J. exp. Biol. (1982), 100, 289–319
With 6 figures
Printed in Great Britain

CONTROL AND CO-ORDINATION OF VENTILATION AND CIRCULATION IN CRUSTACEANS: RESPONSES TO HYPOXIA AND EXERCISE

BY E. W. TAYLOR

Department of Zoology and Comparative Physiology, University of Birmingham, P.O. Box 363, Birmingham B15 2TT

SUMMARY

The functional morphology, nervous and hormonal control and co-ordination of the cardiovascular and ventilatory systems in decapodan crustaceans is reviewed. Pacemaker function reflects the reliance of crustaceans on small numbers of large, multipolar neurones. Respiratory gas exchange and transport may be limited by the potential diffusion barrier presented by chitin on the gills and by the relatively low O_2 capacity of the haemolymph, though this is compensated by the relatively high O_2 affinity of haemocyanin and the large volume of the haemocoel. Haemolymph buffering capacity is attributable to haemocyanin and to bicarbonate, including an internal source of fixed base, possibly the exoskeleton.

The typical hypoxic response includes a bradycardia and hyperventilation resulting in a respiratory alkalosis and resultant increase in O_2 affinity of the haemocyanin. Diffusive conductance may increase. When O_2 transport is limiting there is a switch to anaerobiosis with normoxic recovery including repayment of an O_2 debt. Some species are facultative air-breathers and compensate for a respiratory and metabolic acidosis when in air by elevation of buffer base. Central and peripheral O_2 receptors may be involved in determining respiratory and cardiovascular responses to hypoxia and air-breathers may respond to changes in haemolymph pH. Exercise induces a rapid increase in ventilation, diffusive conductance improves and O_2 consumption is elevated. There is also a major anaerobic contribution causing a metabolic acidosis and recovery includes prolonged repayment of an O_2 debt.

INTRODUCTION

The phylum Arthropoda, by virtue of number of species, biomass, range of adaptability, economic importance, apparent ease of sampling and many other criteria has been a popular alternative group to the vertebrates for physiological study. The major class Insecta typically transport respiratory gases directly to and from the tissues in the tracheal system, by-passing the circulatory system. This puts them outside the scope of this review which considers some members of the class Crustacea. Research into the respiratory and circulatory physiology of crustaceans has largely

concentrated on the suborder Reptantia of the order Decapoda (the lobsters, crayfish and crabs). The range of environments they inhabit includes the abyssal, sublittoral and littoral marine, estuarine, freshwater and terrestrial and they may walk, run, climb, swim or burrow (Warner, 1977). Individual species show wide ranges of activity levels, are highly adaptable to variables such as temperature (recently reviewed by Taylor, 1981), salinity and oxygen tension and show behavioural modifications including annual and diurnal migrations which affect the range of variables they encounter. This review is restricted to the Reptantia and considers the exchange of respiratory gases in relation to: the functioning and control of the open circulatory system or haemocoel, which typically contains the respiratory pigment haemocyanin in solution conferring on the haemolymph a relatively high affinity for oxygen but a relatively low and variable capacity both for O_2 and the buffering of CO_2; ventilation of the respiratory gas exchange surfaces, which are covered by a thin but possibly relatively impervious layer of the chitinous exoskeleton. The physiological adjustments observed when O_2 demand outstrips supply during hypoxia, aerial exposure and exercise are described. Symbols used to denote respiratory variables and indices are chiefly those recommended by Dejours (1975) and are defined in the text when first employed.

CIRCULATION

Functional anatomy of the circulatory system

The general features of the circulatory system in crustaceans were reviewed by Maynard (1960) and are illustrated in Fig. 1(*a*). In the Decapoda there is no separation between interstitial fluids and the circulation, which is an open haemocoel. The circulated fluid is termed haemolymph. Haemolymph volume is relatively large and varies with mass from 20–50% of total volume (e.g. Taylor & Wheatly, 1982). The main propulsive organ is the dorsal, single-chambered heart which is composed of striated muscle and operates in a pericardial haemocoelic space from which it draws haemolymph at diastole via valved ostia. The heart is suspended from ligaments and contracts against their elasticity at systole. Diastolic filling is relatively slow and due primarily to elastic recoil in the ligaments returning the heart to its relaxed volume and causing haemolymph to enter from the surrounding pericardial space. Haemolymph is thus aspirated into the heart, which functions as a force-suction pump. Sheets of alary muscles connect the septum, forming the floor of the pericardial space, to the exoskeleton and may by contraction control the volume of the space and the tension on the suspensory ligaments thus influencing venous return and diastolic filling (Wilkens, 1981). Both cardiac stroke volume (SV_H) and heart rate (f_H) increase when the heart is stretched (Izquierdo, 1931) obeying Starling's Law of the heart.

At systole the heart delivers haemolymph into several elastic walled but non-muscular arteries which are valved to prevent backflow and supply organs such as the C.N.S., appendages, gills, bladder and genitalia. The haemolymph runs into interstitial spaces or lacunae in the tissues then collects in large sinuses bordered by connective tissue. In larger and more active species some arteries terminate in fine vessels 2–10 μm in diameter and resemble capillaries (Sandeman, 1967). These are found in organs such as the C.N.S., the osmoregulatory green gland and the gastrolith

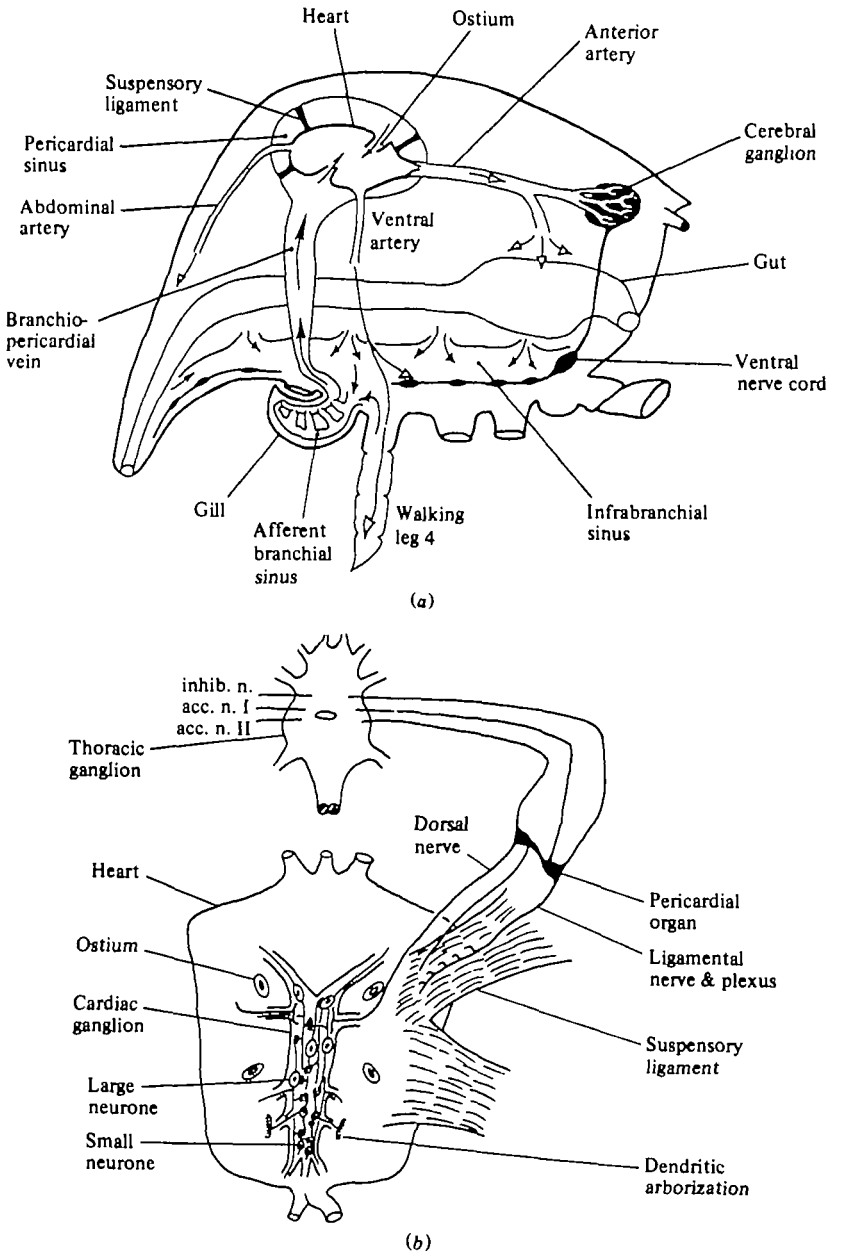

Fig. 1. Diagram of the functional anatomy of the cardiovascular system in decapodan crustaceans. (*a*) The general form of the circulation in a crab. Haemolymph flowing from the heart is indicated by open arrows and haemolymph which has perfused the tissues and is collecting in sinuses to be returned to the heart via the gills is indicated by closed arrows. The supply of haemolymph to one thoracic appendage and its associated gill is indicated; these are lateral whereas the C.N.S. is medio-ventral. (*b*) The heart plus cardiac ganglion. Cardioregulator nerves from the C.N.S. travel dorsally in 3 nerve trunks which supply the pericardial gland and suspensory ligaments on each side. A pair of dorsal nerves to the heart contain the inhibitor and 2 accelerator fibres. The cardiac ganglion, which is drawn disproportionately large, contains 9 neurones, 4 small posterior cells and 5 larger anterior cells all in synaptic contact. A more detailed description of both (*a*) and (*b*) is given in the text.

fields of the stomach wall which are the sites of calcium storage whose possible significance is considered below. The haemolymph drains from the systemic circulation into several large sinuses which then open into an infrabranchial sinus running ventrally along either side of the body. In each segment of the thorax this sinus receives haemolymph from the locomotory appendage and supplies haemolymph to the afferent branchial sinuses in the gills. From the branchial lacunae the oxygenated haemolymph collects in the branchiopericardial veins which connect back to the pericardial sinus, and from there it enters the heart to be recirculated.

Measurements of the pressures and flows generated in the haemocoel have recently been summarized and compared with other invertebrates and fish by McMahon & Wilkens (1982). In the lobster *Panulirus interruptus* ventricular systolic pressure was 36 mmHg and diastolic pressure was 16 mmHg (Belman, 1975, 1976). Elastic compliance kept arterial pressure close to systolic pressure. Mean pressure in the infrabranchial sinus was 19 mmHg and in the pericardial sinus 18 mmHg. Blatchford (1971) measured lower pressures throughout the haemocoel of *Carcinus maenas* and a pressure differential of approximately 2 mmHg across the branchial vasculature. These low pressures are accompanied by a relatively high cardiac output which implies that peripheral resistance in the circulation is low. The high cardiac output, which is 3–4 times higher than in fish if equivalent mass relates to the relatively low carrying capacity of the haemolymph for oxygen, though the total capacity per unit mass is similar for crustaceans and fish because haemolymph volume is approximately 10 times higher than blood volume and both comprise a similar venous reserve of oxygen for use during periods of oxygen lack or increased demand.

The action of the heart appears sufficient to account for flow through the entire circulatory system (Burger & Smythe, 1953; Blatchford, 1971; Belman, 1976), though perfusion of the gills, which receive haemolymph after its passage through the systemic circulation, may be aided by the aspiration of haemolymph from the branchiopericardial veins into the pericardial sinus, which shows pulsatile reductions in pressure as the volume of the heart decreases at systole (Belman, 1976). Another factor possibly aiding flow through the branchial circulation is the subambient hydrostatic pressure generated in the branchial chambers by the scaphognathites during forward ventilation, which may cause distension of the vasculature and further reduce resistance to flow (Burger & Smythe, 1953; Blatchford, 1971). Direct evidence of this effect has recently been obtained (L. E. Burnett – personal communication) and is referred to below. Progressively lower pressures are generated during periods of hyperventilation and if this were reflected in further reductions in branchial vascular resistance it could represent a direct physical mechanism matching ventilatory and perfusion flows to satisfy a demand for increased rates of gas exchange.

Movements of the locomotory appendages by active animals may promote the flow of haemolymph through the branchial circulation by aiding venous return, though the increased pressures in the limb sinuses during movement may not cause directional flow through the gills if no valves are present (Burger & Smythe, 1953). Recent observations indicate some rectification of flow through the branchial circulation of *Carcinus* gills, possibly attributable to valve-like structures identified at the openings into the efferent, hypobranchial vessels (H. H. Taylor and E. W. Taylor, unpublished observations).

The anatomical arrangement of the circulatory system renders direct measurement of haemolymph flow extremely difficult. Measurements of flow using a thermodilution technique (Burnett *et al.* reported by Wilkens, 1981) indicated that cardiac stroke volume (SV_H) varied widely in three species of crabs. The range of variations in heart rate (f_H) observed in response to disturbance, hypoxia and exercise is often compensated or amplified by apparent changes in SV_H which seems to be the more important variable. Wilkens (1981) explored the theoretical reasons, based on the mechanics of heart pumping, for this observed relationship. Clearly, measurements of f_H cannot be a reliable guide to cardiac output.

Estimations of haemolymph flow based on the Fick principle may be suspect as the popular sampling site at the base of a walking leg cannot yield a mixed venous sample and measurements of O_2 content should be referred to as C_v,O_2 levels, rather than $C_{\bar{v}},O_2$ (Taylor *et al.* 1977*a*; Taylor & Butler, 1978). Another objection to sampling haemolymph from this site is that it often involves removing aquatic crustaceans from water, which rapidly results in internal hypoxia and consequent major distortion of blood gas measurements (Taylor *et al.* 1973). Use of the Fick principle necessitates continuous monitoring of heart beat as cardiac arrhythmia and arrest, associated with ventilatory changes, are common in both settled (e.g. Butler *et al.* 1978), and disturbed crustaceans, and this rapidly leads to a decline in haemolymph P_{O_2} (e.g. Taylor *et al.* 1973).

The cardiac pacemaker

In crustaceans muscle contraction is induced primarily by small, cumulative depolarisations of the muscle fibre membranes called junctional potentials (Fatt & Katz, 1953) which arise from a number of motor endplates on each fibre (Hoyle & Wiersma, 1958). Propagated muscle action potentials are not necessary for contraction.

