

GILL VENTILATION VOLUMES, OXYGEN CONSUMPTION AND RESPIRATORY RHYTHMS IN *CARCINUS MAENAS* (L.)

BY K. D. ARUDPRAGASAM* AND E. NAYLOR

Department of Zoology, University College of Swansea

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INTRODUCTION

In a previous paper (Arudpragasam & Naylor, 1964) it has been shown for *Carcinus* that reversals of the respiratory current form an integral part of the pattern of gill ventilation, and it seemed that there might therefore be a direct relationship between reversal rate and the rate of pumping of water through the gill chamber. Thus it seemed worth while to attempt to devise some means of measuring gill ventilation volumes, particularly since the number of instances where such measurements have been made in decapod crustacea are very limited (Wolvekamp & Waterman, 1960). Some indirect estimates of respiratory activity have been made in decapods by measuring the rate of beating of the scaphognathite, either by direct recording with a lever attachment (Kalmus, 1930; Segaar, 1934) or by visual counting of the beats of the exposed tip (Johnson, 1936; Van Heerdt & Krijgsman, 1939; van Weel, Randall & Takata, 1954), but results obtained in this manner are often conflicting and unreliable (Larimer, 1961). Moreover, direct measurements of gill ventilation volume so far appear to have been made only in macrurous forms such as *Astacus fluviatilis* (Lindroth, 1938), *Homarus vulgaris* (Thomas, 1954) and *Procambarus simulans* (Larimer, 1961), and no information on this important parameter of respiration seems to be available for any brachyurous decapod. The present paper describes a method for measuring gill ventilation volumes of crabs. It demonstrates that there are variations in the rate of gill ventilation both during normal respiratory activity of *Carcinus maenas* and during conditions of respiratory stress and it indicates that there is a direct relationship between ventilation volume and the rate of reversal of the respiratory current. In addition the results illustrate the relative importance of the various inhalant respiratory openings.

MATERIALS AND METHODS

To measure ventilation volumes it is necessary to isolate the exhalant stream of the respiratory current, which is relatively easy in the more elongate macrurous forms such as have been studied previously (see above). In the shorter brachyurous forms such as *Carcinus*, however, the shortening of the body and the close proximity of the anterior inhalants and the exhalants make the separation of inhalant and exhalant streams rather more difficult. The method used here was to enclose the anterior part of the crab within a polythene hood which was held in position by a rubber band

* Present address: Department of Zoology, University of Ceylon, Colombo 3, Ceylon.

passing around the body just anterior to the most anterior inhalant opening. The exhalant respiratory current was thus limited to the confines of the hood, the free end of which was secured to a short piece of polythene tubing, again by means of a rubber band.

The apparatus (Fig. 1) consisted of two Perspex chambers of equal dimensions joined together by a short piece of glass tubing which, in the animal chamber, served as the point of attachment for the hood attached to the crab. On the exhalant side the connecting tube opened into a small cubical chamber, open only on the upper side, from which samples of exhaled water were taken for analysis. Each chamber was provided with an overflow so that water exhaled by the crab displaced an equal volume down the overflow tube in the exhalant chamber and into a periodic siphon which recorded on a kymograph. In most experiments a continuous flow of sea water was maintained through the animal chamber, but some were carried out with a limited volume of water and in these cases all the overflow water from the exhalant side was returned to the animal chamber to equalize the head of water on each side.

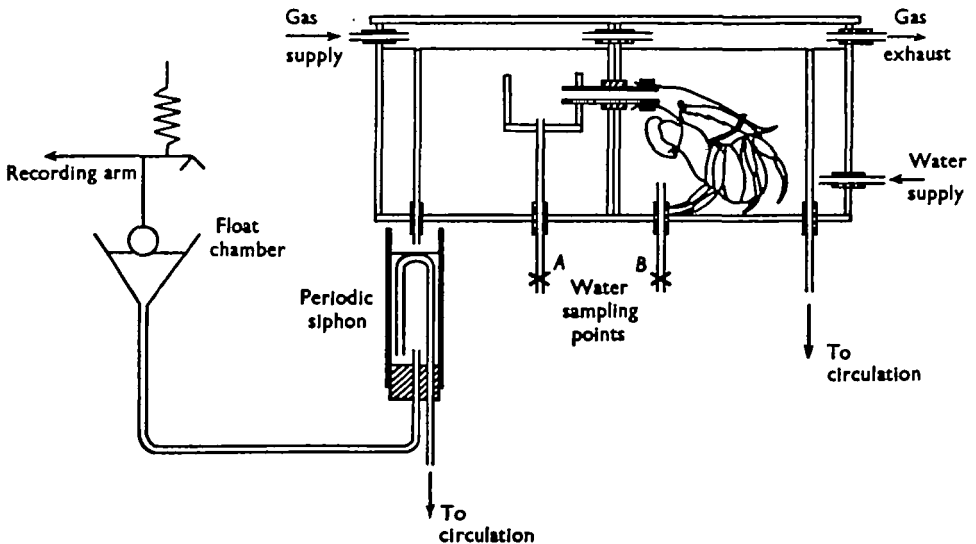


Fig. 1. Apparatus for recording continuously the gill ventilation volume of crabs.

