ON RESPIRATION IN THE DRAGONET
CALLIONYMUS LYRA L.

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INTRODUCTION

In spite of the increased number of studies made during recent years on quantitative aspects of gill ventilation in fish, there are relatively few measurements of the performance of the respiratory pumps. On theoretical grounds it has become clear (Hughes & Shelton, 1962; Hughes, 1964; Rahn, 1966) that, for a full analysis of the gaseous exchange, data is required on the frequency and volume of both the water and blood flowing through the gills, together with their O₂ and CO₂ content. Ideally all the variables should be determined independently and ultimately we must aim at the analysis of a single respiratory cycle as is at present being achieved for the mammalian lung.

This will require even finer techniques for the implantation of electrodes, catheterization of blood vessels, and development of smaller and more rapidly responding $P_{O_2}$ and $P_{CO_2}$ electrodes. To achieve these aims in a fish breathing normally and free swimming will be extremely difficult and perhaps impossible experimentally. Several workers have recently measured the ventilation volume and frequency of the respiratory pump but the methods used have usually restricted the movements of the system (van Dam, 1938; Hughes & Shelton, 1962) or have been indirect (Saunders, 1962).

In this paper an attempt is described to measure the volumes and frequency of the respiratory pump simultaneously with the oxygen content of the water before and after the gills. On the blood side of the exchanger, changes in heart rate have been recorded but no attempt has been made to record its volume flow and O₂ content. In order to do this in an unanaesthetized and relatively unrestricted fish, use has been made of the adaptations of a bottom-living fish Callionymus in which the opening from each opercular cavity is single and dorsally-directed. Water leaving through this opening can be collected by means of a light rubber tube attached to the fish so that the respiratory pumps were scarcely affected. It seems possible that this preparation will be of value in further quantitative studies of the exchange between the water and blood.

MATERIALS AND METHODS

The animals used were mainly males of the dragonet (Callionymus lyra L.) weighing from 70 to 140 g. which had been kept in the sea-water circulation at the Plymouth Laboratory. The experiments were carried out in March and April 1965. Before each experiment the fish was anaesthetized in MS222 and fixed in an experimental set-up

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similar to that used in the dogfish (Hughes & Umezawa, 1968). Because of the small and circular nature of its dorsally directed opercular opening, this species was more amenable to this form of experimentation (Hughes, 1966a). Rubber ‘horns’ were moulded into suitable shapes and fixed to the surface of the fish by means of Eastman 910 adhesive and formed good water-tight connexions about the opercular openings whose valves continued to function normally. The fish was confined in a plastic cage which restricted its movements in the experimental tank, but once it had settled the fish scarcely ever attempted to move.

The expired water was collected in rubber tubes and led into a small chamber containing an oxygen electrode. The volume flowing across the gills was determined directly by displacement from an inclined beaker which had the same water level as the experimental tank, as was checked by a pair of water manometers. The inertial load imposed on the respiratory pumps by the system of collecting the water has been shown to have only a small effect on the O₂ consumption of the fish (Hughes & Knights, 1968). The sea water formed a closed circuit and its gas content could be varied by changing the composition of the gas which bubbled up the exchange column. Reductions in oxygen partial pressure (P₀₂) were produced by bubbling 100% nitrogen and this water was fed into a small plastic bottle one side of which was partly cut away, and the head of the fish was inserted into the opening. In this way the volume of water into which water of lowered P₀₂ was delivered was minimized and hence produced more rapid changes in P₀₂ of the inspired water. The P₀₂ of this water could be monitored by leading it over the same oxygen electrode as was used to determine the P₀₂ of the expired water. Use of the same electrode reduced errors due to any variation in electrode characteristics and this was further reduced by carrying out the experiments in a constant-temperature room at 11–12° C. The micro-oxygen electrode was of the type described by Silver (1963) and was used with a Times electrometer amplifier type AAA.

Normally the volume of water pumped across the gills by the fish was collected for 0.5 or 0.25 min. periods and at the same time the respiratory frequency was counted. In some experiments the pressure gradient of water across the gills was varied by adjusting the level of the beaker into which the water was collected. This pressure gradient (Δp) was measured by the water manometers, positive values being when the pressure on the mouth side was greater than that in the chambers collecting water from the opercular openings. The electrocardiogram (ECG) was led off by a pair of insulated steel pins, amplified by a Tektronix 122 preamplifier and recorded on a Kelvin Hughes or Ediswan pen recorder, as was the output of the oxygen electrode.