These characteristics rule out the possibility of a functional myogenic pacemaker, as described in mammals. Intracellular recordings of voltage changes in myocardial cells during contraction are superficially similar to those recorded from the mammalian heart but consist of summated junctional potentials which arise from activity in 4 or 5 nerve axons supplying each muscle fibre (Van der Kloot, 1980). The simultaneous contraction of the whole myocardium at systole is achieved by a burst of propagated action potentials travelling from a group of neurones embedded in the dorsal wall of the heart, and called the cardiac ganglion, which constitute the neurogenic pacemaker of the heart (Fig. 1*b*). Early descriptions of its form and function were reviewed by Maynard (1960), and its characteristics are summarized in Fig. 3. Typically, it consists of 9 neurones; 4 posteriorly placed, small cells around 50 μm in diameter and 5 anteriorly placed larger cells, 100–200 μm in diameter. Each cell is multipolar with numerous axons, collaterals and complex dendrites, termed dendritic arborizations and speculatively assigned the function of stretch receptors. There is anatomical evidence for reciprocal contact at sites on the various processes and soma of all 9 neurones. Extracellular recordings from the trunk of the cardiac ganglion of the crab *Portunus sanguinolentus* consisted of spontaneous nervous activity organized into regularly patterned, rhythmic bursts of action potentials from small and large cells (Tazaki & Cooke, 1979). Activity in the processes of small cells started and ended each burst and they fired trains of impulses throughout the bursts which were not

synchronized with other cells. The 5 large cells fired trains of impulses which were synchronized, possibly due to electrotonic coupling (Watanabe & Bullock, 1960) and slower than the small cell trains. Intracellular recordings from the soma of small cells showed a slow, 'pacemaker' depolarization to a plateau on which were superimposed attenuated action potentials which were passing along the processes of the cell but not invading its soma. Intracellular recordings from large cell soma showed post-synaptic potentials which corresponded with spiking activity in small cells, attenuated spikes and an underlying slow depolarization during bursts with no pacemaker depolarization apparent between bursts. The morphological distinction between small and large cells appeared to reflect a functional difference, with the small cells comprising the primary pacemaker, determining bursting rate (Hagiwara & Bullock, 1957), possibly by acting as endogenous burst oscillators (Otani & Bullock, 1959). The system seems essentially two-layered with electrotonic and synaptic contact from the small pacemaker cells serving to drive the large motor neurones which act as 'follower cells' innervating the myocardium (Mayeri, 1973). The subsequent driver potential which arose on the large cell was the source of the depolarizing current which initiated its burst of action potentials and in turn caused the myocardium to contract. Injection of depolarizing and hyperpolarizing currents into large cell soma at various phases of the cycle of bursting activity in the ganglion revealed that the interburst interval related to the previous driver potential duration and that various phase shifts could be induced which indicated that the cardiac ganglion functioned as a 'relaxation oscillator' with pacemaker cell function modified by electrotonic feedback from the follower cells (Benson, 1980). When large cell driver potentials were eliminated with octopamine small cell activity increased in frequency suggesting that the small cells were held in a depolarized state by electrotonic spread of the large cell driver potentials and that their duration may be the factor determining the frequency of the cardiac rhythm. This description renders the cardiac ganglion susceptible to entrainment, by virtue of induced phase shifts, in response to externally applied current pulses and comprises a mechanism for the potential synchronization of cardiac activity with other rhythmic behaviours.

Action potentials in the neurones of the cardiac ganglion do not invade the soma so that two separate impulses may travel simultaneously in different processes from the same neurone without interference (Bullock & Terzuolo, 1957). The crustacean heart is known to respond to distension with an increase in rate and amplitude and if this can be demonstrated to be modification of motor output to the myocardium arising from stimulation of the 'dendritic arborizations' then they represent the afferent limb of a single-neurone reflex arc (Maynard, 1960).

Cardioregulatory nerves

The crustacean heart receives inhibitor and accelerator nerves from either the suboesophageal or thoracic ganglia which run in separate trunks to the pericardial sinus where some axons supply a pair of neurohaemal, pericardial organs, others supply a plexus on the suspensory ligaments and one fibre from each trunk is combined into a dorsal nerve which enters the heart to innervate the cardiac ganglion as shown in Fig. 1*b* (Alexandrowicz, 1932; Maynard, 1953, 1960). Peripheral electrical

stimulation of the inhibitor nerve trunks causes a marked bradycardia followed by adaptation with no marked after effect. The inhibitory transmitter may be γ amino butyric acid (Florey, 1963). The accelerators show no adaptation and a prolonged after effect (Wiersma & Novitski, 1942; Maynard, 1953; Florey, 1960) which is mimicked by acetylcholine though the transmitter is possibly an indol alkylamine (Florey, 1963). Maynard (1960) concluded that the cardioregulatory nerves were probably involved in brief reflex inhibition and acceleration of the heart. They are, however, continuously active in the prepared animal (Taylor, 1970; Field and Larimer, 1975*a*; Young, 1978) and may exert a tonic control over heart rate similar to the vagal tone operating on the fish heart (e.g. Taylor, Short & Butler, 1977).

The cardioregulatory effects are imposed directly upon the cardiac ganglion. Intracellular recordings from the large follower cells in *Panulirus interruptus* included i.p.s.p. resulting from stimulation of inhibitor nerve trunks which were either hyperpolarizing or depolarizing depending upon the membrane potential, and showed both facilitation and summation (Terzuolo & Bullock, reported by Maynard, 1961). The i.p.s.p. could either block or potentiate the development of the generator potential and consequent spiking potentials, though stimulation of the inhibitor nerves typically caused a drop in the frequency of the trains of impulses from the ganglion plus a reduction in the number and frequency of impulses within each train (Maynard, 1961).

Interneurones, referred to as cardiac command fibres by Field and Larimer (1975*b*), have been identified in the circumoesophageal connectives which when stimulated electrically cause a tachycardia (the accelerators), cardiac arrest (the strong inhibitors) or a bradycardia (the weak inhibitors) often followed by a post-stimulation rebound (Wiersma & Novitski, 1942; E. W. Taylor, unpublished observations). They are tonically active (Wilkins *et al.* 1974) and when stimulated either directly or by sensory input may induce reciprocal activity in inhibitor and accelerator outputs (Field & Larimer, 1975*a*, *b*).

Cardioregulatory hormones

Substances which affect the beating of the heart have been extracted from a number of potential sites of hormone production (Maynard, 1960). The pericardial organs (P.O.) located in the pericardial space on either side of the heart, which receive axons from the cardioregulatory nerve trunks, appear to be directly involved in hormonal control of the heart. Extracts of P.O. increase the frequency and amplitude of heart beat and may restore steady beating to an arrhythmic preparation (Alexandrowicz & Carlisle, 1953). Cooke (1966) identified the site of action of the extracts as the cardiac ganglion and Cooke & Hartline (1975) pinpointed the effect to trigger zones near the soma of the neurones, particularly the small pacemaker cells, where application caused increases in the rate and duration of the bursts of spiking potentials. Electrical stimulation of the P.O. caused graded cardioacceleration proportional to the number of stimuli given (Cooke, 1964).

The effect of P.O. extract was mimicked by 5-hydroxytryptamine (5HT) (Carlisle, 1956; Maynard & Welsh, 1959) and the P.O. produces a range of biogenic amines including HT, octopamine and dopamine. All three amines cause cardioacceleration in the crayfish *Astacus leptodactylus* with HT the most effective (Florey & Rathmayer,

1978). Berlind and Cooke (1968) concluded that 5-HT and dopamine levels in the P.O. of *Libinia* were too low to be effective in cardioregulation and attributed this role to peptides which were released from the P.O. by electrical stimulation at levels causing cardioacceleration. This confirmed the identification of cardioexcitor peptides from extracts of P.O. (Belamarich & Terwilliger, 1966). A substance similar in properties to proctolin, a putative peptide transmitter from insect gut, was isolated from the P.O. of *Cardisoma* and shown to have an inotropic effect on the heart (Sullivan, 1979). Neurones in the C.N.S. which produce biogenic amines respond to sensory input, are coupled together electrotonically, subject to autoregulation and become spontaneously active above 14 °C (Konishi & Kravitz, 1978), firing bursts of impulses at high temperatures similar to those described in the cardioaccelerator nerve trunks which supply the P.O. (Taylor, 1970).

The site of release of these hormones by the P.O. is directly upstream of the heart and they are aspirated from the pericardial space into the heart at diastole. A similar functional location has been described for the chromaffin tissue which produces biogenic amines in the cardinal sinuses of elasmobranch fishes (Butler & Taylor, 1975). It is possible that tonic control of heart rate and possibly cardiac stroke volume may be exerted by hormones released from the P.O. possibly by the bursts of activity recorded from the accelerator nerve trunks of the crayfish, which corresponded to periodic variations in cardiac 'tone' (Taylor, 1970). Hormones produced by the P.O. may coordinate heart and scaphognathite beating as discussed below.

VENTILATION

The gills

The exchange of respiratory gases between the environment and circulatory system of decapod crustaceans is by passive diffusion and is virtually restricted to the elaborate gills, developed as outpushings of the body wall associated with the bases of the major appendages and enclosed in branchial chambers formed by folds of the body wall termed branchiostegites (Figure 2*a*). Consequently it may be adequately described by derivations from Fick's Law of diffusion (Dejours, 1975). The functional morphology of the gills combines minimum diffusion distance with maximum surface area for exchange thus ensuring a high diffusing capacity favouring effective gas exchange. The gills may possess regularly stacked flattened lamellae as in the phyllobranchiate gills of most brachyuran crabs or consist of filaments which may be single (trichobranchiate) as in the crayfish or branched (dendrobranchiate) as in some shrimps.

The fine structure of phyllobranchiate gills has been described by Taylor & Butler (1978) and Taylor & Greenaway (1979). As they are extensions of the outer surface, the gills are covered with a thin layer of chitin 2–5 μm thick. The shortest diffusion distance is 5–8 μm which includes processes of epithelial cells. This is similar to the diffusion barrier described on fish gills (Hughes, 1972) and other aspects of gill structure such as the arrangement of pillar cells and blood spaces are superficially similar to the structure of fish gill secondary lamellae (e.g. Laurent & Dunel, 1980) though the exchange surfaces on crustacean gills are the morphological equivalents of the primary lamellae. Chitin on the gills presents a special problem as its diffusion

constant for oxygen is reportedly 10% of the value for tissue (Krogh, 1919) so that the effective diffusion barrier over *Carcinus* gills may be 5–10 times higher than over fish gills with 80% of it attributable to chitin (Taylor & Butler, 1978). Compensation for this potential problem may be reflected in the large gill areas in aquatic crustaceans relative to their mass and oxygen requirements. Weight specific gill areas for a number of crustacean species (Gray, 1957) fall within the range given for teleost fish by Hughes & Morgan (1973) with the relatively sluggish crustaceans having gill areas similar to those of more active fish species. The chitin layer may be relatively thin over the gills of animals with a high O_2 demand such as the swimming crab *Callinectes* (Booth *et al.* 1982) or a limited O_2 supply such as *Gnathophausia*, which inhabits a hypoxic environment (Belman & Childress, 1976) and is 300 nm over the inner wall of the branchiostegite which functions as a 'lung' in the land crab *Holthusiana* (Taylor & Greenaway, 1979).

Ventilation of the gills

Ventilation of the branchial chambers on each side of the animal is accomplished by a baler called the scaphognathite, a specialized appendage which morphologically is a flattened exopodite of the second maxilla, one of the mouthparts (Fig. 2*b*). The blade of the scaphognathite oscillates dorsoventrally with a complex sinusoidal action (Young, 1975) in the narrow exhalent channel at the front of each branchial chamber (Fig. 2*a*). In the typical forward mode of ventilation the scaphognathite generates a pulsatile hydrostatic pressure which is below ambient by 1–5 cm H_2O, depending on the mass of the animal and rate of ventilation (e.g. McDonald *et al.* 1977; Taylor & Wheatly, 1980). Consequently water is sucked into the branchial chambers and over the gills via a series of openings around the bases of the walking legs. In brachyuran crabs such as *Carcinus maenas* up to 80% of total ventilatory flow enters through the Milne-Edwards openings at the bases of the chelipeds to supply the anterior 7 gills on each side (Hughes *et al.* 1969). Pressure recordings from the branchial chamber of a number of aquatic crabs (Hughes *et al.* 1969; Taylor *et al.* 1973; McMahon & Wilkins, 1977) lobsters (McMahon & Wilkins, 1975; Butler *et al.* 1978) and crayfish (McMahon *et al.* 1974; Taylor & Wheatly, 1980) demonstrate a typical biphasic waveform. Both strokes of the scaphognathite generate forward force (Wilkens & McMahon, 1972; Young, 1975) and are equally involved in movement of water (McDonald *et al.* 1977; Batterton & Cameron, 1978). Most species ventilate the gills predominantly in the forward direction and a functional counter-current flow of water and blood was described over the lamellae of the phyllobranchiate gills of *Carcinus maenas* in this mode (Hughes *et al.* 1969) though P_{a,O_2} values are typically lower than P_{E,O_2} (e.g. Wheatly & Taylor, 1981) and the benefits of counter-current exchange may be masked by a large ventilatory dead-space in the branchial chambers (Johansen *et al.* 1970; McMahon & Wilkens, 1982).