Oxygen concentrations in inhaled and exhaled water were determined by a modified Winkler method (Fox & Wingfield, 1938) and values for oxygen consumption were calculated using corresponding values of ventilation volume to give figures for total available oxygen. pH was measured by introducing the electrodes of a pH meter directly into the animal chamber and corresponding values of total carbon-dioxide concentration were derived from a pH/CO₂ curve constructed using the carbon-dioxide titration method of Beyers & Odum (1959). In some experiments oxygen tensions were reduced by bubbling nitrogen through the water before it was led into the animal chamber and in others the concentration of carbon dioxide was increased by injecting water saturated with carbon dioxide into both chambers. In these and some other cases an airtight seal was maintained using glass covers sealed

temporarily with Vaseline, whilst air above the water was replaced with nitrogen. In most experiments the temperature of the water used was about 16° C. and the salinity about 32‰.

Though the crabs were tethered during the experiments they were able to move to some extent and could adopt a normal posture. Moreover, specimens survived, apparently without ill effects, in some experiments which lasted for several days. Most specimens were kept in aquaria before use in experiments, but in some long-term experiments only freshly collected animals were used.

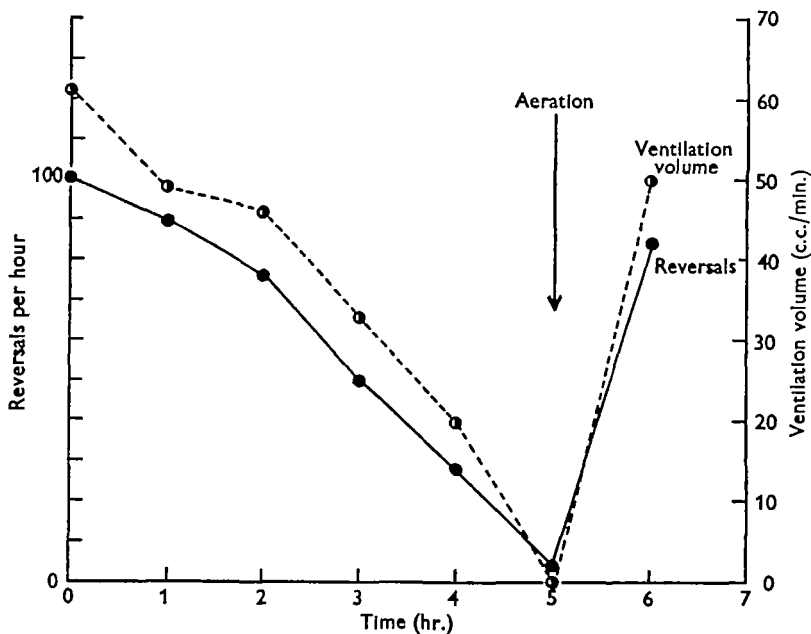


Fig. 2. Gill ventilation volumes in relation to the frequency of reversal of the respiratory current.

RESULTS

Ventilation volume and reversal rate

In these experiments which were carried out in a limited volume of water the ventilation volume was recorded for 5 min. every $\frac{1}{2}$ hr. whilst reversal frequency was recorded throughout by the method described previously (Arudpragasam & Naylor, 1964). Between the times of each measurement of the overflow the two chambers were in open communication by means of an additional connecting tube which was closed off again prior to each measurement. The results of a typical experiment, carried out with an atmosphere of nitrogen above the water in each chamber, are plotted in Fig. 2 in which it is clear that there is a direct relationship between reversal rate and ventilation volumes. The highest reversal rate was associated with the highest values for forward transport of water, and the diminution of reversal frequency associated with progressive stagnation of the water was accompanied by a similar fall in ventilation volume. Towards the end of the experiment reversals were almost completely

suspended and ventilation volume was reduced to an unmeasurable level. Nevertheless, aeration at this stage resulted in sharp rises in both reversal rate and ventilation volumes to values approximating to those at the beginning of the experiment.

The role of Milne-Edwards's openings

In these experiments, a crab was allowed to acclimatize in the apparatus for $\frac{1}{2}$ hr. before gill ventilation volumes were measured over a further period of 10 min. Milne-Edwards's openings at the bases of the chelipeds were then blocked by securing the polythene hood slightly further back around the body and measurements of the volume pumped were made for an additional 15 min. The results obtained, using a number of different crabs, are listed in Table 1, in which it is apparent that closure of Milne-Edwards's openings consistently resulted in an approximately 80% reduction of the amount of respiratory water taken in. Clearly therefore, these openings play a major role in normal gill ventilation.

Table 1. *Normal ventilation volumes compared with those when Milne-Edwards's openings were experimentally closed*

Normal ventilation (c.c./min.)	Ventilation volume with Milne-Edwards's openings closed (c.c./min.)	
	Total	Percentage
60	10	16.6
48	9	18.7
44	7	16.0
50	11	22.0
54	11	20.3
56	11	19.9
35	7	20.0
37	7	19.0

Ventilation volume and oxygen consumption

Fig. 3 shows the gill ventilation volumes of a series of crabs of both sexes ranging in weight from 18 to 60 g. The animals used were kept in aquaria for a few days before the experiments and in each case the animal was allowed to acclimatize for $\frac{1}{2}$ hr. in the apparatus before measurements were made. The ventilation volumes given are averages of the volume pumped in 10 consecutive minutes after the period of acclimatization. There was some variation between individuals and in the same individual at different times but in general the larger crabs pumped about 1 c.c./g./min. and smaller specimens up to about 1.5 c.c./g./min.