RESULTS

Although the pressure changes in the respiratory chambers have been recorded in Callionymus (Hughes, 1960), there has been relatively little work on other aspects of its respiration. This fish has several advantages for this purpose, notably the way it rests quietly on the bottom of a tank during experiments and the relatively low frequency (10–20 per min.) of its respiratory movements. The main disadvantages are its small size and that not all specimens survive for long periods in the laboratory.
(1) Relationship between the timing of the heart beat and respiratory movements

Preliminary observations were made using fish either unrestrained or held in a head clamp. The clearest respiratory movement is a contraction of the respiratory chambers during which the increased pressure forces water out through the opercular openings in the form of an almost vertical jet. There seems to be a tendency for the heart to beat shortly after this phase of the respiratory cycle (Fig. 1a, b).

However, the heart beat did not always coincide with a particular phase of the cycle (Fig. 1f). Where there were several heart beats during each respiratory cycle, those nearest the positive pressure phase seemed to be more constant in phasing than the others (fig. 1b). In some preparations, where there were two beats to each cycle, often

![Diagram](image)

Fig. 1. Relationship between the cardiac and respiratory rhythms analysed from a number of different fish. The respiratory cycle is shown by the buccal pressure curve below each figure and this cycle is divided into ten equal intervals. The frequency of occurrence of the ECG in these intervals is plotted in each instance. In some experiments the fish was under very light MS 222 anaesthesia (b, d, e, f), but in other cases the fish had been allowed to recover from the anaesthetic for many hours (a, c).

both tended to be close to the positive phase, one shortly before and one shortly after (Fig. 1d), and this produced the appearance of doublets in the ECG recording. In other cases where the cardiac:respiratory ratio was also 2:1, the heart beats were equally spaced with respect to one another.

Normally the respiratory frequency was 15–20 per min. and the heart rate two or three times greater, but in some cases the ratio became 1:1. Ratios as high as five beats:respiratory cycle were found and in these cases the position of the ECG in a given cycle was more variable (Fig. 1e). Although it was quite common for a fairly close
coupling to occur between the cardiac and respiratory cycles, there were many preparations in which there did not seem to be quite such a close coupling. For example, in the experiment analysed in Fig. 2a, it is clear that a ratio of 2:1 exists and that each heart beat occurs at a fairly constant time over a long period. For another fish, however, Fig. 2b shows the way in which, although there is again a ratio of about 2:1, in this case the position of the two cycles relative to the buccal pressure curve gradually shifts with each cycle, the heart beat tending to occur slightly later in successive respiratory cycles.

![Graphs showing cardiac and respiratory rhythms](image)

Fig. 2. More detailed analysis of the relationship between cardiac and respiratory rhythms of two different specimens. The position of the ECG in each of a successive series of respiratory cycles is shown. In (a) the fish had recovered from an anaesthetic for some time but it shows that the ECG fell very regularly twice during each respiratory cycle. In (b), however, there was a gradual shift in the position of the heart beat although the general ratio of 2:1 was the same as that for a. Specimen (b) was under very light MS 222 anaesthesia.

These variations do not appear to depend on the experimental treatment and often seem to be due to individual variations. It has sometimes been suggested, and shown in certain cases, that the close coupling arises as a result of MS 222 anaesthesia. The recording shown in Fig. 2a was taken from an experiment in which the fish, though anaesthetized initially for placement of the ECG electrodes, had been in sea water without anaesthetic for many hours. On the other hand, the recording shown in Fig. 2b was taken when the fish was under very light (1 g. in 50,000 c.c.) anaesthesia. Other indications of changes in the degree of coupling of the two rhythms were observed in unrestrained fish resting quietly on the bottom, when spontaneous changes in heart
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rate were recorded, although respiration continued at the normal rate. In such cases (Fig. 3d) there is a slowing of the heart although the respiratory frequency remains fairly constant. Then following a sort of 'cough' there is a marked increase in the cardiac frequency which declines again and this sort of pattern tends to be repeated in this particular fish. The fast records in Figs. 3a and b show the normal rhythm and again show how the heart rhythm is interrupted during these atypical respiratory manoeuvres. Increases in heart rate could often be obtained by directing a jet of water into the mouth when the animal was recovering from the anaesthetic. When the cardiac frequency changed under these and other conditions, there was a tendency for one of

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**Fig. 3. Callionymus lyra.** Recordings of pressures in the respiratory cavities and the electrocardiogram. (a) and (b) showed a regular 2:1 rhythm and the spontaneous change in the relationship between the two rhythms resulting from a cough. (d) shows other spontaneous changes in the heart rhythm which are to some extent related to the changes in the pressure curves. In (c) the effect of holding the mouth open on the rhythm of the heart seems to be a slowing during this experiment, but was followed by speeding up when the mouth was allowed to close again.