The beat of the scaphognathite is periodically reversed, in some species, particularly macrurans, for 1 or 2 beats (e.g. Wilkens & McMahon, 1972; Taylor & Wheatly, 1980), in others, typically the brachyuran crabs, for bursts of several beats (e.g. Hughes *et al.* 1969; Taylor *et al.* 1973). Several roles have been speculatively attributed to scaphognathite reversals including clearing the gills or apertures of detritus, flushing

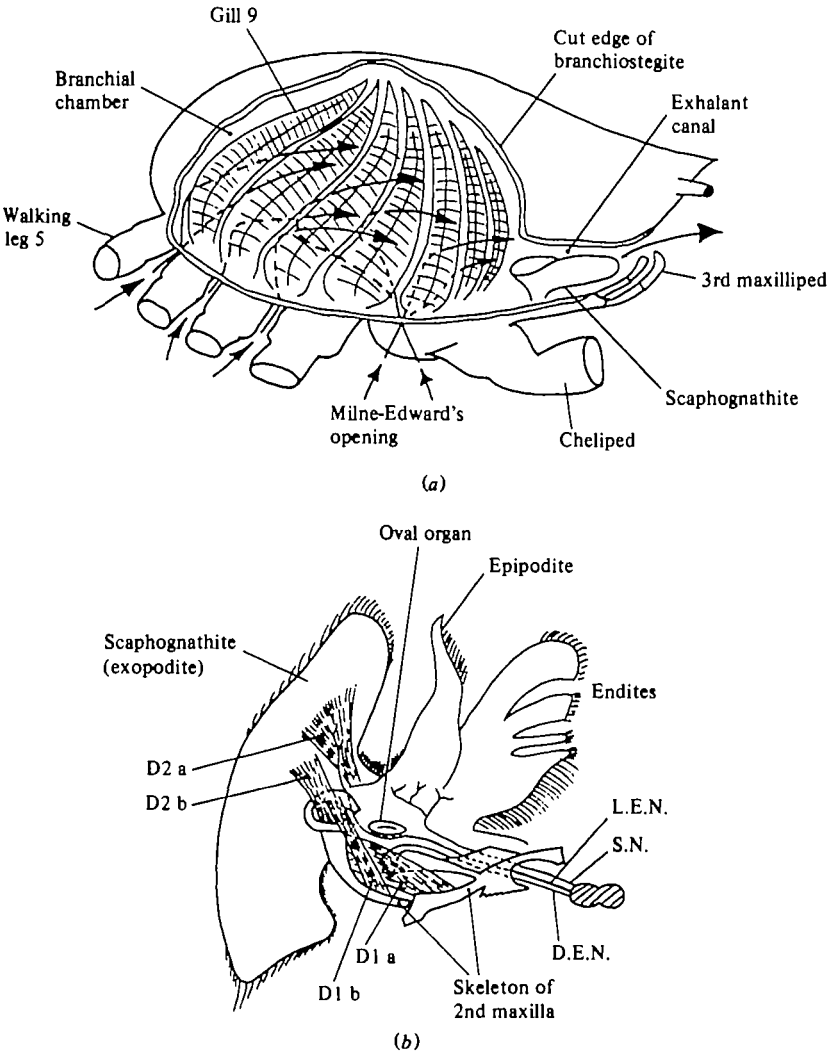

Fig. 2. Diagrams of the functional anatomy of the ventilatory system in decapodan crustaceans. (*a*) Pattern of water flow through the branchial chamber of a crab; the branchiostegite has been removed to reveal the gills. Water enters around the limb bases and flows from the ventral hypobranchial space over the gill lamellae into the epibranchial space from which it is drawn forwards by the scaphognathite to be expelled anteriorly. (*b*) The second maxilla, one of the mouthparts, which bears the scaphognathite, a flattened exopodite. Parts of the complexly articulated skeletal system and some of the muscles which depress the blade of the scaphognathite, D 1*a*, *b* and D 2*a*, *b*, are indicated; together with 3 nerves: LEN, a mixed nerve supplying levator muscles plus D 2*a* and the oval organ; DEN, a motor nerve supplying depressor muscles and SN, a sensory nerve supplying the endites (based on Pasztor, 1968, 1969; Young, 1975). Each system is described in greater detail in the text.

poorly ventilated areas of the branchial chambers or sampling the water ahead of the animal (Borradaile, 1922; Arudpragasam & Naylor, 1964*a*; Hughes *et al.* 1969). Reversals may predominate in buried crabs when forward ventilation is precluded (Arudpragasam & Naylor, 1966; Bridges, 1976). The frequency and duration of reversals increased during progressive hypoxia in *Carcinus*, and were employed to aerate the branchial chamber (Taylor & Butler, 1973).

Immediately after experimental manipulation crustaceans typically ventilate both branchial chambers continuously. After settling in the experimental regime they often show prolonged respiratory pauses or unilateral ventilation (McDonald *et al.* 1977; Butler *et al.* 1978). Pauses may serve to avoid detection by a possible predator (McMahon and Wilkens, 1977) and *Carcinus* has been observed to show immediate cessation of ventilation, with an associated bradycardia in response to the appearance of the investigator (Taylor *et al.* 1973). They also decrease the energy cost of ventilation for the resting animal without necessarily depleting O_2 supply to the tissues which may be maintained for short periods due to the relatively large venous reserve of O_2 in the circulating haemolymph (see below).

The flow of water or air through the various apertures and the chambers is relatively complex (e.g. Hughes *et al.* 1969) and subject to control by movements of accessory organs such as the limb bases, particularly the 1st maxilliped which forms the floor of the exhalent canal (Wilkens, 1981) and the epipodite of the 3rd maxilliped which varies the size of the Milne–Edwards openings and may control the direction of water flow into the branchial chambers in brachyuran crabs (Borradaile, 1922). Movements of these organs may alter the resistance to flow of the apertures and chambers, particularly during reversals (McDonald *et al.* 1977). The medial, epimeral wall of the branchial chambers is flexible and can be pulled inward, enlarging the chamber and causing subambient pressures which may aid ventilation (Wilkens & McMahon, 1972), and is utilized by a number of air-breathing crabs (see below). Though the work of Batterton & Cameron (1978) established a relationship between f_R and $\dot{V}_W$ in *Callinectes sapidus* there are many examples of changes in $\dot{V}_W$ independent of a change in f_R which implies that the stroke volume (SV_R) of the scaphognathite is variable (e.g. Arudpragasam & Naylor, 1964*b*, Wheatly & Taylor, 1981). Beat by beat measurements revealed that SV_R and f_R varied widely and often independently in crayfish and lobsters (Mercier & Wilkens, reported by Wilkens, 1981). Measurements of f_R alone cannot be a useful guide to relative rates of gill ventilation which vary during hypoxia, aerial exposure and exercise. Other factors which render indirect measurements of $\dot{V}_W$ hazardous are the ventilatory reversals and pauses. Calculation of $\dot{V}_W$ from measurements of $\dot{M}_{O_2}$, P_{I,O_2} and P_{E,O_2}, assuming the Fick relationship is applicable, ignores the possibility that a water sample collected from in front of the exhalent opening may give a fallaciously high value for apparent P_{E,O_2} during a reversal or pause in ventilation (e.g. Butler *et al.* 1978), and similar sampling problems were encountered in air-breathing crabs during intermittent ventilation (Wood & Randall, 1981*a*). Many authors have restrained crustaceans in order to collect expired water (e.g. Arudpragasam & Naylor, 1964*b*; Taylor, 1976); this is undesirable as it is unlikely that they will show settled rates of ventilation. Other studies have used light hoods which separate the inhalent and exhalent streams without restraining the animals (e.g. Butler *et al.* 1978; Taylor & Wheatly, 1980) or small funnels located in the expiratory stream (Taylor *et al.* 1977*a*). These have seemed satisfactory, yielding values for percentage extraction of available O_2 from the inspired water (% $Extn_W$) of between 30 and 40%, but have recently been criticized by J.-C. Massabuau (personal communication) who, sampling directly from a cannula inserted in the exhalent canal of the crayfish *Astacus leptodactylus*, obtained low P_{E,O_2} values and a % $Extn_W$ of approximately 80%.

Control of the scaphognathites

The scaphognathite is powered by the complex musculature of the second maxilla (Fig. 2*b*) and studies of its motor control have established the functional role of these muscles in the rhythmic beating of the scaphognathite (e.g. Pasztor, 1968; Pilkington & Simmers, 1973). Young (1975) recognized 10 muscles responsible for scaphognathite movements and classified them into sets according to their functions. These functional divisions were reflected in their innervation and in the organization of bursting activity in the motor nerves from the C.N.S. During the beating cycle the muscles showed sharply defined bursts of excitatory junctional potentials in particular phases of the scaphognathite beat, leading to contraction and alternating with completely silent periods. The peak frequencies of spiking within the bursts were synchronized within muscle sets but coincidental with a trough in the temporally adjacent set, indicating positive synchronizing interaction between motor units within a set, possibly by electrotonic coupling, and negative interaction between units in temporally adjacent groups. Young (1975) related the sequence of burst patterns in the ventilatory muscles with the movements of the scaphognathite in both the forward and reversed modes and the reader is referred to his excellent account and to a review by Wilkens (1976) for an understanding of scaphognathite function and control.

The second maxilla receives a single nerve from the C.N.S. which divides into 3 trunks, one sensory, one mixed, the other predominantly motor (Fig. 2*b*). Each muscle is innervated by 2 or 3 excitatory neurones with apparently no peripheral inhibitory fibres (Pasztor, 1968; Young, 1975; Pilkington & McFarlane, 1978). Young (1975) concluded that the rhythmicity of the system was determined centrally at premotoneuronal level by sinusoidal input from an oscillator. Mendelson (1971) identified pacemaker neurones in the subeosophageal ganglion of lobsters and hermit crabs and their existence was verified by Simmers (1979) who recorded intracellularly from spiking and non-spiking and non-spiking neurones in the thoracic ganglion of *Carcinus* which showed oscillatory activity in phase with ventilation. Pilkington (1976) entrained scaphognathite rhythm to a slowly alternating current applied to the ganglion which presumably drove the pacemaker. Young (1975) suggested that the phase constancy of the motor units, which gives rise to the fixed sequential contractions of the ventilatory muscles, was dependent upon the different thresholds for depolarization by the pacemaker of the depressor motoneurones supplying muscles which depressed the scaphognathite and activation of the levator motoneurones by rebound during the relatively repolarized phase of the pacemaker (Mendelson, 1971). He also speculated that there may be interneurones which modulate the cycling rate of the driver oscillator or pacemaker which could feed forward onto the levator motoneurones and would themselves be subject to feedback from the pacemaker. Young (1975) presented a model for control of the scaphognathite which proposed that its beating is determined centrally by the modulated but fundamentally intrinsic rhythmicity of a pacemaker, though the motoneuronal output is interactive. Reversal of scaphognathite beating may be achieved by a command input which by-passes the pacemaker and changes the relative threshold of the motoneurone sets causing a rephasing of the cycles of depolarization and recruiting some alternative muscles.

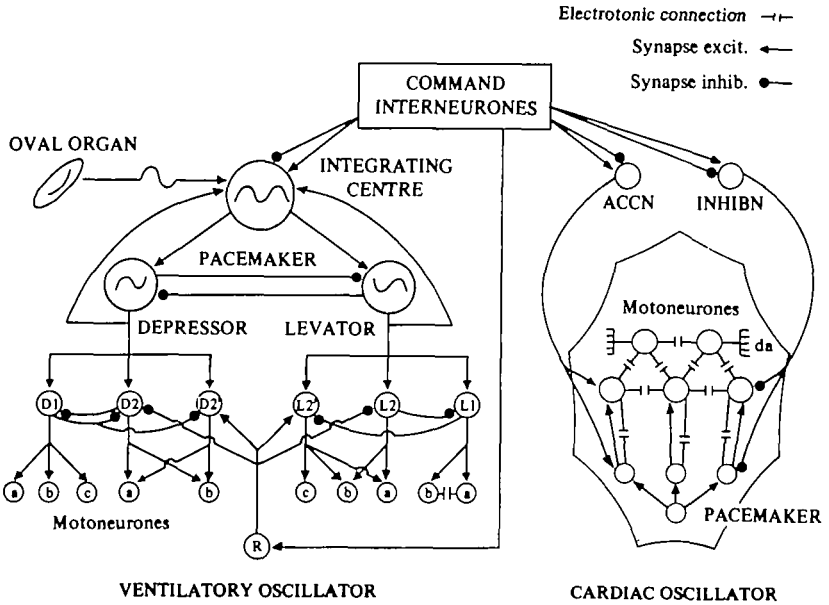

Fig. 3. Diagram of the possible functional organization of the neuronal pacemaker mechanisms determining ventilatory and cardiac rhythmicity in decapodan crustaceans. The ventilatory oscillator resides in the C.N.S. and consists of silent neurones with membrane potentials which vary spontaneously in synchrony with depression or levation of the scaphognathites and show reciprocal inhibition. These drive depressor (D) or levator (L) interneurones which innervate sets of motoneurones (*a*, *b*, *c*) each supplying specific scaphognathite muscles whose contraction sequence is determined by the relative threshold for depolarization of the interneurones by the oscillators. The endogenous rhythmicity of the oscillator neurones may be entrained to a central integrating centre which receives information on scaphognathite movements from the oval organ. Reversal of the ventilation may be achieved by a command input (R) which by-passes the pacemaker, changes the relative threshold of the motoneurone sets, causing a rephasing of the cycles of depolarization, and recruits alternative interneurones (D_2' and L_2').

The neurogenic pacemaker of the crustacean heart is the cardiac ganglion. Cardiac pacemaker function has been ascribed to the 4 small cells in the cardiac ganglion, which show pacemaker potentials and initiate regular bursts of activity in the ganglion. These drive the 5 large follower motoneurones which are electrotonically coupled together to produce co-ordinated bursts of activity which drive the myocardium. The rhythm determined by the pacemaker neurones may be influenced by electrotonic feedback of the duration of driver potentials on the follower cells, tonic input via inhibitor or accelerator fibres from the C.N.S. and a possible stretch reflex arising within the heart from stimulation of the dendritic arborizations (da). Co-ordination of ventilation and perfusion is achieved by command interneurones which override the pacemakers and may cause simultaneous changes in rate or cessation of the two pumps in response to sensory stimulation or changes in activity levels.

Simmers & Bush (1980) located two non-spiking interneurones in the thoracic ganglion of *Carcinus* with membrane potentials which oscillated in phase with activity in either the depressor or levator motoneurones and may show reciprocal inhibition. This replaces the proposed existence of a single oscillator and is included in a version of Young's model as part of Figure 3.

Pasztor (1969) identified and characterized a unique receptor, the oval organ, on the dorsal surface of the scaphognathite (Fig. 2*b*) which is innervated by large axons discharging in patterned bursts during scaphognathite movements (Pasztor, 1969;

Young & Coyer, 1979). Motor output to the scaphognathite can be entrained to movements imposed upon it, suggesting that afferent input can exert a phasic influence on the central pacemaker (Young & Coyer, 1979). The input from the oval organ consists of both impulses and graded receptor potentials which showed a linear relationship with the amplitude of stretch applied to connective tissue strands on the organ (Pasztor & Bush, 1982). These potentials may provide the basis for a tonic influence over scaphognathite motoneurones attributed to the afferent input by Pasztor (1968), Mendelson (1971) and Wilkens & Young (1975).

During active forward ventilation of the branchial chambers there is often significant phase coupling between the ventilatory cycles of the two scaphognathites following either drift and lock or absolute phase-locked co-ordination (Wilkens & Young, 1975; Young & Coyer, 1979). Often the scaphognathites beat in synchrony but other phase relationships also occur. This may imply some advantage from coupling of the rhythms which could result in increased stability and regularity of pumping (Young & Coyer, 1979). Cross-ganglionic motoneuronal processes which could mediate this co-ordination have been described in the lobster (Wilkens & Young, 1975) and crab (Pilkington & MacFarlane, 1978). At other times the scaphognathites beat independently at different intrinsic rates (Batterton & Cameron, 1978) and in settled, inactive animals ventilation may become unilateral for long periods in both water-breathers (McDonald *et al.* 1977; Butler *et al.* 1978) and air breathers (Wood & Randall, 1981*a*). Reversals may occur simultaneously on both sides or independently (Taylor *et al.* 1973; Batterton & Cameron, 1978).