In a number of other experiments the oxygen tension of inhaled and exhaled water were estimated after 30 min. and after 60 min., whilst ventilation volumes were recorded continuously. Two sets of values could thus be calculated for percentage utilization of available oxygen and for total oxygen consumption in relation to body weight, and Table 2 shows the averages of these two sets of values for each crab used. Smaller crabs seemed to consume oxygen at a higher rate than larger ones, with a 23 g. specimen consuming about 0.108 c.c./g./hr. and a 70 g. specimen consuming about 0.03 c.c./g./hr. Average utilization values ranged from 9.3 to 22.9%, but these varied more with ventilation rate than with the size of the animal, for the highest

values of efficiency of utilization were related to low pumping rates and vice versa. However, there was a broad relationship between body weight and the volume of water pumped, so percentage utilization was, on average, higher in small crabs than in large specimens.

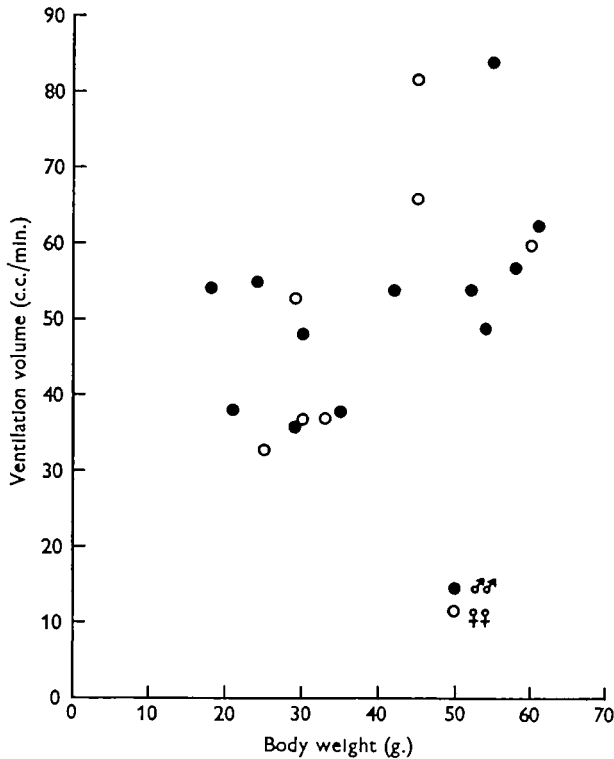


Fig. 3. Gill ventilation volumes recorded in crabs of various weights (see text for method).

Table 2. *Ventilation volume, percentage utilization and oxygen consumption in crabs of various weights*

Weight (g.)	Sex	Ventilation volume (c.c./min.)	% Utilization	Oxygen consumption (c.c./g./hr.)
21	♂	30	19.5	0.093
23	♂	32	22.9	0.108
34	♀	56	12.6	0.070
41	♂	60	12.0	0.058
43	♂	63	13.1	0.066
43	♂	47	20.4	0.076
48	♀	36	21.0	0.053
70	♂	68	9.3	0.030

Tidal and 24 hr. rhythms of respiration

Crabs used in these experiments were freshly collected from the shore and kept in continuous artificial light in water at a fairly constant temperature of about 16° C. Fig. 4 shows the results of one of these experiments in which, in addition to records of ventilation volumes, determinations of oxygen tensions in inhaled and exhaled water

were made at intervals of 30 min. It can be seen that ventilation volumes were greatest shortly after the times of high tide, whilst pumping activity was minimal between these times. Percentage utilization on the other hand varied more or less inversely to the rate of ventilation and, as one might expect, there was a smaller percentage depletion when water flowed most rapidly across the gills. Thus the highest efficiency of about 50% utilization occurred just before the times of high tide when ventilation rates were very low, whilst the lower values of between 30 and 40% depletion tended to coincide with peaks of pumping activity. The curve for oxygen consumption, calculated as the product of ventilation volume and oxygen depletion, closely parallels that for ventilation volume.