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**Fig. 4.** Plot of the interval between respiratory and cardiac cycles showing the effect of closing the mouth. Both rhythms slow down but return to the original level when the mouth was released.
the heart beats between the positive respiratory pressure phases to drop out or for others to be interpolated in this part of the cycle.

Experiments were also carried out in which the mouth was forced open or held closed, and under these conditions there was clear evidence of a correlation between respiratory and cardiac rhythms. During mouth closing there tended to be a decrease in heart rate (Fig. 4) but this effect was variable. Opening of the mouth produces a reduction in the size and frequency of the respiratory pressures and a slowing of the heart which usually speeds up very markedly when the lower jaw is released (Fig. 3c). In some preparations the mouth was held open by a short length (1 cm.) of rubber tubing placed between the jaws, and produced a very clear slowing of the heart. During one such experiment the ratio passed, for example, from 2:1 to 1:1.

In most of the experiments in which changes were made in the oxygen content of the water inspired by the fish there did not seem to be any definite effect on the coupling between the heart and respiratory rhythms. In some cases, however, it was observed that at low P O2's bradycardia was associated with a closer coupling between the two rhythms which sometimes fell into a 1:1 relationship.

In all experiments on the relationship between heart and ventilation rhythms it was observed that individuals differed from one another and were not consistent during an experiment.

(2) The pressure/flow relationship across the gills

When the pressure in the tubes collecting water from the opercular cavities was adjusted to be the same as that in the experimental tank, normal ventilation volumes of about 30 c.c./min. were measured for a fish of about 100 g. By varying the height of the beaker into which the water flowed, it was possible to alter the gradient (Δp) in hydrostatic pressure between the water entering the mouth and that outside the external gill openings. Experiments of this type on dogfish (Hughes & Umezawa, 1968) showed a fairly linear relationship between the flow across the gills and the imposed pressure gradient over the range —0.7 to +2.0 cm. H2O. Many experiments of this type were carried out with Callionymus and again a fairly linear relationship was obtained between flow and pressure gradient. However, in most preparations it was found that the precise nature of the pressure/flow relationship differed on the two sides of zero. Usually a larger change in flow occurred for a given pressure change when the pressure in the mouth was made greater than that on the opercular side, i.e. a positive gradient.

It was found that many specimens could still pump water out of the opercular cavity even against adverse or negative gradients of 2 cm. of water. This seems to correlate fairly well with the large positive phase of the opercular pressure curve which sometimes reaches 2 cm. of water in Callionymus.

A series of plots for a number of specimens is given in Fig. 5, and they give some indication of the range obtained from different individuals. It can be seen that on the positive side of zero the slope is approximately 30 c.c./min./cm. H2O. On the negative side, however, this is reduced to 10–15 c.c./min./cm. H2O.

These gradients were fairly constant in different specimens and seem to indicate some property of the gill resistance. It is also of interest that the gradient on the positive side gives approximately the normal minute volume (30 c.c./min.) for a pressure gradient of 1 cm. of water, which is the mean pressure difference normally
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measured across the gills. In Fig. 6a two sets of data obtained from the same fish at different times during a given experiment are shown. At the beginning of the experiment the fish was hyperventilating, and it is of interest that the slope of the curve is different to that obtained 6 hr. later when the fish was fully equilibrated and in a resting state. During the hyperventilating phase the slope of the line was very much the same on both sides of zero but the difference between them was present later. In the latter

Fig. 5. Effect of changing the gradient (Δ\(p\)) of hydrostatic pressure across the gills on the volume of water pumped by four different specimens. Notice that Δ\(p\) = 0 is the normal situation with the same pressure on the mouth and opercular sides. This normally gave a minute volume of 20–35 c.c./min.