Berlind (1976) injected extracts of pericardial organs into crabs and crayfish and obtained an acceleration of scaphognathite rate which he attributed to peptides rather than amines. Injection of 5 HT into *Carcinus maenas* reduced f_R and increased reversal frequency (Berlind, 1977). When 5 HT was applied to the thoracic ganglion it reduced bursting frequency in motoneurones supplying the scaphognathite indicating that the effect was on the central oscillator. Increased reversal frequency, induced by addition of particulate matter to the water was blocked by a 5 HT antagonist. Glutamate and possible acetylcholine increased reversal frequency but dopamine, noradrenaline, octopamine and γ aminobutyric acid were without effect. In later experiments (Wilkens, 1981) 5 HT, dopamine and octopamine each caused a long lasting increase in f_R and f_H in settled *Carcinus*. Clearly, these results demonstrate hormonal control of scaphognathite function attributable to biogenic amines already implicated in control of the heart.

Co-ordination of ventilation and perfusion

The control and co-ordination of bilateral ventilation and its relationships to perfusion of the gills with haemolymph delivered by the heart has been the subject of a number of studies. Hypoxic or hypercapnic water and solutions of L-glutamic acid or NaCl applied externally to one side of the crayfish *Procambarus simulans* produced inhibition of the homolateral scaphognathite accompanied by a simultaneous bradycardia or cardiac arrest (Larimer, 1964*b*) demonstrating that the scaphognathites can function separately and that changes in their activity are often reflected in responses of the heart. Introduction of sugars such as glucose into the ventilatory stream of the crayfish caused bilateral slowing of the scaphognathite and short-term cardiac arrest

Ashby & Larimer, 1965). Settling after a period of disturbance is often accompanied by a progressive reduction in f_R and f_H culuminating in long periods of unilateral ventilation, respiratory pauses and an irregular heart beat (e.g. McDonald *et al.* 1977; Butler *et al.* 1978). Exposure to diluted seawater caused a cardioacceleration, typically accompanied by a slowing in scaphognathite beating in *Carcinus maenas* (Hume & Berlind, 1976) whereas hypoxia typically results in a bradycardia and hyperventilation, as described below. Ventilatory pauses and reversals are often accompanied by changes in heart rate (e.g. McMahon & Wilkens, 1972; Taylor *et al.* 1973). Part of this co-ordination could result from a physical link between haemolymph flow through the gills and ventilation of the branchial chambers. The effective increase in hydrostatic pressure in the branchial chambers during ventilatory pauses or reversals may flush haemolymph from the gills or alternatively temporarily halt flow when noxious stimuli appear at the gills (McMahon & Wilkens, 1977), and could result in selective perfusion of the ventilated gills during unilateral ventilation. In *Cancer anthonyi* rate of perfusion of an isolated gill with saline at constant pressure was maximum at a subambient external pressure of -2 cm H_2O, which mimicked forward ventilation. Perfusion was slower at ambient pressure, equivalent to a ventilatory pause and slowest at a superambient external pressure of $+2$ cm H_2O, equivalent to a ventilatory reversal (L. E. Burnett, personal communication).

The onset of a respiratory pause is often accompanied by an immediate reduction in heart rate (McMahon & Wilkens, 1972, 1977; Taylor *et al.* 1973). In *Carcinus maenas* respiratory pauses are typically accompanied by cardiac arrest, with the heart stopping instantaneously at the onset of the pause (E. W. Taylor, unpublished observation). The closely co-ordinated nature of this response suggests a neural link between the ventilatory oscillators and the cardioregulatory centres in the C.N.S. Wilkens *et al.* (1974) identified command fibres in the circumoesophageal connectives of *Cancer magister* which were active during induced changes in cardiac or scaphognathite rhythms. When these fibres were stimulated electrically 69% produced responses in both the heart and scaphognathites, 28% in scaphognathites alone and 3% in the heart alone. By varying the frequency of electrical stimulation they established an order of response thresholds for both the heart and scaphognathites in the sequences: bradycardia < cardiac arrest and decreased rate and amplitude of forward ventilation < reversed ventilation < ventilatory pause, which resembled observed behavioural responses to increasing levels of disturbance. Reversals often followed stimulation of one command fibre whilst pauses required high frequency stimulation of several fibres inferring the involvement of both spatial and temporal summation. The sequence of responses and their co-ordination implied an endogenous programme as suggested by McMahon & Wilkens (1977).

Presumably the command fibres stimulated by Wilkens *et al.* (1974) are the same as those separately identified as affecting the cardioregulatory centres (Wiersma & Novitski, 1942) and the central ventilatory oscillator (Mendelson, 1971). The majority of them are bivalent, innervating two anatomically distinct but functionally correlated systems. Very few command fibres affected the heart alone and 90% of them caused cardioinhibition which is a common response to sudden disturbance in crustaceans (McMahon & Wilkens, 1972; Wilkens *et al.* 1974), though it may indicate that f_H was near maximum due to experimental manipulation (McMahon & Wilkens, 1982).

A prolonged burst of activity in the cardioinhibitory nerve of the lobster, *Nephrops norvegicus*, caused initial cardiac arrest, followed by adaptation and a postinhibitory rebound, plus persistent cessation of ventilation (Young, 1978). Continuous recordings revealed an inverse relationship between ventilation and activity in the cardioinhibitory nerves indicating that the cardioregulatory centre interacts with the ventilatory pacemaker. In *Portunus* bursts of activity in the cardioinhibitor nerve may be associated with ventilatory reversals rather than pauses which agree with the observation that reversals in *Carcinus* are often accompanied by cardiac arrest (Taylor *et al.* 1973). Spiking activity in cardioregulator nerves often occurs in preferred phases of the ventilatory cycle (Young, 1978) which is a possible basis for the bimodal and trimodal phase coupling between the heart and scaphognathites described by Young & Coyer (1979).

Transport of respiratory gases by the haemolymph

Most decapod crustaceans possess the respiratory pigment haemocyanin in solution or colloidal suspension in the haemolymph. The concentration is limited, possibly by the effect of colloid osmotic pressure on water fluxes (Mangum & Johansen, 1975) which sets an upper limit on the O_2 carrying capacity of the haemolymph. Bound O_2 ($C^{max}_{Hcy\,O_2}$) varies around 1 vol % (approximately 0·5 μ mol l^{-1}) which is 2–4 times the dissolved level for a whole range of aquatic crustaceans (Fig. 4). Higher values have been reported from land crabs whose gills are not in contact with a ventilatory stream of water (e.g. Wood & Randall, 1981*b*). Haemocyanin is an important buffer against pH variation in the haemolymph so that similar limits are set on non-HCO_3^- buffering capacity, which varies in direct proportion to O_2 capacity (e.g. Wood & Randall, 1981*b*). Both are low relative to vertebrates which package high concentrations of circulating haemoglobin in erythrocytes.

Crustacean haemocyanins typically have a relatively high affinity for O_2 with P_{50} varying from 6 mmHg in the crayfish *Pacifastacus leniusculus* (Rutledge, 1981) to 34 mmHg in the spider crab *Maia squinado* (W. E. Taylor, unpublished observation). The apparent paradox of an animal such as the lobster living in well aerated sublittoral waters and yet possessing a respiratory pigment with a relatively high affinity for O_2 was attributed to the diffusion barrier presented by chitin at the gas exchange surfaces. Low haemolymph P_{O_2} values were reported in animals taken from normoxic water (Redmond, 1955). These results now seem erroneous, due possibly to removal of the animals into air during sampling procedures, and Johansen *et al.* (1970) reported very high P_{a,O_2} values from *Cancer magister*, though it is probable that these crabs were hyperventilating due to recent disturbance. Routinely active crustaceans show wide variations in haemolymph P_{O_2} levels with P_{a,O_2} varying around the P_{SATN} level for the haemocyanin. P_{v,O_2} levels are normally around or above the P_{50} level, leaving a considerable venous reserve of oxygen available for periods when O_2 demand outstrips supply during exposure to hypoxic water, cessation of ventilation, movement into air or bouts of exercise, as described below (Fig. 4).

For accurate assessments of respiratory gas transport it is necessary to measure the important variables directly. It is not possible to infer O_2 content from measurements of O_2 tension because O_2 capacity varies in individuals with nutritive state and the moulting cycle (e.g. Zuckerkandl, 1957) and the relatively high affinity and coopera

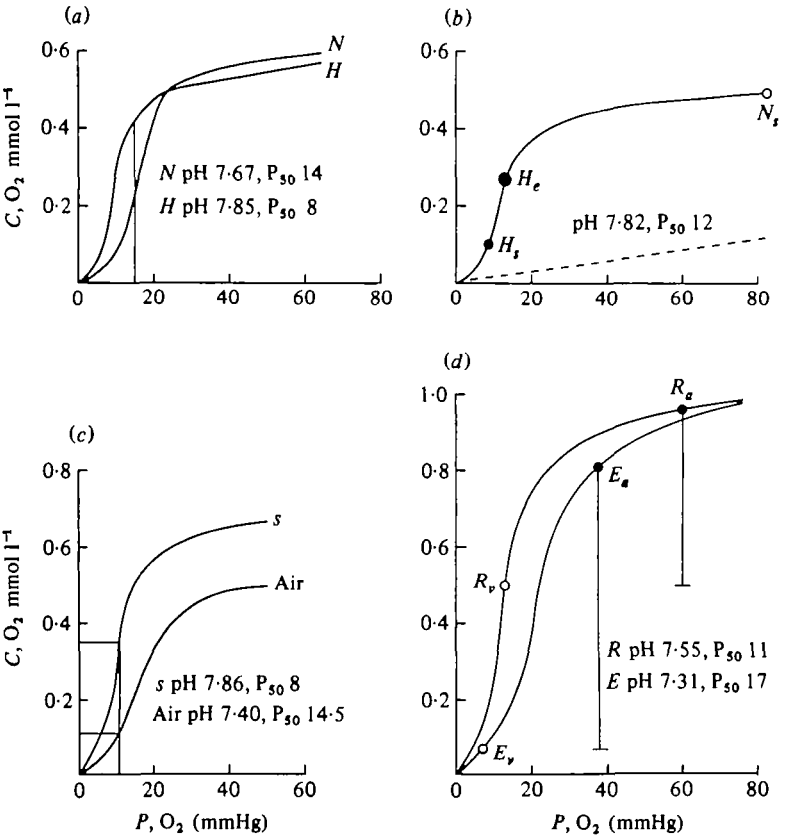

Fig. 4. Oxygen equilibrium curves for haemolymph from 4 species of decapodan crustaceans: (*a*) *Homarus vulgaris, in vitro* curves of haemolymph from animals settled for 48 h in normoxic water (N) and 3 h after subsequent exposure to hypoxia (H) at 15 °C, the vertical line denotes hypoxic P_{a,O_2} (redrawn from Butler *et al.* 1978); (*b*) *Carcinus maenas, in vivo* curve of haemolymph from crabs submerged in normoxic seawater at 17 °C (Ns), submerged in hypoxic water (Hs) and 10 min after emerging into air to aerate the water surrounding the gills (He), the points indicate mean values and the divided line dissolved O_2 (taken from Taylor *et al.* 1973); (*c*) *Austropotamobius pallipes, in vitro* curves on haemolymph collected from crayfish submerged in normoxic water at 15 °C (s) and following 3 h exposure in air (air), the vertical line is at the P_{a,O_2} value whilst the animal was in air and indicates the increased capacity to transport oxygen arising from compensation for the acidosis experienced on initial aerial exposure (redrawn from Wheatly, 1980); (*d*) *Cardisoma carnifex*, approximated *in vivo* curves for resting (R) and exercising (E) crabs at 25 °C with the mean values for postbranchial (*a*) and prebranchial (*v*) haemolymph superimposed, the vertical lines indicate the relative *a*–*v*, O_2 content difference for the two groups (redrawn from McMahon, 1981; based on data from Wood & Randall, 1981*b*).

tivity of haemocyanin measured *in vitro* reveals that content varies widely over a narrow range of tension values at the functional range of the pigment. This range is highly variable as crustacean haemocyanin is characterized by a large Bohr shift with pH variation. Affinity also changes with temperature and salinity (e.g. Truchot, 1973) and is effected by concentration of specific ions such as calcium and some metabolites (e.g. Truchot, 1981). Acid-base balance and CO_2 capacity is similarly complex. Haemocyanin shows a measurable Haldane effect causing pH and CO_2 capacity to vary with degree of oxygenation (Truchot, 1976) and the buffering of a metabolic acidosis by carbonate may generate CO_2 (e.g. Wood and Randall, 1981*b*). Production of free

amino acids during hyperosmotic exposure in *Pacifastacus leniusculus* led to a reduction in haemocyanin levels and consequent reduction in $C^{max}_{Hcy\,O_2}$, compensated by an increase in affinity and cooperativity which were not reproduced *in vitro* at measured levels of pH and ionic concentration, implicating other factors in the *in vivo* situation (Wheatly & McMahon, 1982). Recent studies emphasize the multifactorial and interactive influences effecting gas transport in crustacean haemolymph.

Hypoxia and air breathing

Oxygen levels are variable in many aquatic environments including those inhabited by crustaceans, such as intertidal pools which may be hyperoxic or hypoxic (Taylor & Butler, 1973; Truchot & Duhamel-Jouve, 1980). Periods of hypoxia may be accompanied by increased temperatures and varying salinities such that the animal's oxygen demand may increase in the face of a reduced supply.

The range of responses to hypoxia shown by invertebrates was recently reviewed (Herreid, 1980). Some species maintain $\dot{M}_{O_2}$ independent of P_{O_2} down to low levels whilst in others $\dot{M}_{O_2}$ is dependent upon P_{O_2} over the whole range. The distinction between oxygen regulators and conformers is, however, not clear cut (Mangum & Van Winkle, 1973) and the degree of independence within a species can vary with environmental variables such as temperature or salinity (e.g. Weins & Armitage, 1961; Taylor *et al.* 1977*b*; Taylor, 1981) and intrinsic variables such as the moulting cycle (Thompson & Pritchard, 1969). The experimental regime is also critical. When recently disturbed the lobster was an oxyconformer (Thomas, 1954) whilst after 48 h of settling in a respirometer $\dot{M}_{O_2}$ was maintained at its normoxic level in moderate levels of hypoxia (Butler *et al.* 1978) and Spoek (1974) found that restraining lobsters caused them to become oxyconformers. For many species the degree of independence of reduced P_{O_2} relates to the level of $\dot{M}_{O_2}$ (Herreid, 1980).