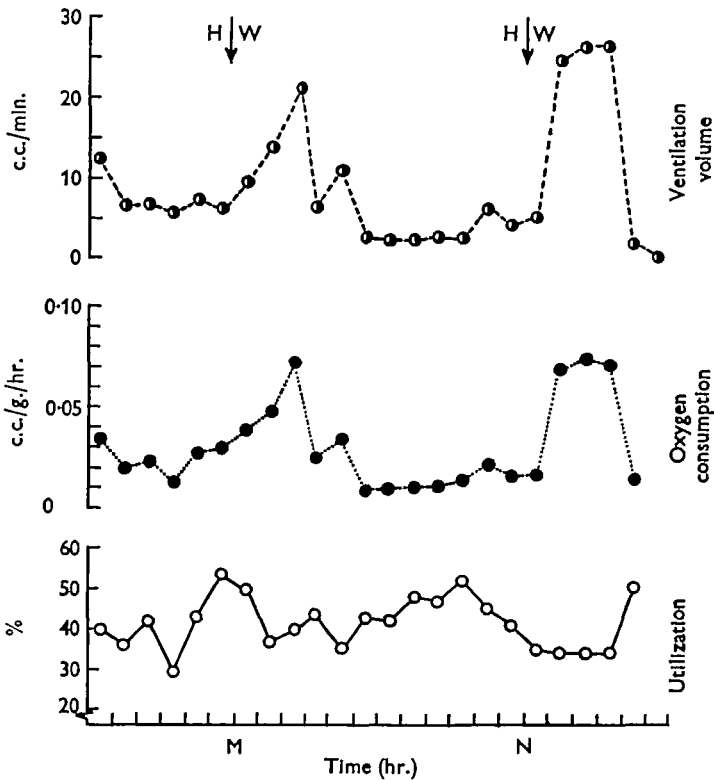


Fig. 4. Gill ventilation volumes, oxygen consumption and percentage utilization of a freshly collected crab during a period of 24 hr. HW, High tide; M, midnight; N, noon.

The existence of a tidal rhythm of gill ventilation activity was confirmed in a number of longer-term experiments and the results of two of these, lasting for 4 and 5 days respectively, are illustrated in Fig. 5. The summation of results in 12 hr. periods centred on the times of high tide (Fig. 5, inset) clearly confirms that the time of greatest pumping activity occurred at high and early ebb tide, with minimum pumping about 2 or 3 hr. before high tide. In addition these results, and perhaps also those in Fig. 4, indicate that pumping activity was often greater after a day-time high tide than after a night-time one, suggesting that there may have been a 24 hr. rhythm superimposed upon the tidal cycle. The rhythms were usually maintained for

about 5 days, during which time the total volume of water pumped tended to decrease each day. After about 5 days the rhythm was no longer overtly apparent in an individual crab and periods of pumping became irregular.

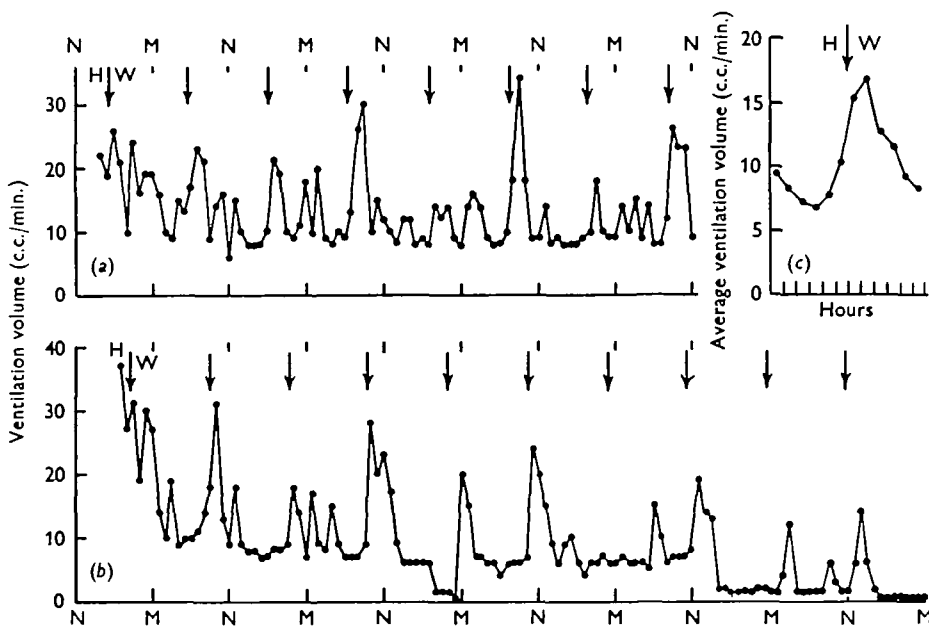


Fig. 5. Spontaneous changes in gill ventilation volume in two freshly collected crabs: (a) over a period of 4 days, (b) over a period of 5 days. Inset (c) presents the average ventilation volume in relation to the time of high tide. (Symbols as in Fig. 4.)

Responses to oxygen depletion

The effects of oxygen depletion on gill ventilation rates and the related changes in efficiency of utilization of oxygen were studied in a number of crabs of similar weights (40–43 g.). These animals were kept overnight in a little sea water which usually ensured that they would show a predictably high ventilation volume at the start of the experiments. In the control of one such experiment (Fig. 6*b*) in which the oxygen tension was maintained at a high level by aeration, ventilation volume was initially about 40 c.c./min. and fell off gradually to about 10 c.c./min. after 6 hr. At first the efficiency of utilization was low, related to the high pumping rate, but as the pumping rate decreased so utilization rose from an initial level of around 8% to a value of 35%. Throughout most of the experiment oxygen consumption remained fairly constant, fluctuating around 0.05 c.c./g./hr., though it fell off at the lowest pumping rates. In the experimental animal (Fig. 6*a*) a reduction in oxygen from 6 to about 4 c.c./l. was correlated with a sharp increase in ventilation volume. Moreover, whereas in the control such a rise would normally be accompanied by a drop in efficiency of utilization, there was also in this case a marked rise in percentage utilization. This therefore resulted in a particularly sharp increase in the total oxygen consumption in the early stages of oxygen depletion, though consumption fell sharply with a further decrease in available oxygen. Continued reduction in oxygen was correlated with a persistently high rate of gill ventilation so that even after 6 hr. when the oxygen tension was as low

as 1.5 c.c./l., the ventilation volume was four or five times greater than the control. However, pumping was abruptly suspended in experiments in which the oxygen tension was reduced to below 1 c.c./l. for longer than about 1 hr.