Fig. 6. Relationship between the volume of water pumped across the gills and the inspired hydrostatic pressure gradient (Δ\(p\)). (a) Beginning of the experiment, this fish was hyperventilating (----); 6 hr. later (-----), the normal ventilation volume was reduced to half. In the latter position the difference between the gradients of this curve on the two sides of zero began to show itself, though not so markedly as is typical (Figs. 5, 6b). (b) More details of a minute volume/Δ\(p\) plot for a given specimen in which the arrows indicate the direction in which pressure gradient changes were made. It is clear that changes from positive to negative always lie below those from negative to positive Δ\(p\)'s.
condition, of course, the relationship was such that the volume for a given \( \Delta p \) was lower than during the hyperventilation stage, presumably because of a reduction in the proportion of the water shunted between the tips of the filaments.

During the experiments in which changes were made in the \( \Delta p \) and minute volume measured, it was customary to make changes alternately from the zero pressure in the positive and the negative directions. In this way it was hoped to avoid any unnecessary loading of the system, and where this was done by an adverse gradient, immediately to help to restore normal conditions with a gradient assisting ventilation. The different \( \Delta p \)'s were maintained for about 5–10 min. or until a reasonably steady flow resulted. In some cases, however, changes were made steadily in one direction to a maximum and then returned to zero before the changes were made in the opposite direction. If, when plotting the results of such an experiment (Fig. 6b), account was taken of the order in which the measurements were made, a hysteresis was often found in the curve. Thus the minute volume was generally less for a particular pressure gradient when the change was made from a high positive level down towards the

![Diagram](image-url)

Fig. 7. Effect of changes in the rate of water flow across the gills on the heart rate (-----) and percentage utilization (------). When the minute volume increased as a result of a greater \( \Delta p \) there was no change in heart rate (●) but a marked fall in utilization (■). Increased flow resulting from a lowering of the inspired \( P_{O_2} \), however, resulted in a marked fall in both heart rate (○) and utilization (□).
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negative side. Also, when the flow had been slow and the gradient was gradually increased, the flow obtained for a given pressure was above that obtained previously. The difference may well be due to a difference in the degree of expansion of the gill sieve under these conditions and it might be expected to be maximal under the high pressure gradients but minimal with adverse gradients and there would tend to be

\[ \Delta p = +2 \text{ cm.} \]

\[ \Delta p = 0 \]

\[ \Delta p = -1.8 \]

Fig. 8. Recordings of the electrocardiogram from a fish during a change in flow produced by different \( \Delta p \)'s. Respiratory movements make rhythmic artifacts on the recordings. For full description, see text.

some time-lag before this became modified in relation to the new flow. If this interpretation is correct, it suggests a passive effect on the gills rather than an active response of a mechanism regulating the orientation of the gills as a direct response to the flow.

During experiments of this kind measurements were also made of the oxygen removed by the gills in relation to changes in the volume of water flow brought about
by changing the $\Delta p$. As can be seen from Fig. 7, this clearly showed a fall in percentage utilization with the increased flow. It is notable, however, that there was no marked change in the heart rate in these experiments. Thus in Fig. 8, the centre record (b) is with the normal pressure relationships and the water pumped by a fish was 53 c.c./min. When the $\Delta p$ was increased to +2 cm. the flow increased to 120 c.c./min., but when it was nearly $-2.0$ cm. the flow was reduced to 2.5 c.c./min. The water inspired by the fish was saturated with air and its $P_{O_2}$ was consistently about 155 mm. Hg. But after it passed over the gills, it was reduced to 115, 90 and 50 mm. respectively for the three different rates of flow. Thus, at lower flows there was a more marked lowering of the oxygen content, i.e. the percentage utilization was increased. The heart and respiratory frequencies can be made out from these records and are shown on the right-hand side of Fig. 8; the cardiac frequency changed relatively little but in this case the respiratory rate fell more than usual, from 21 to 14 per min. This lowering of the respiratory rate probably resulted from the poor oxygenation of the blood at these low ventilation volumes.

In some experiments a fish was made to pump against a pressure head of more than 1 cm. of water for longer periods. When the normal pressure gradient was restored there was usually a marked increase in the oxygen consumption above the resting level, which suggests the paying off of an oxygen debt as a result of the extra work done by the respiratory pumps during the period of working against the gradient.