The physiological mechanisms which compensate for reduced P_{O_2} during regulation serve to increase the conductance of the gas exchange organs, and circulatory system. They may be typified by describing the responses of the crayfish *Austropotamobius pallipes* to moderate hypoxia recently studied by Wheatly & Taylor (1981). At 15 °C $\dot{M}_{O_2}$ was maintained independent of P_{O_2} down to 40 mmHg (Fig. 5). Progressive hypoxia was accompanied by hyperventilation, with increases in both f_R and SV_R. The convection requirement for water ($\dot{V}_W/\dot{M}_{O_2}$) increased markedly. Despite the increased rate of delivery of water to the gills both % $Extn_W$ and effectiveness of removal of O_2 from the water (E_W) rose, due to an improvement in the ability of the respiratory surfaces to transfer O_2 assessed as $\dot{M}_{O_2}/\Delta P_{O_2}$ and termed the transfer factor (T_{O_2}) which more than doubled during moderate hypoxia. This implies recruitment of a greater area for gas exchange, and/or a change in the flow of water or haemolymph at the exchange surface, which served to increase the effective diffusive conductance or eliminate shunts. A similar improvement in T_{O_2} during hypoxia was suggested by the results of earlier studies (e.g. Thomas, 1954; Larimer, 1964; Arudpragasam & Naylor, 1964*b*; McMahon *et al.* 1974; Taylor *et al.* 1977*b*; Batterton & Cameron, 1978) and the phenomenon merits further investigation.

As well as serving to increase the rate of delivery of O_2 to the gills, hyperventilation in the crayfish also reduced haemolymph CO_2 levels, resulting in a respiratory

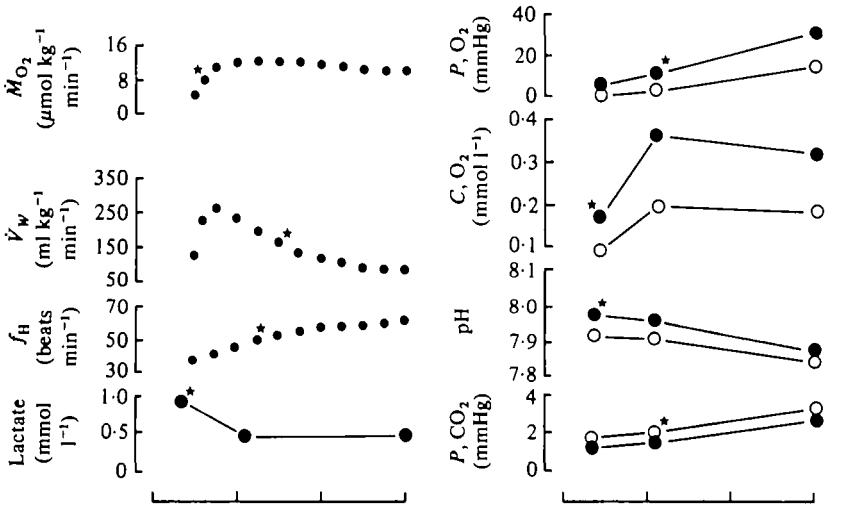

Fig. 5. Responses of the freshwater crayfish, *Austropotamobius pallipes* to progressive hypoxia at 15 °C. The curves are from above downward, on the left: rate of oxygen consumption ($\dot{M}_{O_2}$); ventilation volume ($\dot{V}_w$); heart rate (f_H); haemolymph lactate concentration; and on the right prebranchial (○) and postbranchial (●) values of : O_2 tension (P, O_2); O_2 content (C, O_2); pH; CO_2 tension (P, CO_2). The asterisks indicate significant variation from the normoxic value ($P < 0{\cdot}05$). Data taken from Wheatly & Taylor (1981).

alkalosis (Wheatly & Taylor, 1981). A rise in pH during hypoxia was noted previously (e.g. Truchot, 1975*a*; McMahon *et al.* 1978; Burnett, 1979). This in turn caused an increase in O_2 affinity of the circulating haemocyanin, due to a Bohr shift (Fig. 4*a*). Despite reductions in pre- and postbranchial O_2 tensions by 50% the arteriovenous O_2 content difference was maintained (Fig. 5), the effectiveness of removal of O_2 into the haemolymph (E_b) remained high and the venous reserve of O_2 was retained. The 'blow-off' of CO_2 and resultant alkalosis was a vital component of this response and may be the underlying significance of the hypoxic hyperventilation which is generally considered merely to increase delivery of O_2 to the exchange surfaces, its utility in this regard being limited by the high respiratory cost of ventilation (Jones, 1971). In the settled lobster during long-term hypoxia an initial period of hyperventilation eased after 24 h (Butler *et al.* 1978) presumably to reduce the respiratory cost of ventilation (McMahon *et al.* 1974), but the alkalosis in the haemolymph was maintained by elevation of bicarbonate levels and thus oxygen affinity remained above the normoxic level (McMahon *et al.* 1978).

Hypoxic hyperventilation was accompanied in the crayfish by a bradycardia, though haemolymph flow was maintained by an increase in SV_H (Wheatly & Taylor, 1981). Nevertheless the ventilation perfusion ratio $\dot{V}_W/\dot{V}_b$ increased. Bradycardia is a common feature of the hypoxic response in aquatic crustaceans (e.g. Larimer, 1962; McMahon & Wilkens, 1975; Taylor *et al.* 1977*b*) and in air-breathers (Herreid *et al.* 1979). In settled lobsters f_H was relatively low and did not change on exposure to moderate hypoxia (Butler *et al.* 1978). It is possible that the bulk of observations of a marked bradycardia during hypoxia were taken from disturbed animals with elevated f_H (McMahon & Wilkens, 1982).

At P_{O_2} levels below 40 mmHg the crayfish became an oxyconformer (Wheatly & Taylor, 1981). Hyperventilation ceased, arteriovenous O_2 content difference decreased, the venous reserve of O_2 was depleted and as the haemocyanin was no longer saturated with O_2 during its passage through the gills E_b was reduced. As a consequence $\dot{M}_{O_2}$ fell and was substituted by a switch to anaerobic metabolism with lactic acid accumulating in the haemolymph (Fig. 5). The lactate levels measured in the haemolymph of *Carcinus maenas* during hypoxia appeared sufficient to replace aerobic energy production and measured activity levels were unchanged (Taylor *et al.* 1977*b*). There is a trend towards oxyconformity as temperature increases in many crustaceans and this may be accompanied by enzymic changes favouring lactic acid production in the tissues (Taylor, 1981).

On return to normoxia after hypoxic exposure $\dot{M}_{O_2}$ is often elevated in crustaceans, possibly reflecting the replenishment of the venous reserve of O_2, regeneration of phosphagens and eventual repayment of an O_2 debt as lactic acid is reoxidized, though changes in recovery $\dot{M}_{O_2}$ may not parallel reduction in lactate levels (Bridges & Brand, 1980). Some crustaceans appear to repay an accumulated O_2 debt in full (Teal & Carey, 1967; Taylor *et al.* 1977*b*), others repay only part of the debt (Bridges & Brand, 1980) and some, despite accumulating lactic acid during hypoxia, appear not to repay an O_2 debt (Spoek, 1974). Lobster claw muscle accumulated both alanine and lactate during anaerobiosis (Trausch, 1976) indicating the availability of alternative metabolic pathways, which was suggested by the results of Butler *et al.* (1978). These may provide a greater net yield of ATP (Hochachka & Somero, 1973) which could be available during exercise as lactate constituted only 23% of the metabolic acids accumulated by exercising *Gecarcinus* (Smatresk *et al.* 1979).

Instead of reducing activity levels or accumulating an O_2 debt during hypoxia some primarily aquatic crustaceans may become facultative air-breathers thus exploiting a source of O_2 which requires little energy for ventilation. The shore crab *Carcinus maenas* raised its normally exhalent apertures from shallow hypoxic water and ventilated the water surrounding its gills by prolonged reversed beating of the scaphognathites causing bubbles to stream from the Milne-Edwards openings (Taylor & Butler, 1973). Although the crab remained internally hypoxic this behaviour was accompanied by an immediate recovery tachycardia and increased $C_{a.O_2}$ (Fig. 4*b*) which restored O_2 supply to the tissues (Taylor *et al.* 1973). Very little CO_2 accumulated as contact with water was retained, and haemolymph pH stayed at normoxic submerged levels during partial emersion from hypoxic water at 15°C (Wheatly & Taylor, 1979). On exposure to relatively high temperatures *Carcinus* moved into air (Taylor & Wheatly, 1979) and the freshwater crayfish *Austropotamobius pallipes* similarly left water to breathe air during progressive hypoxia (Taylor & Wheatly, 1980).

The chitin covering the gas exchange surfaces in crustaceans could provide mechanical support and resistance to dehydration in air. Despite this apparent preadaptation aquatic crustaceans become hypoxic and hypercapnic and accumulate lactic acid when taken into air. In the sublittoral spider crab *Maia squinado* an accumulating metabolic and respiratory acidosis remained uncompensated and the animal died within 24 h, apparently from asphyxia (E. W. Taylor & P. J. Butler, unpublished

observations). The lobster *Homarus vulgaris* from the sublittoral fringe compensated for the potential acidosis by mobilizing an internal source of HCO_3^- with a concomitant increase in haemolymph calcium levels (E. W. Taylor, unpublished observations). Facultative air-breathers such as *Carcinus* metabolize aerobically and compensate for a respiratory acidosis by elevation of buffer base (Truchot, 1975*b*) when in air. The crayfish *Austropotamobius* experienced an initial combined metabolic and respiratory acidosis when first taken into air, which recovered over 24 h due to a reduction in lactate level, which appeared to be sequestered in the tissues as it reappeared on submersion, and elevation of HCO_3^- from an internal source of fixed base which may be $CaCO_3$ as calcium accumulated in the haemolymph during aerial exposure (Taylor & Wheatly, 1982). The recovery in pH served to restore O_2 transport by reversal of a Bohr shift as shown in Fig. 4*c* (Taylor & Wheatly, 1981). Both the shore crab and crayfish maintain $\dot{M}_{O_2}$ and f_H at submerged normoxic levels whilst in air. Ventilation rate in air ($\dot{V}_A$) was 5% of normoxic $\dot{V}_W$ in *Austropotamobius*, reflecting the increased O_2 content and diffusion rate (Dejours, 1975) and minimizing evaporative water loss which appears to limit their survival in air to about 72 h at 15 °C, due possibly to reduction in circulating haemolymph volume (Taylor & Wheatly, 1982). Land crabs may maintain low resting levels of $\dot{V}_A$ for similar reasons (Wood & Randall, 1981*a*). Obligate air-breathers have reduced gill areas and exchange respiratory gases over the well vascularized and thin-walled internal surfaces of the branchiostegites (Greenaway & Taylor, 1976). *Birgus latro* survives after removal of its gills though this delays recovery after exercise indicating that they retain a role in acid-base balance (Smatresk & Cameron, 1981). Injection of radioactive microspheres into the haemolymph of *Holthusiana* indicated that flow to the wall of the branchiostegite may be enhanced after 24 h in air (H. H. Taylor & P. Greenaway, personal communication). The scaphognathite retains its role in ventilation in air in some facultative (e.g. Taylor & Butler, 1978) and obligate (e.g. Cameron & Mecklenberg, 1973) air-breathers. In *Holthusiana* ventilation is accomplished by alternate expansion and retraction of the epimeral wall into each branchial chamber (Greenaway & Taylor, 1976) and epimeral retractor muscles may cause some air movement in *Coenobita* (McMahon & Burggren, 1979) and *Cardisoma* (Wood & Randall, 1981*a*).

Fully adapted air-breathing crustaceans may have relatively high haemolymph P_{O_2} values (e.g. Cameron & Mecklenberg, 1973; Wood & Randall, 1981*a*) though in others it is routinely low (e.g. McMahon & Burggren, 1979). Haemolymph CO_2 levels are high in many air-breathers and in the absence of compensation this may result in a low pH. In *Birgus latro* haemolymph pH was 7·54 and $[HCO_3^-]$ 5·7 m-equiv. l^{-1}, whilst *Coenobita* has a pH of 7·84 and $[HCO_3^-]$ of 11·0 m-equiv. l^{-1}. This specific difference resembles the progressive change in pH and $[HCO_3^-]$ observed in *Austropotamobius* during 24 h exposure in air (Taylor & Wheatly, 1981) and confirms the relationship between pH and $[HCO_3^-]$ in crustaceans, which is also apparent in aquatic species over a range of temperatures (Truchot, 1978). The non-bicarbonate buffering capacity which varies with haemocyanin concentration is also characteristically high in terrestrial crustaceans (Wood & Randall, 1981*b*). *Coenobita* may also minimize CO_2 accumulation by retaining a reservoir of water in its adopted shell (McMahon & Burggren, 1979). In the brachyuran land crab *Cardisoma carnifex*

the branchial chamber is normally partly filled with water which is renewed every few minutes when the crab has access to pools of water. This water is flicked over the gills by the flabellum (mastigobranch of the first maxilliped) and CO_2 equilibrates between the gas and water phases so that it provides a significant sink for CO_2 (Wood & Randall, 1981*a*). Excretion of CO_2 is facilitated by a catalysed HCO_3^- dehydration reaction in the gill epithelium which contains carbonic anhydrase (Randall & Wood, 1981).

There is circumstantial evidence for the involvement of O_2 sensitivity at a number of morphological sites in the physiological responses of crustaceans to hypoxia and in particular the initiation of the hypoxic bradycardia. The effect of hypoxia (Stiffler & Pritchard, 1972) or metabolic inhibitors (Livengood & Kusano, 1973) suggested a direct sensitivity of the myocardium or cardiac ganglion to reduced O_2. The latency of cardiac and ventilatory responses to changes in branchial chamber P_{O_2} (McMahon & Wilkens, 1972, 1975) and the ventilatory responses to an induced cardiac arrest (Larimer, 1964*a*) suggested a role for central P_{O_2} receptors in the heart and C.N.S. and it seems likely that the cardiac and central ventilatory pacemaker neurones may respond to variations in P_{O_2}.