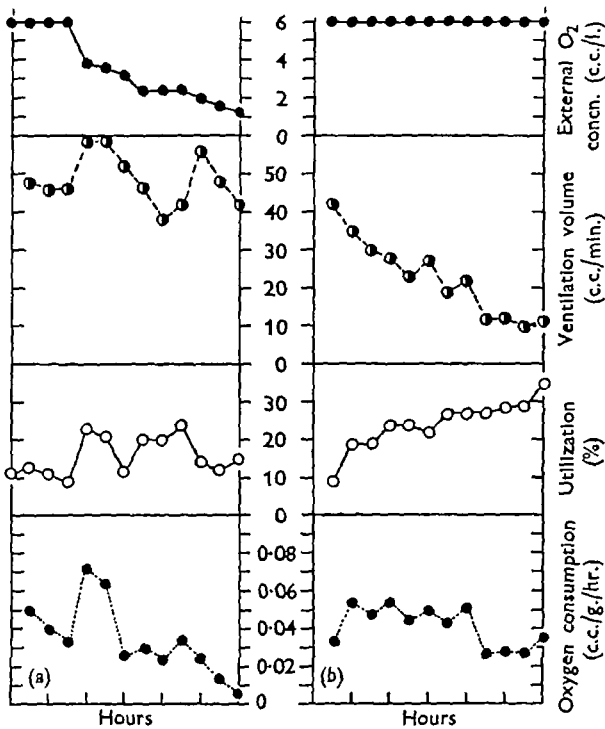


Fig. 6. Effects of oxygen depletion on gill ventilation, oxygen consumption and percentage utilization.

Responses to increased carbon dioxide

The effects of a sudden temporary increase in carbon-dioxide concentration on crabs kept in well-oxygenated water and in partly de-oxygenated water are illustrated in Fig. 7. The typical response to increased carbon dioxide in well-oxygenated water (Fig. 7a) was an immediate inhibition of gill ventilation lasting for 2 or 3 min., followed by a considerably increased pumping rate for a short period. There then followed a fall in pumping rate before the final rise to a fairly steady level at the end of the experiment, by which time, since water circulated continuously, carbon-dioxide concentration had returned to near the starting values. The reaction to carbon dioxide at low oxygen concentrations (Fig. 7b) was essentially similar except that the lower oxygen concentration apparently resulted in consistently higher ventilation rates and thus enhanced the responses to increased carbon dioxide.

In experiments in which the carbon-dioxide concentration was progressively increased in a limited volume of non-circulating water the immediate effects of each addition of carbon dioxide were similar to those described above, though recovery after each successive addition was progressively less marked (Fig. 8). At high oxygen tensions ventilation was completely suspended about 80 min. after the first addition

of carbon-dioxide at a carbon-dioxide concentration of about 225 c.c./l. (Fig. 8a). On the other hand, at low oxygen tensions (Fig. 8b), as would be expected, the pumping rates were already high even before the addition of carbon dioxide. Moreover, though the effects of increased carbon dioxide were similar to those observed at high oxygen concentrations, the animal was still pumping actively at the end of

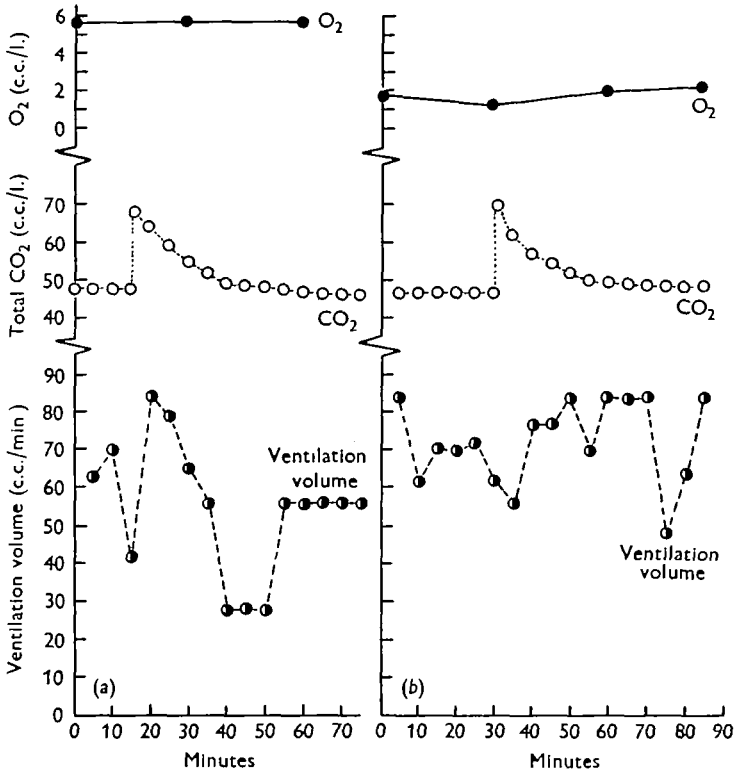


Fig. 7. Effects on gill ventilation of temporary increases in carbon-dioxide concentrations: (a) at normal oxygen tensions, (b) at low oxygen tensions.