(3) The effect of changes in $P_{O_2}$ of the water inspired by the fish

Some experiments were carried out in which the fish was maintained in water of different partial pressures of oxygen for periods of 2 hr. The oxygen consumption was measured when it had reached a more or less constant level and was found to be directly related to the $P_{O_2}$ of the inspired water except at the highest levels where the curve seems to flatten out (Fig. 9). Such a relationship suggests a largely dependent type of respiration similar to that of the toadfish *Opsanus tau* (Hall, 1929). The lowered oxygen consumption with reduction in $P_{O_2}$ is associated with a fall in minute volume brought about by a decrease in stroke volume and respiratory frequency but a rise in utilization.

In most experiments the changes in $P_{O_2}$ were sudden and brief and no observations were made on the effect of varying the rate of change. The results of a typical experiment are shown in Figs. 10 and 11, which show a typical record and all the data determined simultaneously either directly or indirectly. It was found that, following a rapid fall in $P_{O_2}$ of the inspired water, the $P_{O_2}$ of the water which passed over the gills also fell but not proportionately. Consequently there was a fall in percentage utilization of oxygen, and when the fish showed signs of respiratory distress air-saturated water was fed in once more, usually about 4 min. after the experiment had begun. Following the renewed breathing of air-saturated water, the increase of the inspired $P_{O_2}$ was reflected by a rise in the $P_{O_2}$ of the expired water; this rise took much longer before it reached its original level. Consequently, there was a significant increase in the percentage utilization of oxygen following a brief period of hypoxia.

The most obvious respiratory response of the fish to lowering the $P_{O_2}$ of the inspired water was an increase in the volume of water pumped over the gills per minute. This was mainly achieved by increases in stroke volume because the respiratory frequency
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fell at lower $P_{O_2}$'s. The fish was observed to breathe very deeply and in many cases the volume pumped in a respiratory cycle was doubled. During the recovery period, the ventilation rate and stroke volume gradually returned to normal. The oxygen consumption of the fish fell during the period of reduced $P_{O_2}$ as was to be expected, but following

![Graph](image)

Fig. 9. Relationship between oxygen consumption of the fish under standard conditions, and its relation to the $P_{O_2}$ of the ambient water. Each of the points is the mean of three determinations. The oxygen consumption of this particular fish is higher than in most instances when it was 30–50 c.c./kg./hr. at $P_{O_2}$'s of about 150 mm. Hg.

![Graph](image)

Fig. 10. Pen recording showing the effect of lowering the $P_{O_2}$ of the inspired water as a result of bubbling nitrogen through the exchange column. The change in the electrocardiogram clearly shows the marked bradycardia.

the return of the air-saturated water there was an overshoot which suggested that the fish was making up an oxygen debt incurred during the hypoxic period. It is notable that this raised oxygen consumption during recovery was achieved largely as a result of the increased utilization and not by an increase in the volume of water pumped over the gills. If the latter were the case it would have involved a further increase in the oxygen consumption of the fish and hence would be less efficient than that of increasing utilization. In the absence of any measurements one can only surmise that the $P_{O_2}$ of the afferent blood was low during recovery from hypoxia, and hence would increase

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the $P_{O_2}$ gradient across the water/blood interface. In some experiments the increased ventilation persisted for a short time after the fish was breathing air-saturated water once more and occasionally there was only a relatively small change in minute volume during hypoxia, although there were marked changes in the percentage utilization and heart rate.

![Diagram summarizing the effect of lowering the $P_{O_2}$ of the water inspired by the fish.](image)

Fig. 11. Diagram summarizing the effect of lowering the $P_{O_2}$ of the water inspired by the fish. This analysis was produced by superimposing two sets of data in which the $P_{O_2}$ either before or after the gills was determined. From the experimental data, values for the percentage utilization, oxygen consumption, and stroke volume were calculated. All the other parameters were measured directly.

The response of the heart during these experiments was a marked bradycardia, the heart rate falling quite rapidly and ultimately almost to zero. At the lowest partial pressures of oxygen (about 40 mm. Hg) the fish began to make struggling movements
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Fig. 12. Changes in $P_{O_2}$ of the inspired and expired water during hypoxia. The same data are also plotted with respect to the changes in heart rate which occur during the reduction in the $P_{O_2}$ of the inspired water.

