become confused towards the south-west of Britain.

If the first alternative is correct, and only the accumulation of more data can decide, the next few paragraphs can be ignored. For the second, following Broekhuysen (1936), we may postulate a normal winter cycle and a secondary

Table 8. *The breeding season of* C. maenas.

References: (*a*) Rasmussen (1959); (*b*) Broekhuysen (1936); (*c*) Wells (1938); (*d*) Colman and Segrove (1955); (*e*) Williamson (1903); (*f*) Elmhirst (1922); (*g*) Southward (1953); (*h*) Rees (1939); (*i*) Naylor (1962); (*j*) Crothers (1966); (*k*) Lebour (1928); (*l*) Lebour (1947); (*m*) Marine Biological Association (1957); (*n*) Shen (1935); (*o*) Holme (1949) and (*p*) Demeusey (1963).
Most of these data are from at least one annual series: any casual data are bracketed.

No. (see Map)		Ref.	Copulation	Berried Females main	Berried Females subsid.	Zoeae hatching	Zoeae in plankton	Megalopae in plankton	Settlement	Young Crabs
1	Isejford	a		May–June						
2	Den Helder	b	July–Sept.	Nov.–May	May–	May–				
3	Thames Estuary	c					Mar.–July	August (July–Aug.)		
4	Robin Hood's Bay	d								
5	Aberdeen	e		"most of the year" Oct.–May	Apr.–Sept.	Apr.–July	Mar.–July			
6	Clyde	f		Nov.–May	May, July		Apr.–Sept.			Aug.–Oct.
7	Isle of Man	g							(June–Oct.)	
8	Cardiff	h					July–Sept.	August		
9	Swansea	i	July–Sept.	Feb.–June (max. Apr.)						
10	Milford Haven	j	July–Sept.	Jan.–Apr.	August		all months	May–July		Mar.–Apr.
11	Plymouth	k–n		all year Feb.–Mar.		larvae in the plankton all through the year: numbers maximal in spring minimal from October to December				July–Sept.
12	Exmouth	o							(July)	(July–Aug.)
13	Luc-sur-Mer	p		spring (young adults) Dec.–Feb.	spring (older crabs)					



Sketch-map to show the positions of the places mentioned in Table 8.

summer one. Under adverse conditions only one may appear, and under very favourable conditions the two become merged into a continuous breeding season.

The normal cycle in southwest Britain appears to be: copulation, July/September: eggs, January/April: zoeae, April/June: megalopae, June/July: settlement of young crabs, July/August.

Females physiologically unable to produce eggs at the "normal" time (usually the younger crabs—see Demeusey, 1963) form the secondary summer cycle which takes a shorter length of time because of the warmer water. Berried females are found from late spring until August. Many of their larvae will not develop fast enough to metamorphose by October and so either settle in small numbers throughout the winter or overwinter as zoeae to settle early the following year. So far there is no evidence for either of these suggestions, but Table 8 shows a very limited season for the occurrence of megalopae.

Data from localities away from southwest Britain are slightly out of phase with the cycle outlined above. In the colder water to the north and east the cycles will take longer and in most cases the winter cycle predominates. In the North Sea the lower winter temperatures appear to require a longer period for egg development, for berried females appear earlier (in October/December rather than January/February). Naylor mentions a mechanism which could produce this when he suggests that a drop in temperature might be necessary to stimulate breeding (Naylor, 1965). It is only a short step further to suggest that the earlier (or the greater) the drop in sea temperature, the earlier the onset of breeding.

Where environmental conditions prevent the winter cycle the summer cycle predominates. In part of the Kattegat studied by Rasmussen (1959) the mean salinity—of 19‰—would prevent normal development of the eggs at temperatures below 17° C. (Broekhuysen, 1936). In other estuarine habitats the berried females move into more saline water, but perhaps this is impossible in the Kattegat—so the summer cycle alone can succeed.

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