2 hr. in water of very high concentrations of carbon dioxide. It would appear, therefore, that the increased rate of gill ventilation, brought about by reduced oxygen concentrations (see p. 315), was not completely over-ridden by the long-term inhibitory effects of increased carbon dioxide. Inhibition was, however, brought about at fairly high oxygen tensions by longer exposures to increased carbon dioxide, for ventilation was inhibited after a period of 3 hr. in stagnant water in which the concentration of carbon dioxide was increased experimentally to only 72 c.c./l. (Fig. 9a). Under conditions of gradual stagnation in a limited volume of sea water the combined responses to decreasing oxygen and increased carbon dioxide often resulted in an initial slight increase in ventilation volume, followed by a gradual falling off until pumping was eventually suspended at a carbon-dioxide concentration of about 50 c.c./l. and an oxygen concentration of about 2 c.c./l. (Fig. 9b).

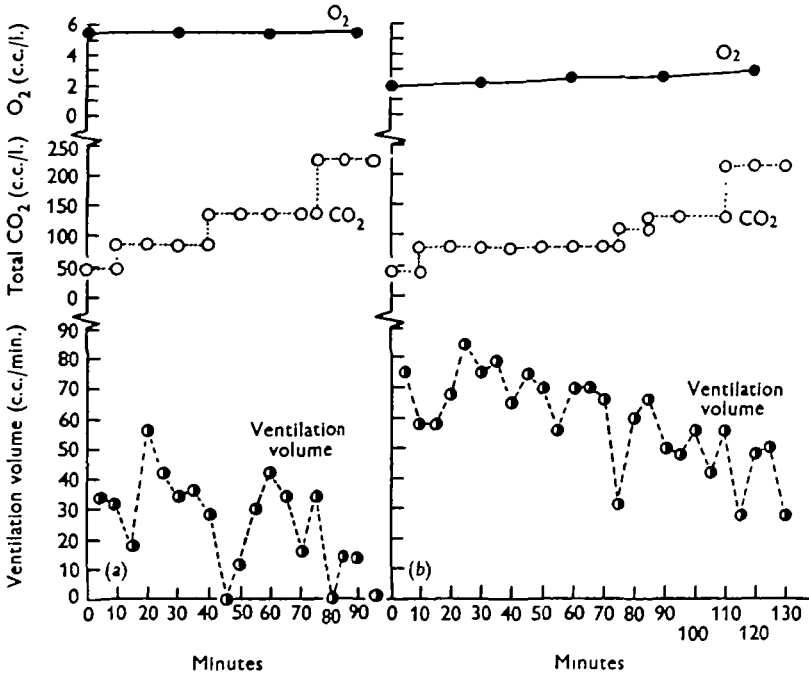


Fig. 8. Effects on gill ventilation of progressively increased exposure to carbon dioxide: (a) at normal oxygen tensions, (b) at low oxygen tensions.

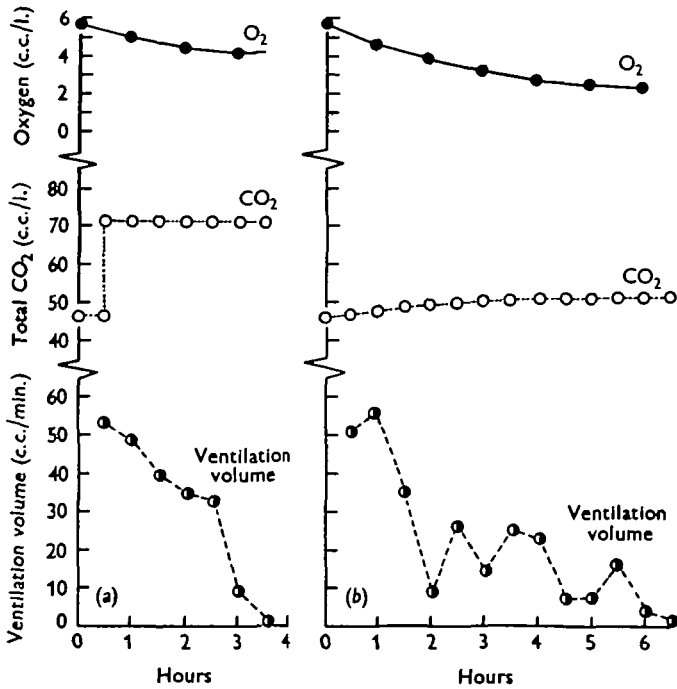


Fig. 9. (a) Effects on gill ventilation of prolonged exposure to moderately high concentrations of carbon dioxide. (b) Effects of stagnation on gill ventilation.