Fig. 13. Plots to show heart rate (●) and ventilation frequency (▲) in relation to the changes in minute volume which occur during a reduction in the inspired $P_{O_2}$ and its subsequent return to the normal level.
and it was essential to return the $P_{O_2}$ to normal. Analysis of the relationship between changes of heart rate and $P_{O_2}$ of the water before and after its passage over the gills suggests that the heart rate is most closely linked to the $P_{O_2}$ of the inspired water as shown by plotting the $P_{O_2}$ of the inspired and expired water against heart rate (Fig. 12). Thus although the heart rate and $P_{O_2}$ of the inspired water returned to their original level fairly quickly after a period of hypoxia, this was not the case for the $P_{O_2}$ of the expired water. The effect on respiratory frequency is not so marked though it generally fell at low $P_{O_2}$'s. The frequency was usually unaffected in most experiments in which the volume of water flowing through the gills was changed by altering $\Delta p$.

The possibility that the change in flow resulting from the hypoxia was the effective stimulus producing changes in both the heart rate and utilization is an obvious one. Figs. 13 and 14 show plots of the relationship between minute volume during lowered $P_{O_2}$ of the inspired water in relation to the percentage utilization, heart rate and respiratory frequency. As has just been indicated, Fig. 13 shows that there is a lowering of the heart rate which is associated with the increase in ventilation volume and there is also a significant fall in ventilation frequency. In Fig. 14, however, account is taken of the

![Graph showing changes in utilization and heart rate](image-url)
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time relationships of the points and they are joined up to form hysteresis loops. Both percentage utilization and heart rate fall as the ventilation volume increases with lowering of the inspired $P_{O_2}$. During the increasing phase of the inspired $P_{O_2}$ there is a rapid return of both parameters to the original level although there is no marked change in minute volume. The subsequent reduction in ventilation volume during recovery is not associated with very large changes in heart rate or utilization, but the latter finally falls to its original level at the same minute volume. These observations support the view that neither percentage utilization nor heart rate during the recovery phase is directly dependent on the change in minute volume.

**DISCUSSION**

From the results described in this and subsequent papers (Hughes & Ballintijn, 1968; Hughes & Knights, 1968), it is clear that *Callionymus* has much to recommend it as an experimental animal for studies of this kind; its particular advantages include a normal habit of resting on the sea bottom for long periods and a convenient anatomical arrangement for measuring the ventilation volume directly. It is not quite ideal, however, as it is relatively small, and a larger fish of this kind might prove more suitable. When considering the results of this work, it must be remembered that *Callionymus* is specialized in relation to its mode of life.

Some of the observations reported here are of general interest in relation to the respiratory mechanism of fish. For example, the frequency of the heart is more rapid than that of respiration, which is opposite to the situation found in most fishes previously investigated.

Ratios as high as 5:1 were observed and only in very rare instances was the cardiac frequency less than that of the respiratory movements. This situation is related to the low frequency of the latter and the particular mechanism of gill ventilation involving a slow expansion of the opercular cavities and a relatively large stroke volume. It is therefore possible for quite a large volume of blood to be pumped through the gills and to be effectively oxygenated during this period. As the heart is relatively small it must beat more frequently if an efficient relationship is to be maintained between the $O_2$ capacities and the rates of flow of the blood and the water. The results obtained on the relationship of these rhythms have been variable and require further more detailed experimentation before it is possible to be more certain of the conditions under which the two rhythms come into phase with one another. This certainly occurs under MS 222 anaesthesia and hypoxia, but not in all cases.

*Callionymus* has been particularly useful for studying the effect of changing the hydrostatic pressure gradient across the gills on the volume pumped by the fish. Similar experiments were first carried out on *Scyliorhinus* (Hughes & Umezawa, 1968), where the straight line relating flow and pressure was the same for both negative and positive gradients. This was occasionally true for *Callionymus*, as when the fish was hyperventilating, but normally the slope of the curve was much steeper on the positive side. The most probable interpretation is that the steeper slopes represent mainly the passive effect of the gill resistance on the flow, whereas when the gradient is adverse the reduction in slope is accounted for by the extra effort of the fish to continue adequate ventilation of the gills. This difference between the dogfish and *Callionymus*
is illustrated by Table 1 from which it is clear that *Callionymus* is much more able to maintain the ventilation volume with adverse gradients. That the maintenance of the ventilation is an active response is supported by later experiments in which the electromyograms were recorded (Hughes & Ballintijn, 1968). It was also found that the better the condition of the fish, the more able it was to maintain an adequate ventilation of the gills with adverse gradients (Hughes & Knights, 1968). The fall in percentage utilization with increasing water flow is partly due to the increased velocity of water flow between the secondary lamellae, but also to the increased proportion that is shunted past the tips of the filaments as a part of the anatomical dead space (Hughes, 1966b).