Evidence for central receptors does not preclude the existence of peripheral receptors monitoring P_{O_2} levels in the haemocoel or ventilatory stream. Larimer (1964*b*) ascribed initiation of the cardiac and ventilatory responses of the crayfish to hypoxic and hypercapnic water to chemoreceptors located somewhere within the branchial chambers. This suggestion is supported by the instantaneous increase in f_H at the onset of air-bubbling, during the emersion response in *Carcinus maenas* (Taylor & Butler, 1973). Both this recovery tachycardia following emersion and the similarly high f_H level recorded from *Carcinus* in air (Taylor & Butler, 1978) are associated with internal hypoxia, with P_{a,O_2} values below those normally associated with a bradycardia in submerged, hypoxic animals, indicating that the presence of air in the branchial chambers provides a normoxic stimulus to an externally placed O_2 receptor. Direct recordings of O_2 receptor discharge were described from nerves supplying the gills of the chelicerate arthropod *Limulus polyphemus* (Crabtree & Page, 1974) and similar unpublished information from a crustacean was cited by McMahon & Wilkens (1982). The initial bradycardia and hyperventilation during progressive hypoxia are probably nervously mediated and arise from stimulation of as yet uncharacterized reflexogenic areas. When P_{a,O_2} levels fall below the P_{SATN} for haemocyanin both f_R and f_H may fall (McMahon & Wilkens, 1975) and $\dot{V}_W$ is reduced (Wheatly & Taylor, 1981), possibly due to a direct effect of O_2 lack on the functioning of the two pumps, rather than effective co-ordination of their outputs, as this response may be accompanied by a reduction in $\dot{M}_{O_2}$ and a switch to anaerobiosis.

The ability to breathe air, which offers the advantage of a continuously high level of P_{O_2} but the problem of CO_2 elimination, might be expected to result in development of CO_2 sensitivity. This is foreshadowed in aquatic species. Normoxic crayfish show a ventilatory (Massabuau & Dejours, 1981) and associated cardiac (Larimer, 1964*b*) response to increases in dissolved CO_2. Land crabs respond to hypercapnia with an increase in ventilation. *Birgus latro* showed a reduction in $\dot{V}_A$ at low P_{O_2} levels and a linear increase as CO_2 was increased (Cameron & Mecklenberg, 1973) which the authors considered signified that they occupied an intermediate position in an evol-

tionary sequence from water to land. Ventilation increased greatly in response to hypercapnia in *Gecarcinus lateralis* and *Cardisoma guanhami* signifying that they were adapted to function as air-breathers (Cameron, 1975). Injection of buffered CO_2 rich saline into *Birgus* was without effect but injection of an acid saline solution caused an immediate increase in f_R and recovery in post exercise f_R followed recovery in haemolymph pH values rather than P_{CO_2} (Smatresk & Cameron, 1981). This suggests sensitivity to internal pH i.e. $[H^+]$ or $[HCO_3^-]$ which are components of strong ion difference (Stewart, 1978) rather than P_{CO_2} and a parallel may exist in the responses of the vertebrate medulla to the pH of the cerebrospinal fluid (Mitchell & Severinghaus 1965).

Exercise

During exercise animals typically show a marked increase in $\dot{M}_{O_2}$ over settled levels which may be taken as their aerobic metabolic scope for activity. Shortfall in aerobic scope may be taken up by anaerobic metabolism. Homeothermic air-breathing vertebrates characteristically have a high aerobic scope, adjust rapidly to exercise, including lactate production, and recover rapidly whilst poikilothermic, water-breathing vertebrates typically have a lower aerobic scope and recover less rapidly (Bennett, 1978). Crustaceans may be limited in their aerobic scope by the potential problems of diffusive conductance of O_2 over the chitin on the gills and convective conductance via the open haemocoel. Oxygen uptake and acid base balance during activity in decapod crustaceans were recently reviewed by McMahon (1981).

Changes in O_2 demand and transfer, anaerobic metabolism and acid-base balance following 20 min of exhausting activity enforced by violent disturbance of the relatively sluggish aquatic crab *Cancer magister* were described by McMahon *et al.* (1979) and McDonald *et al.* (1979). The overall responses resembled those described for the land crab *Cardisoma carnifex* running sideways on a treadmill at close to maximum burst velocity for short periods. Similar short sprints were undertaken by crabs seeking the shelter of their burrows (Wood & Randall, 1981*a*).

In *Cardisoma* 10 min of exhausting activity at 25 °C caused a 3 times increase in $\dot{M}_{O_2}$. This degree of aerobic scope resembled that of a relatively sluggish fish; whereas, in the crayfish, *Pacifastacus leniusculus*, maximum aerobic scope, attained at 20 °C, was 10 times the resting rate, an increase which approaches that of a moderately active fish such as the bass, *Micropterus salmoides* (Rutledge & Pritchard, 1981).

The increased $\dot{M}_{O_2}$ was partially attributable to increased ventilation with $\dot{V}_A$ 5 times resting level and a similar increase in f_R. % Extn_A was low in resting crabs at 12% and further decreased to 3% during exercise. A smaller proportional increase in f_H of approximately 20% occurred and Herreid *et al.* (1979) reported a reduction in f_H and cardiac arrhythmia during 'heavy exercise' in *Cardisoma guanhami*. This could imply that $\dot{M}_{O_2}$ during exercise is limited by ventilation and diffusive conductance over the chitin covered exchange surfaces, rather than by perfusion, though $\dot{V}_b$ estimated by the Fick principle increased during exercise, independently of f_H. This indicates an increased SV_H or possibly improved perfusion of the gills due to movement of the legs improving venous return via the gills from the infrabranchial haemocoelic spaces.

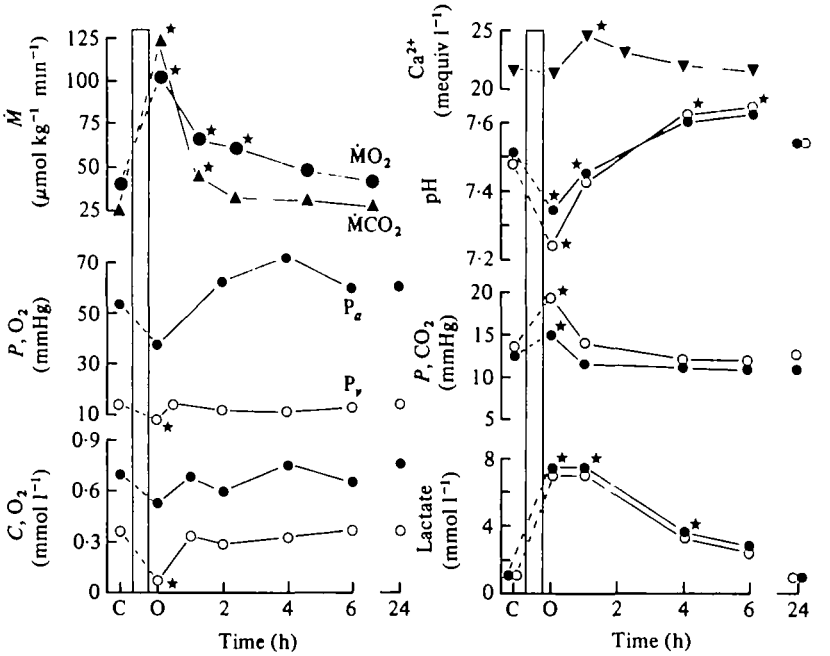

Fig. 6. Changes associated with 10 min of severe exercise in the land crab *Cardisoma carnifex*. The horizontal, time axis indicates mean control (C) resting levels, the 10 min exercise period is indicated by the vertical bar and subsequent recovery is followed for 6 h with a break to a 24 h recovered value. The curves are from above, downward, on the left: rate of O_2 consumption ($\dot{M}_{O_2}$) and CO_2 production ($\dot{M}_{CO_2}$); haemolymph O_2 tension (P, O_2); O_2 content (C, O_2) and on the right haemolymph Ca^{2+} concentration; pH; CO_2 tension (P, CO_2); lactate concentration. The open and filled circles denote prebranchial and postbranchial haemolymph levels respectively. The asterisks indicate the mean values which vary significantly from control values. Redrawn from Wood & Randall (1981*a*, *b*).

The maintenance of gas exchange during exercise was partially explained by an increase in ΔP_{O_2} over the gills due to reduced P_{O_2} levels in the haemolymph. P_{v,O_2} was reduced by the exercising tissues and P_{a,O_2} fell, due possibly to reduced transit time through the gas exchange organs (Fig. 6). This approximately 30% improvement in ΔP_{O_2} was insufficient to explain the increased $\dot{M}_{O_2}$ and diffusive conductance expressed as T_{O_2}, doubled during exercise. The reduced P_{a,O_2} levels had little effect on C_{a,O_2} with saturation of the postbranchial haemolymph (Sa, O_2) decreasing from 87% to 71%. The reduced P_{v,O_2} levels were, however, indicative of a marked reduction in C_{v,O_2} with S_{v,O_2} reduced from 45% to 9% as tissue O_2 consumption shifted the P_{O_2} range in the haemolymph onto the functional portion of the haemocyanin O_2 equilibrium curve, thereby utilizing up to 90% of the available venous reserve of O_2. Up to 70% of this reduction in S_{v,O_2} was due to the fall in P_{v,O_2} with the other 30–40% due to a marked Bohr shift induced by an acidosis (Fig. 4*d*).

The sharp increase in $\dot{M}_{O_2}$ during exercise infers an increase in $\dot{M}_{CO_2}$ which rose to 5 times the settled level in *Cardisoma* (Wood & Randall, 1981*b*). Despite this increase, P_{CO_2} values were little affected and remained around 1·5 mmHg (Fig. 6) which is approximately half that recorded in poikilothermic vertebrates such as turtles which breathe in the intermittent manner characteristic of land crabs (Burggren & Shelton,

1979). Elimination of CO_2 from this air-breathing crab is enhanced by carbonic anhydrase in the gill epithelium (Randall & Wood, 1981) and the presence of a reservoir of water held in the branchial chambers (Wood & Randall, 1981*a*). The main contributor to acid-base variation during exercise was the accumulation of lactic acid in anaerobically metabolizing tissues. Anaerobic energy production due to lactate fermentation accounted for 80% of the energy utilized by *Cardisoma*, and lactic acid accumulated to 7 times the resting level in the haemolymph. Following severe exercise *Cardisoma* showed a combined respiratory and metabolic acidosis which recovered within 2 h to be followed by an alkalosis. Lactate levels in the haemolymph were still elevated at 6 h and it is probable that the recovery and overcompensation in pH was attributable to the reduced $\dot{M}_{CO_2}$ and elevation of bicarbonate buffer by mobilization of calcium carbonate from the exoskeleton or gastrolith fields in the gut which are supplied with arteries and may be involved in calcium regulation. Calcium levels in the haemolymph increased during recovery to a peak 1 h after exercise which was when the apparent discrepancy between lactate levels and relative acidity was greatest (Fig. 6). An internal source of fixed buffer is particularly important in land crabs which have lost external seawater as a source of HCO_3^-. During periods of inactivity the $CaCO_3$ may be replenished by retention of respiratory CO_2 which could explain the abnormally low value for gas exchange ratio R measured from *Cardisoma* (Wood & Randall, 1981*b*).

The responses of *Cardisoma* during short sprints may be contrasted with the swimming crab *Callinectes sapidus* which is active for long periods without fatigue (Booth *et al.* 1982). *Callinectes* has a relatively large weight specific gill area and short minimum diffusion distance over the gills of approximately 1 μm (Aldridge & Cameron, 1979) which may account for its ability to maintain $\dot{M}_{O_2}$ and % $Extn_W$ (40–50%) at high levels during prolonged exercise. At the onset of induced swimming it showed rapid increases in f_R, f_H and $\dot{M}_{O_2}$. Lactic acid accumulated to 14 times the resting level, inducing a large metabolic acidosis. P_{a,O_2} and P_{v,O_2} levels were unchanged but C_{v,O_2} decreased significantly due to a marked Bohr shift which was opposed by a specific effect of lactate ions increasing the O_2 affinity of haemocyanin (Truchot, 1981). The amount of haemocyanin bound O_2 released to the tissues rose but a large proportion of the venous reserve remained intact and the increase in O_2 delivery to the tissues was attributed to a 2·3 times increase in cardiac output (Booth *et al.* 1982).

There was a virtually instantaneous increase in f_R at the onset of swimming in *Callinectes* and running in *Cardisoma* which suggests that neural control, possibly involving proprioceptive feedback from the locomotory appendages, may initiate the respiratory responses which enhance O_2 uptake during exercise.

CONCLUSION

The functional morphology and physiology of the respiratory and cardiovascular systems in decapod crustaceans differ widely from the relatively well documented vertebrate systems. Nevertheless, there are qualitative similarities in their adaptive responses to problems of O_2 supply or demand. This is a flourishing branch of comparative physiology at present and some aspects which merit further attention are: functioning and control of the circulatory system, including the role of the alary

muscles; details of gill ventilation, including the role of the epimeral muscles; localization and characterization of the receptors initiating the responses to hypoxia and exercise; a critical reappraisal of the supposed diffusion barrier presented by chitin; the factors contributing to the improvement in T_{O_2} during hypoxia and exercise; the role of active transport over the gills in HCO_3^- and NH_4^+ elimination; the combined roles of haemocyanin in O_2 transport, acid-base balance and osmoregulation, including the associated roles of free amino acids and their contribution to oxidative phosphorylation; the biochemistry of anaerobic metabolism; the partitioning of lactate and H^+ between the tissues and haemolymph and control of $CaCO_3$ mobilization during exercise and aerial exposure; changes in any of these variables during moulting.

I am grateful to the following authors for providing me with manuscripts or information prior to publication: Charles Booth, Brian Bush, Brian McMahon, Valerie Pasztor, Dave Randall and Michèle Wheatly. I am also indebted to Jean Hill for typing and Deborah Barrett for proof reading the manuscript.

REFERENCES

ALDRIDGE, J. B. & CAMERON, J. N. (1979). CO_2 exchange in the blue crab *Callinectes sapidus* (Rathbun). *J. exp. Zool.* **207**, 321–328.

ALEXANDROWICZ, J. S. (1932). The innervation of the heart of the Crustacea. I. Decapoda. *Quart. J. micr. Sci.* **75**, 181–249.

ALEXANDROWICZ, J. S. & CARLISLE, D. B. (1953). Some experiments on the function of the pericardial organs in Crustacea. *J. mar. biol. Ass. U.K.* **32**, 175–192.