DISCUSSION

Present observations on *Carcinus* which demonstrate that as much as 80% of respiratory water enters the gill chamber through Milne-Edwards's openings, anterior to the large posterior gills, seem to support the view (Arudpragasam & Naylor, 1964) that current reversals form an integral part of the mechanism of gill ventilation by forcing water back across the gills. This, together with the fact that reversal frequency is directly proportional to the rate of forward transport of water (p. 311), suggests that measurements of reversal frequency as well as measurements of ventilation volume should give a more reliable indication of respiratory responses than, say, counts of scaphognathite beat which are sometimes unreliable (van Weel, Randall & Takata, 1954; Larimer, 1961). Thus though Johnson (1936) recorded irregular respiratory responses in *Carcinus* by counting scaphognathite beats, present measurements of ventilation volume and those of reversal frequency (Arudpragasam & Naylor, 1964) suggest that there are predictable responses to both oxygen lack and carbon-dioxide accumulation in that species. One possible disadvantage of the present method of measuring ventilation volumes is the fact that the animals were tethered, which might have affected their normal respiratory behaviour, though the animals certainly had more freedom of movement than those in the experiments of some previous workers (e.g. Thomas, 1954; Larimer, 1961). Moreover, freshly collected animals consistently showed apparently normal long-term rhythms of respiration and gill ventilation, so the results obtained are perhaps reasonably representative.

Average pumping rates for *Carcinus* kept previously in aquaria in this investigation were of the order of 1.0 c.c./g./min. as has also been recorded for two other brachyurous decapods, *Cancer pagurus* and *Portunas puber* (Arudpragasam, unpublished observations). These values are of the same order as, but slightly higher than, values of about 0.6 c.c./g./min. obtained for *Procambarus simulans* (Larimer, 1961), and 0.3 c.c./g./min. for *Homarus vulgaris* (Thomas, 1954). The rate of oxygen consumption is also of the same order as that reported for other crustacea (Wolvekamp & Waterman, 1960) and in *Carcinus* it varies from about 0.03 c.c./g./hr. in large crabs (70 g.) to about 0.108 c.c./g./hr. for smaller specimens (23 g.). Unlike the present results, previous accounts give no indication of possible rhythmic changes in ventilation volumes such as occur in *Carcinus*.

Values of percentage utilization of oxygen for animals kept previously in aquaria have been given as 60–70% for *Astacus* (Lindroth, 1938) and *Procambarus* (Larimer, 1961) and 40% for *Homarus* (Thomas, 1954). These compare with values of 10–25% for *Carcinus* kept under similar conditions in the present experiments, but such low values seem to be correlated with the slightly higher rates of gill ventilation in this species. More realistic values are perhaps seen in freshly collected *Carcinus* (see p. 314) which at first consumed about 40% of the available oxygen. Furthermore, it is important to note that the percentage utilization was inversely proportional to the rate of gill ventilation, which showed striking spontaneous increases at the times of high tide (see p. 314). Rhythmical changes in gill ventilation do not seem to have been previously reported in decapods though the existence of tidal and 24 hr. rhythms of oxygen consumption have been demonstrated in the fiddler crabs *Uca pugilator* and *Uca pugnax* (Brown, Bennett & Webb, 1954). In this respect it is of interest to

note that the times of greatest respiratory activity in *Uca* and *Carcinus* occur just after the times of greatest locomotor activity, which coincide with periods of low tide in *Uca* (Bennett, Shriner & Brown, 1957) and with high tide in *Carcinus* (Naylor, 1958, 1962). In *Carcinus*, however, it remains unexplained as to why periods of greatest respiratory activity occur just after times of daytime high tides, whilst periods of greatest locomotor activity coincide with night-time high tides (Naylor, 1958).

The respiratory responses of *Carcinus*, which show increased gill ventilation in low oxygen and inhibited ventilation in high concentrations of carbon dioxide, agree in general with those reported for other crustacea (Wolvekamp & Waterman, 1960), though carbon dioxide is not apparently always inhibitory (von Schlieper & Peters, 1957; Larimer, 1961). However, previous authors mainly reviewed the effects on scaphognathite beat so it is worth while also to consider the separate effects of stress upon percentage utilization of oxygen in addition to those upon ventilation volume. *Homarus vulgaris*, for example, shows a fairly constant rate of ventilation in lowered oxygen tensions, but percentage utilization rises steeply (Thomas, 1954). In contrast, *Procambarus simulans* shows increased ventilation rates at oxygen tensions down to about 1.5 c.c./l., but percentage utilization remained fairly constant over the whole range (Larimer, 1961). In *Carcinus*, too, the ventilation rate rises when oxygen tension begins to fall and is maintained at a fairly constant high level down to oxygen tensions of about 1 c.c./l., but in this species, unlike *Procambarus*, the rise in ventilation rate is also accompanied by a rise in percentage utilization. The simultaneous increases in ventilation volumes and percentage utilization of oxygen under conditions of stress are of particular interest, for under normal conditions percentage utilization tends to vary inversely with ventilation volume (see above). Perhaps, therefore, ventilation activity and oxygen uptake are under separate physiological control in *Carcinus* as they appear to be in *Procambarus* (Larimer, 1961) and in *Homarus* (Thomas, 1954). In *Homarus*, unlike *Procambarus* and *Carcinus*, the ventilation volume does not increase under conditions of stress (Thomas, 1954), but that species does seem to recirculate water over the gills as an additional regulatory mechanism (Arudpragasam, unpublished observations). In none of the above species does there seem to be a striking rise in percentage utilization at a critical oxygen tension such as has been demonstrated in a variety of decapods by van Weel *et al.* (1954); but *Carcinus* did show an abrupt suspension of ventilation activity at a critically low oxygen tension (see p. 316).