Table 1. Effect of negative pressure gradients on minute volume of Callionymus and Scyliorhinus

<table>
<thead>
<tr>
<th>∆p</th>
<th>Callionymus (c.c./min.)</th>
<th>Scyliorhinus (c.c./min.)</th>
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<tbody>
<tr>
<td>0</td>
<td>30</td>
<td>70</td>
</tr>
<tr>
<td>−0.7 cm. H₂O</td>
<td>27</td>
<td>0</td>
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<tr>
<td>−2.0 cm.</td>
<td>20</td>
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The results of the oxygen measurements confirmed that bradycardia occurred during reduction of the Pₒ₂ of the inspired water, as reported by Randall & Shelton (1963) for the tench. In their case, however, they were unable to measure the minute volume under these conditions and they assumed that it would increase as did the amplitude and frequency of the respiratory movements. In the present experiments it was possible to measure this directly and, unlike most other fish, *Callionymus* shows a decrease in respiratory frequency with lowering of the Pₒ₂ while maintaining or even increasing the minute volume. The stroke volume consequently increases a great deal. Analysis of the recordings has shown that the change in heart rate is related to the Pₒ₂ of the inspired water and lends further support to the view that the bradycardia is initiated as a response to oxygen receptors on the gills. The possibility that the changes in heart rate are directly related to changes in the rate of water flow through the respiratory system has been ruled out by the present experiments because during such changes resulting from alterations in the hydrostatic pressure gradient the heart rate was almost constant in contrast to the very marked bradycardia during hypoxia, although the changes in minute volume were comparable in the two instances.

As indicated earlier, the main information that is lacking for a more complete interpretation of the present results is the Pₒ₂ of the afferent and efferent blood. However, some deductions can be made about this from the changes in the percentage utilization. During recovery from the rapid lowering of Pₒ₂ the utilization maintains a more or less steady level about 55–60%, whereas before it was about 40%, and as the ventilation volume remains the same, these differences are probably due to modifications on the blood side of the exchanger. The heart rate also recovers to the same level and so there must have been changes in cardiac stroke volume or in the Pₒ₂ of the blood going to the gills, so as to increase the gradient for oxygen diffusion across the secondary lamellae.

All the experiments tend to indicate that *Callionymus* shows a conforming type of respiration and therefore the differences noted above relative to those, for example, in
the trout by Holeton & Randall (1967) and Randall, Holeton & Stevens (1967), can perhaps be attributed to this difference. In general, Callionymus tends to show an oxygen uptake which is directly related to the ventilation volume and to the $P_{O_2}$ of the inspired water.

**SUMMARY**

1. The usefulness of a bottom-living fish, the dragonet (*Callionymus lyra*), in experiments on fish respiration is described. The position and nature of its opercular opening made it possible to determine directly the volume of water pumped over the gills and the $P_{O_2}$ of the mixed expired water. The normal ventilation volume for a 100 g. fish was about 30 c.c./min.

2. The relationship between cardiac and respiratory rhythms was investigated and showed a variety of ratios. The heart usually beats more than once during each respiratory cycle. Individual variations in the coupling between these rhythms was common and close couplings were observed in the absence of anaesthetic and at normal $P_{O_2}$s.

3. Changes in minute volume produced by altering the hydrostatic pressure across the respiratory system did not affect the heart rate. Percentage utilization fell at higher flow rates. Changes in flow per cm. of water pressure gradient was less with negative gradients than when the static pressure on the mouth side exceeded that in the opercular collecting chamber.

4. Oxygen consumption of the fish is directly related to the ambient $P_{O_2}$ over a wide range (30–120 mm. Hg). Sudden lowering of the $P_{O_2}$ in the inspired water leads to compensatory responses in which the minute volume is maintained or increased as a result of a rise in stroke volume and lowered respiratory frequency: there is also a marked bradycardia. During recovery the increased oxygen consumption of the fish resulted from a rise in utilization rather than a change in the respiratory rate or ventilation volume.

5. Analysis of the time course of the changes in heart rate and ventilation volume in experiments in which $P_{O_2}$ was changed supports the view that the receptors mediating bradycardia occur on the gills and respond directly to the change in $P_{O_2}$ rather than to the secondary increase in flow produced by the hypoxia.

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**REFERENCES**