ARUDPRAGASAM, K. D. & NAYLOR, E. (1964*a*). Gill ventilation and the role of reversed respiratory currents in *Carcinus maenas* (L.). *J. exp. Biol.* **41**, 299–307.

ARUDPRAGASAM, K. D. & NAYLOR, E. (1964*b*). Gill ventilation volumes, oxygen consumption and respiratory rhythms in *Carcinus maenas* (L.). *J. exp. Biol.* **41**, 309–321.

ARUDPRAGASAM, K. D. & NAYLOR, E. (1966). Patterns of gill ventilation in some decapod Crustacea. *J. zool. Soc. Lond.* **150**, 401–411.

ASHBY, E. A. & LARIMER, J. L. (1965). Modification of cardiac and respiratory rhythms in crayfish following carbohydrate chemoreception. *J. cell. comp. Physiol.* **65**, 373–380.

BATTERTON, C. V. & CAMERON, J. N. (1978). Characteristics of resting ventilation and response to hypoxia, hypercapnia and emersion in the blue crab *Callinectes sapidus* (Rathbun). *J. exp. Zool.* **203**, 403–418.

BELAMARICH, F. A. & TERWILLIGER, R. C. (1966). Isolation and identification of cardio-excitor hormone from the pericardial organs of *Cancer borealis*. *Amer. Zool.* **6**, 101–106.

BELMAN, B. W. (1975). Some aspects of the circulatory physiology of the spiny lobster *Panulirus interruptus*. *Mar. Biol.* **29**, 295–305.

BELMAN, B. W. (1976). New observations on blood pressure in marine Crustacea. *J. exp. Zool.* **196**, 71–78.

BELMAN, B. W. & CHILDRESS, J. J. (1976). Circulatory adaptations to the oxygen minimum layer in the bathypelagic mysid *Gnathophausia ingens*. *Biol. Bull. mar. biol. Lab., Woods Hole* **150**, 15–37.

BENNETT, A. F. (1978). Activity metabolism in the lower vertebrates. *Ann. Rev. Physiol.* **40**, 447–469.

BENSON, J. A. (1980). Burst reset and frequency control of the neuronal oscillators in the cardiac ganglion of the crab, *Portunus sanguinolentus*. *J. exp. Biol.* **87**, 285–313.

BERLIND, A. (1976). Neurohumoral organ extracts affect the ventilation oscillator in crustaceans. *J. exp. Zool.* **195**, 165–170.

BERLIND, A. (1977). Neurohormonal and reflex control of scaphognathite beating in the crab *Carcinus maenas*. *J. comp. Physiol.* **116A**, 77–90.

BERLIND, A. & COOKE, I. M. (1968). Effect of calcium omission on neurosecretion and electrical activity of crab pericardial organs. *Gen. comp. Endocrinol.* **11**, 458–463.

BLATCHFORD, J. G. (1971). Hemodynamics of *Carcinus maenas* (L.). *Comp. Biochem. Physiol.* **39A**, 193–202.

BOOTH, C. E., MCMAHON, B. R. & PINDER, A. W. (1982). Oxygen uptake and the potentiating effects of increased haemolymph lactate on oxygen transport during sustained exercise in the blue crab *Callinectes sapidus*. *J. comp. Physiol.* (In the press).

BORRADAILE, L.-A. (1922). On the mouthparts of the shore crab. *J. Linn. Soc. (Zool.)* **35**, 115–143.

BRIDGES, C. R. (1976). The respiratory physiology of *Galathea strigosa* (L.) and *Corystes cassivelaunus* (Pennant). Ph.D. thesis. University of Liverpool. 168 pp.

BRIDGES, C. R. & BRAND, A. R. (1980). The effect of hypoxia on oxygen consumption and blood lactate levels of some marine Crustacea. *Comp. Biochem. Physiol.* **65**A, 399–409.

BULLOCK, T. H. & TERZUOLO, C. A. (1957). Diverse forms of activity in the somata of spontaneous and integrating ganglion cells. *J. Physiol., Lond.* **138**, 341–364.

BURGER, J. W. & SMYTHE, C. M. (1953). The general form of circulation in the lobster *Homarus*. *J. cell. comp. Physiol.* **42**, 369–383.

BURGGREN, W. W. & SHELTON, G. (1979). Gas exchange and transport during intermittent breathing in chelonian reptiles. *J. exp. Biol.* **82**, 75–92.

BURNETT, L. E. (1979). The effects of environmental O_2 levels on the respiratory function of haemocyanin in the crabs *Libinia emarginata* and *Ocypode quadrata*. *J. exp. Zool.* **210**, 289–300.

BUTLER, P. J. & TAYLOR, E. W. (1975). The effect of progressive hypoxia on respiration in the dogfish (*Scyliorhinus canicula*) at different seasonal temperatures. *J. exp. Biol.* **63**, 117–130.

BUTLER, P. J., TAYLOR, E. W. & MCMAHON, B. R. (1978). Respiratory and circulatory changes in the lobster (*Homarus vulgaris*) during long term exposure to moderate hypoxia. *J. exp. Biol.* **73**, 131–146.

CAMERON, J. N. (1975). Aerial gas exchange in the terrestrial Brachyura *Gecarcinus lateralis* and *Cardisoma guanhami*. *Comp. Biochem. Physiol.* **52**A, 129–134.

CAMERON, J. N. & MECKLENBURG, T. A. (1973). Aerial gas exchange in the coconut crab *Birgus latro*, with some notes on *Gecarcoidea lalandii*. *Respir. Physiol.* **19**, 245–261.

CARLISLE, D. B. (1956). An indole alkylamine regulating heart beat in Crustacea. *Biochem. J.* **63**, 32–33P.

COOKE, I. M. (1964). Electrical activity and release of neurosecretory material in crab pericardial organs. *Comp. Biochem Physiol.* **13**, 353–366.

COOKE, I. M. (1966). The sites of action of pericardial organ extract and 5-hydroxytryptamine in the decapod crustacean heart. *Amer. Zool.* **6**, 107–121.

COOKE, I. M. & HARTLINE, D. K. (1975). Neurohormonal alteration of integrative properties of the cardiac ganglion of the lobster *Homarus americanus*. *J. exp. Biol.* **63**, 33–52.

CRABTREE, R. L. & PAGE, C. H. (1974). Oxygen sensitive elements in the bookgills of *Limulus polyphemus*. *J. exp. Biol.* **60**, 631–641.

DEJOURS, P. (1975). *Principles of Comparative Respiratory Physiology*. New York: American Elsevier Publishing Co.

FATT, P. & KATZ, B. (1953). The electrical properties of crustacean muscle fibres. *J. Physiol.* **120**, 171–204.

FIELD, L. H. & LARIMER, J. L. (1975*a*). The cardioregulatory system of crayfish: neuroanatomy and physiology. *J. exp. Biol.* **62**, 519–530.

FIELD, L. H. & LARIMER, J. L. (1975*b*). The cardioregulatory system of crayfish: role of circumoesophageal interneurones. *J. exp. Biol.* **62**, 531–543.

FLOREY, E. (1960). Studies on the nervous regulation of the heart beat in decapod Crustacea. *J. gen. Physiol.* **43**, 1061–1081.

FLOREY, E. (1963). Pharmacology of the crayfish heart. In *Problems in Biology* (ed. G. A. Kerkut), Oxford: Pergamon Press.

FLOREY, E. & RATHMAYER, M. (1978). The effects of octopamine and other amines on a heart and on neuromuscular transmission in decapod crustaceans: further evidence for a role as neurohormone. *Comp. Biochem. Physiol.* **61***C*, 229–237.

GRAY, I. E. (1957). A comparative study of the gill area of crabs. *Biol. Bull. mar. biol. Lab., Woods Hole* **112**, 23–42.

GREENAWAY, P. & TAYLOR, H. H. (1976). Aerial gas exchange in Australian arid-zone crab, *Parathelphusa transversa* Von Martens. *Nature, Lond.* **262**, 711–713.

HAGIWARA, S. & BULLOCK, T. H. (1957). Intracellular potentials in pacemaker and integrative neurons of the lobster cardiac ganglion. *J. cell. comp. Physiol.* **50**, 25–47.

HERREID, C. F. (1980). Hypoxia in invertebrates. *Comp. Biochem. Physiol.* **67**A, 311–319.

HERREID, C. F., LEE, L. L. & SHAH, G. M. (1979). Respiration and heart rate in exercising land crabs. *Respir. Physiol.* **36**, 109–120.

HOCHACHKA, P. W. & SOMERO, G. N. (1973). *Strategies of biochemical adaptation*. Philadelphia: W. B. Saunders.

HOYLE, G. & WIERSMA, C. A. G. (1958). Coupling of membrane potential to contraction in crustacean muscle. *J. Physiol.* **143**, 441–453.

HUGHES, G. M. (1972). Morphometrics of fish gills. *Respir. Physiol.* **14**, 1–25.

HUGHES, G. M., KNIGHTS, B. & SCAMMEL, C. A. (1969). The distribution of P_{O_2} and hydrostatic pressure changes within the branchial chambers of the shore crab *Carcinus maenas* L. *J. exp. Biol.* **51**, 203–220.

HUGHES, G. M. & MORGAN, M. (1973). The structure of fish gills in relation to their respiratory function. *Biol. Rev.* **48**, 419–475.

HUME, R. I. & BERLIND, A. (1976). Heart and scaphognathite rate changes in a euryhaline crab, *Carcinus maenas*, exposed to dilute environmental medium. *Biol. Bull. mar. biol. Lab., Woods Hole* **150**, 241–254.

IZQUIERDO, J. J. (1931). A study of the crustacean heart muscle. *Proc. Roy. Soc. Lond.* B, **109**, 229–250.

JOHANSEN, K., LENFANT, C. & MECKLENBURG, T. A. (1970). Respiration in the crab *Cancer magister*. *Z. vergl. Physiol.* **70**, 1–19.

JONES, D. R. (1971). Theoretical analysis of factors which may limit the maximum oxygen uptake of fish: the oxygen cost of the cardiac and branchial pumps. *J. theor. Biol.* **32**, 341–349.

KONISHI, S. & KRAVITZ, A. (1978). The physiological properties of amine-containing neurones in the lobster nervous system. *J. Physiol.* **279**, 215–229.

KROGH, A. (1919). The rate of diffusion of gases through animal tissues with some remarks on the coefficient of invasion. *J. Physiol.* **52**, 391–408.

LARIMER, J. L. (1962). Responses of the crayfish heart to respiratory stress. *Physiol. Zool.* **35**, 179–186.

LARIMER, J. L. (1964*a*). Patterns of diffusion of oxygen across the crustacean gill membranes. *J. cell. comp. Physiol.* **64**, 139–148.

LARIMER, J. L. (1964*b*). Sensory-induced modifications of ventilation and heart rate in crayfish. *Comp. Biochem. Physiol.* **12**, 25–36.

LAURENT, P. & DUNEL, S. (1980). Morphology of gill epithelia in fish. *Am. J. Physiol.* **238**, R147–R159.

LIVENGOOD, D. R. & KUSANO, K. (1972). Evidence for an electrogenic sodium pump in follower cells of the lobster cardiac ganglion. *J. Neurophysiol.* **35**, 170–186.

MCDONALD, D. G., MCMAHON, B. R. & WOOD, C. M. (1977). Patterns of heart and scaphognathite activity in the crab *Cancer magister*. *J. exp. Zool.* **202**, 33–44.

MCDONALD, D. G., MCMAHON, B. R. & WOOD, C. M. (1979). An analysis of acid-base disturbances in the haemolymph following strenuous activity in the Dungeness Crab *Cancer magister*. *J. exp. Biol.* **79**, 47–58.

MCMAHON, B. R. (1981). Oxygen uptake and acid-base balance during activity in decapod crustaceans. In *Locomotion and Energetics in Arthropods* (ed. C. L. Herreid and C. R. Fourtner), New York: Plenum Press.

MCMAHON, B. R. & BURGGREN, W. (1979). Respiration and adaptation to the terrestrial habitat in the land hermit crab *Coenobita clypeatus*. *J. exp. Biol.* **79**, 265–281.

MCMAHON, B. R. & WILKENS, J. L. (1972). Simultaneous apnoea and bradycardia in the lobster *Homarus americanus*. *Can. J. Zool.* **50**, 165–170.

MCMAHON, B. R. & WILKENS, J. L. (1975). Respiratory and circulatory responses to hypoxia in the lobster *Homarus americanus*. *J. exp. Biol.* **62**, 637–655.

MCMAHON, B. R. & WILKENS, J. L. (1977). Periodic respiratory and circulatory performance in the red rock crab *Cancer productus*. *J. exp. Zool.* **202**, 363–374.

MCMAHON, B. R. & WILKENS, J. L. (1982). Ventilation, perfusion and oxygen consumption. In *The Biology of Crustacea*, vol. 2 (ed. L. H. Mantel and D. Bliss), New York: Academic Press (in the press).

MCMAHON, B. R., BURGGREN, W. W. & WILKENS, J. L. (1974). Respiratory responses to long-term hypoxic stress in the crayfish *Orconectes virilis*. *J. exp. Biol.* **60**, 195–206.

MCMAHON, B. R., BUTLER, P. J. & TAYLOR, E. W. (1978). Acid-base changes during recovery from disturbance and during long-term hypoxic exposure in the lobster *Homarus vulgaris*. *J. exp. Zool.* **205**, 361–370.

MCMAHON, B. R., MCDONALD, D. G. & WOOD, C. M. (1979). Ventilation, oxygen uptake and haemolymph oxygen transport following enforced exhaustive activity in the Dungeness Crab *Cancer magister*. *J. exp. Biol.* **80**, 271–285.

MANGUM, C. P. & JOHANSEN, K. (1975). The colloid osmotic pressure of invertebrate body fluids. *J. exp. Biol.* **63**, 661–671.

MANGUM, C. P. & VAN WINKLE, W. (1973). Responses of aquatic invertebrates to declining oxygen conditions. *Amer. Zool.* **13**, 529–541.

MASSABUAU, J.-C. & DEJOURS, P. (1981). Ventilatory CO_2 drive in the crayfish. *I.R.C.S. Medical Science*, **9**, 401.

MAYERI, E. (1973). Functional organization of the cardiac ganglion of the lobster, *Homarus americanus*. *J. gen. Physiol.* **62**, 448–472.

MAYNARD, D. M. (1953) Activity in a crustacean ganglion. I. Cardio-inhibition and acceleration in *Panulirus argus*. *Biol. Bull. mar. biol. Lab., Woods Hole* **104**, 156–170.