Finally, van Weel *et al.* (1954) have also suggested that respiratory responses may vary according to whether the animals normally live in well-oxygenated or in poorly oxygenated water, with which some present observations on *Carcinus* are in agreement. Thus *Carcinus* seems to have greater tolerance for high carbon dioxide than some other decapods, which is perhaps to be expected since the species is able to survive in isolated, shallow pools which might rapidly stagnate. This tolerance seems to be additional to the ability of *Carcinus* when in shallow pools to raise the front of the carapace above the water level and to aerate the water retained in the gill chamber by persistent reversals of the scaphognathite (Lim, 1918; Borradaile, 1922; Arudpragasam & Naylor, 1964).

SUMMARY

1. An apparatus is described for continuously measuring gill ventilation volumes in crabs.
2. Large *Carcinus* pump about 1 c.c./g./min. and consume oxygen at the rate of about 0.03 c.c./g./hr. whilst smaller specimens pump up to 1.5 c.c./g./min. and consume up to 0.1 c.c./g./hr. Freshly collected crabs show persistent tidal and 24 hr. rhythms of pumping activity and oxygen consumption.
3. In response to oxygen depletion *Carcinus* shows increased rates of gill ventilation and increased percentage utilization. Prolonged exposure to increased carbon dioxide results in a short-lived inhibition followed by over-compensation and then progressive inhibition of respiratory activity.
4. The results are discussed in relation to previous work on respiration in other decapod crustacea.

REFERENCES

- ARUDPRAGASAM, K. D. & NAYLOR, E. (1964). Gill ventilation and the role of reversed respiratory currents in *Carcinus maenas* (L.). *J. Exp. Biol.* **41**, 299-307.
- BENNETT, M. F., SHRINER, J. & BROWN, F. A., Jr. (1957). Persistent tidal cycles of spontaneous motor activity in the fiddler crab *Uca pugnax*. *Biol. Bull., Woods Hole*, **112** (3), 267-75.
- BEYERS, R. J. & ODUM, H. T. (1959). The use of carbon dioxide to construct pH curves for measurements of productivity. *Limnol. and Oceanogr.* **4**, 499-502.
- BORRADAILE, L. A. (1922). On the mouthparts of the shore crab. *J. Linn. Soc. (Zool.)*, **35**, 115-42.
- BROWN, F. A., Jr., BENNETT, M. F. & WEBB, H. M. (1954). Persistent daily and tidal rhythms of O₂-consumption in fiddler crabs. *J. Cell. Comp. Physiol.* **44** (3), 477-506.
- FOX, H. M. & WINGFIELD, C. A. (1938). A portable apparatus for the determination of oxygen dissolved in a small volume of water. *J. Exp. Biol.* **15**, 437-45.
- HEERDT, P. F. VAN & KRIJGSMAN, B. J. (1939). Die Regulierung der Atmung bei *Eriocheir sinensis* Milne-Edwards. *Z. vergl. Physiol.* **27**, 29-40.
- JOHNSON, M. L. (1936). The control of respiratory movements in crustacea by oxygen and carbon dioxide. *J. Exp. Biol.* **13**, 467-75.
- KALMUS, H. (1930). Untersuchungen über die Atmung des Flusskrebse *Potamobius astacus* Leach. *Z. vergl. Physiol.* **12**, 725-59.
- LARIMER, J. L. (1961). Measurement of ventilation volume in decapod crustacea. *Physiol. Zool.* **34** (2), 158-66.
- LIM, R. K. S. (1918). Experiments on the respiratory mechanism of the shore crab (*Carcinus maenas*). *Proc. Roy. Soc. Edinb.* **38**, 48-56.
- LINDROTH, A. (1938). Atmungsregulation bei *Astacus fluviatilis*. *Ark. Zool.* **30** (3), 1-7.
- NAYLOR, E. (1958). Tidal and diurnal rhythms of locomotory activity in *Carcinus maenas* (L.). *J. Exp. Biol.* **35** (3), 602-10.
- NAYLOR, E. (1962). Seasonal changes in a population of *Carcinus maenas* (L.) in the littoral zone. *J. Anim. Ecol.* **31**, 601-9.
- SCHLIEPER, C. VON & PETERS, F. (1937). Über den Einfluss der O₂- und CO₂-Spannungen des Aussenmediums auf die Atembewegungen von *Astacus fluviatilis* Fabricius. *Zool. Anz.* **120**, 95-9.
- SEGAAR, J. (1934). Die Atmungsbewegungen von *Astacus fluviatilis*. *Z. vergl. Physiol.* **21**, 492-515.
- THOMAS, H. J. (1954). The oxygen uptake of the lobster (*Homarus vulgaris* Edw.). *J. Exp. Biol.* **31**, 228-51.
- WEEL, P. B. VAN, RANDALL, J. E. & TAKATA, M. (1954). Observations on the oxygen consumption of certain marine crustacea. *Pacif. Sci.* **8**, 209-18.
- WOLVEKAMP, H. P. & WATERMAN, T. H. (1960). Respiration. In *The Physiology of Crustacea*, Vol. 1, pp. 35-100. Ed. T. H. Waterman. New York.