MAYNARD, D. M. (1960). Circulation and heart function. In *The Physiology of Crustacea* (ed. T. H. Waterman), New York: Academic Press.

MAYNARD, D. M. (1961). Cardiac inhibition in decapod crustacea. In *Nervous Inhibitions*. Oxford: Pergamon.

MAYNARD, D. M. & WELSH, J. H. (1959). Neurohormones of the pericardial organs of brachyuran crustacea. *J. Physiol.* **149**, 215–227.

MENDELSON, J. (1971). Oscillator neurons in crustacean ganglia. *Science, N.Y.* **171**, 1170–1173.

MITCHELL, R. A. & SEVERINGHAUS, J. W. (1965). Cerebrospinal fluid and the regulation of respiration. *Physiol. Physicians* **3**, 1–7.

OTANI, T. & BULLOCK, T. H. (1959). Effects of presetting the membrane potential of the soma of spontaneous and integrative ganglion cells. *Physiol. Zool.* **32**, 104–114.

PASZTOR, V. M. (1968). The neurophysiology of respiration in decapod crustacea. I. The motor system. *Can. J. Zool.* **46**, 585–596.

PASZTOR, V. M. (1969). The neurophysiology of respiration in decapod crustacea. II. The sensory system. *Can. J. Zool.* **47**, 435–441.

PASZTOR, V. M. & BUSH, B. M. H. (1982). Impulse coded and analog signalling in single mechanoreceptor neurons. *Science, N.Y.* (in the press).

PILKINGTON, J. B. (1976). Experimental coupling of crab (*Carcinus maenas*) second maxilla neural motor to an alternating current. *Experientia*, **32**, 1435–1437.

PILKINGTON, J. B. & MACFARLANE, D. W. (1978). Numbers and central projections of crab second maxilla motor neurones. *J. mar. biol. Ass. U.K.* **58**, 571–584.

PILKINGTON, J. B. & SIMMERS, A. J. (1973). An analysis of bailer movements responsible for gill ventilation in the crab *Cancer novae-zelandiae*. *Mar. behav. Physiol.* **2**, 73–95.

RANDALL, D. J. & WOOD, C. M. (1981). Carbon dioxide excretion in the land crab (*Cardisoma carnifex*). *J. exp. Zool.* **218**, 37–44.

REDMOND, J. R. (1955). The respiratory function of haemocyanin in Crustacea. *J. cell. comp. Physiol.* **46**, 209–247.

RUTLEDGE, P. S. (1981). Effects of temperature acclimation on crayfish haemocyanin oxygen binding. *Am. J. Physiol.* **240**, R93–R98.

RUTLEDGE, P. S. & PRITCHARD, A. W. (1981). Scope for activity in the crayfish *Pacifastacus leniusculus*. *Am. J. Physiol.* **240**, R87–R92.

SANDEMAN, D. C. (1967). The vascular circulation in the brain, optic lobes and thoracic ganglia of the crab *Carcinus*. *Proc. Roy. Soc. Lond.* B, **168**, 82–90.

SIMMERS, A. J. (1979). Oscillatory potentials in crab ventilatory neurones. *J. Physiol.* **287**, 39–40*P*.

SIMMERS, A. J. & BUSH, B. M. H. (1980). Non-spiking neurones controlling ventilation in crabs. *Brain Research* **197**, 247–252.

SMATRESK, N. J. & CAMERON, J. N. (1981). Post-exercise acid-base balance and ventilatory control in *Birgus latro*, the coconut crab. *J. exp. Zool.* **218**, 75–82.

SMATRESK, N. J., PRESLAR, A. J. & CAMERON, J. N. (1979). Post-exercise acid-base disturbance in *Gecarcinus lateralis*, a terrestrial crab. *J. exp. Zool.* **210**, 205–210.

SPOEK, G. L. (1974). The relationship between blood haemocyanin levels, oxygen uptake, and the heart-beat and scaphognathite-beat frequencies in the lobster *Homarus gammarus*. *Neth. J. Sea Res.* **8**, 1–26.

STEWART, P. A. (1978). Independent and dependent variables of acid-base control. *Respir. Physiol.* **33**, 9–26.

STIFFLER, D. F. & PRITCHARD, A. W. (1972). A comparison of *in situ* and *in vitro* responses of crustacean hearts to hypoxia. *Biol. Bull. mar. biol. Lab., Woods Hole* **143**, 247–255.

SULLIVAN, R. E. (1979). A proctolin-like peptide in crab pericardial organs. *J. exp. Zool.* **210**, 543–552.

TAYLOR, A. C. (1976). The respiratory responses of *Carcinus maenas* to declining oxygen tension. *J. exp. Biol.* **65**, 309–322.

TAYLOR, E. W. (1970). Spontaneous activity in the cardioaccelerator nerves of the crayfish, *Astacus pallipes* Lereboullet. *Comp. Biochem. Physiol.* **33**, 859–869.

TAYLOR, E. W. (1981). Some effects of temperature on respiration in decapodan crustaceans. *J. therm. Biol.* **6**, 239–248.

TAYLOR, E. W. & BUTLER, P. J. (1973). The behaviour and physiological responses of the shore crab *Carcinus maenas* during changes in environmental oxygen tension. *Neth. J. Sea Res.* **7**, 496–505.

TAYLOR, E. W. & BUTLER, P. J. (1978). Aquatic and aerial respiration in the shore crab *Carcinus maenas* (L.), acclimated to 15 °C. *J. comp. Physiol.* **127**, 315–323.

TAYLOR, E. W., BUTLER, P. J. & AL-WASSIA, A. (1977*a*). The effect of a decrease in salinity on respiration, osmoregulation and activity in the shore crab, *Carcinus maenas* (L.) at different acclimation temperatures. *J. comp. Physiol.* **119**, 155–170.

TAYLOR, E. W., BUTLER, P. J. & AL-WASSIA, A. (1977*b*). Some responses of the shore crab, *Carcinus*

maenas (L.) to progressive hypoxia at different acclimation temperatures and salinities. *J. com. Physiol.* **122**, 391–402.

TAYLOR, E. W., BUTLER, P. J. & SHERLOCK, P. J. (1973). The respiratory and cardiovascular changes associated with the emersion response of *Carcinus maenas* (L) during environmental hypoxia, at three different temperatures. *J. comp. Physiol.* **86**, 95–115.

TAYLOR, E. W., SHORT, S. & BUTLER, P. J. (1977). The role of the cardiac vagus in the response of the dogfish *Scyliorhinus canicula* to hypoxia. *J. exp. Biol.* **70**, 57–75.

TAYLOR, E. W. & WHEATLY, M. G. (1979). The behaviour and respiratory physiology of the shore crab, *Carcinus maenas* (L.) at moderately high temperatures. *J. comp. Physiol.* **130**, 309–316.

TAYLOR, E. W. & WHEATLY, M. G. (1980). Ventilation, heart rate and respiratory gas exchange in the crayfish *Austropotamobius pallipes* (Lereboullet) submerged in normoxic water and following 3 h exposure in air at 15 °C. *J. comp. Physiol.* **138**, 67–78.

TAYLOR, E. W. & WHEATLY, M. G. (1981). The effect of long-term aerial exposure on heart rate, ventilation, respiratory gas exchange and acid-base status in the crayfish *Austropotamobius pallipes*. *J. exp. Biol.* **92**, 109–124.

TAYLOR, E. W. & WHEATLY, M. G. (1982). The effects of dehydration during aerial exposure on the distribution of water and ions in the freshwater crayfish *Austropotamobius pallipes* (Lereboullet). *J. comp. Physiol.* (in the press).

TAYLOR, H. H. & GREENAWAY, P. (1979). The structure of the gills and lungs of the arid-zone crab, *Holthusiana* (*Austrothelphusa*) *transversa* (Brachyura-Sundathelphusidae) including observations on arterial vessels within the gills. *J. Zool. Lond.* **189**, 359–384.

TAZAKI, K. & COOKE, I. M. (1979). Spontaneous electrical activity and interaction of large and small cells in cardiac ganglion of the crab, *Portunus sanguinolentus*. *J. Neurophysiol.* **42**, 975–999.

TEAL, J. & CAREY, F. (1967). The metabolism of marsh crabs under conditions of reduced oxygen pressure. *Physiol. Zool.* **40**, 83–91.

THOMAS, H. J. (1954). The oxygen uptake of the lobster (*Homarus vulgaris Edw.*). *J. exp. Biol.* **31**, 228–251.

THOMPSON, R. & PRITCHARD, A. (1969). Respiratory adaptations of two burrowing crustaceans, *Callianassa californiensis* and *Upogebia pugettensis* (Decapoda, Thalassinidea). *Biol. Bull. mar. biol. Lab., Woods Hole* **136**, 274–287.

TRAUSCH, G. (1976). Glycolytic activity of the claw and tail muscle homogenates of the lobster, *Homarus vulgaris*. *Biochem. Syst. Ecol.* **4**, 51–54.

TRUCHOT, J.-P. (1973). Fixation et transport de l'oxygène par le sang de *Carcinus maenas*: variations en rapport avec diverses conditions de température et de salinité. *Neth. J. Sea Res.* **7**, 482–495.

TRUCHOT, J.-P. (1975*a*). Changements de l'état acide-base du sang en fonction de l'oxygénation de l'eau chez le crabe *Carcinus maenas* (L.). *J. Physiol., Paris* **70**, 583–592.

TRUCHOT, J.-P. (1975*b*). Blood acid-base changes during experimental emersion and reimmersion of the intertidal crab, *Carcinus maenas* (L.). *Respir. Physiol.* **23**, 351–360.

TRUCHOT, J.-P. (1976). Carbon dioxide combining properties of the blood of the shore crab *Carcinus maenas* (L.): CO_2 dissociation curves and the Haldane effect. *J. comp. Physiol.* **112**, 283–293.

TRUCHOT, J.-P. (1978). Mechanisms of extracellular acid-base regulation as temperature changes in decapod crustaceans. *Respir. Physiol.* **33**, 161–176.

TRUCHOT, J.-P. (1981). Lactate increases the oxygen affinity of crab haemocyanin. *J. exp. Zool.* **214**, 205–208.

TRUCHOT, J.-P. & DUHAMEL-JOUVE, A. (1980). Oxygen and carbon dioxide in the marine intertidal environment: diurnal and tidal changes in rockpools. *Respir. Physiol.* **39**, 241–254.

VAN DER KLOOT, W. (1980). The electrophysiology of muscle fibres in the hearts of decapod crustaceans. *J. exp. Zool.* **174**, 367–380.

WARNER, G. F. (1977). *The Biology of Crabs*. London: Paul Elek (Scientific Books) Ltd.

WATANABE, A. & BULLOCK, T. H. (1960). Modulation of activity of one neuron by subthreshold slow potentials in another in lobster cardiac ganglion. *J. gen. Physiol.* **43**, 1031–1045.

WEINS, A. W. & ARMITAGE, H. B. (1961). The oxygen consumption of the crayfish *Orconectes immunis* and *Orconectes nais* in response to temperature and oxygen saturation. *Physiol. Zool.* **34**, 39–54.

WHEATLY, M. G. (1980). The problems of respiratory gas exchange and acid-base balance in water and air in two amphibious decapodan crustaceans. Ph.D. thesis, University of Birmingham.

WHEATLY, M. G. & MCMAHON, B. R. (1982). Responses to hypersaline exposure in the euryhaline crayfish *Pacifastacus leniusculus* (Dana). II. Modulation of haemocyanin binding *in vitro* and *in vivo*. *J. exp. Biol.* (in the press).

WHEATLY, M. G. & TAYLOR, E. W. (1979). Oxygen levels, acid-base status and heart rate during emersion of the shore crab *Carcinus maenas* (L.) in air. *J. comp. Physiol.* **132**, 305–311.

WHEATLY, M. G. & TAYLOR, E. W. (1981). The effect of progressive hypoxia on heart rate, ventilation, respiratory gas exchange and acid-base status in the crayfish *Austropotamobius pallipes*. *J. exp. Biol.* **92**, 125–141.

KIERSMA, C. A. G. & NOVITSKI, E. (1942). The mechanism of the nervous regulation of the crayfish heart. *J. exp. Biol.* **19**, 255–265.

WILKENS, J. L. (1976). Neuronal control of respiration in decapod crustacea. *Fed. Proc.* **35**, 2000–2006.

WILKENS, J. L. (1981). Respiratory and circulatory coordination in decapod crustaceans. In *Locomotion and Energetics in Arthropods* (ed. C. F. Herreid and C. R. Fourtner), New York: Plenum Press.

WILKENS, J. L. & MCMAHON, B. R. (1972). Aspects of branchial irrigation in the lobster *Homarus americanus*. I. Functional analysis of scaphognathite beat, water pressures and currents. *J. exp. Biol.* **56**, 469–479.

WILKENS, J. L. & YOUNG, R. E. (1975). Patterns and bilateral co-ordination of scaphognathite rhythms in the lobster *Homarus americanus*. *J. exp. Biol.* **63**, 219–235.

WILKENS, J. L., WILKENS, L. A. & MCMAHON, B. R. (1974). Central control of cardiac and scaphognathite pacemakers in the crab, *Cancer magister*. *J. comp. Physiol.* **90**, 89–104.

WOOD, C. M. & RANDALL, D. J. (1981*a*). Oxygen and carbon dioxide exchange during exercise in the land crab (*Cardisoma carnifex*). *J. exp. Zool.* **218**, 7–22.

WOOD, C. M. & RANDALL, D. J. (1981*b*). Haemolymph gas transport, acid-base regulation, and anaerobic metabolism during exercise in the land crab (*Cardisoma carnifex*). *J. exp. Zool.* **218**, 23–36.

YOUNG, R. E. (1975). Neuromuscular control of ventilation in the crab *Carcinus maenas*. *J. comp. Physiol.* **101**, 1–37.

YOUNG, R. E. (1978). Correlated activities in the cardiovascular nerves and ventilatory system in the Norwegian lobster, *Nephrops norvegicus* (L.). *Comp. Biochem. Physiol.* **61**A, 387–394.

YOUNG, R. E. & COYER, P. E. (1979). Phase co-ordination in the cardiac and ventilatory rhythms of the lobster *Homarus americanus*. *J. exp. Biol.* **82**, 53–74.

ZUCKERKANDL, E. (1957). La tenue d'oxygène en hémolymphe artérielle de *Maia squinado* aux divers stades d'intermue. *C.r. Soc. Biol.* **151**, 524–528.