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THE USE OF A NEW TILTING TUNNEL RESPIROMETER TO INVESTIGATE SOME ASPECTS OF METABOLISM AND SWIMMING ACTIVITY OF THE PLAICE (*PLEURONECTES PLATESSA* L.)

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SUMMARY

1. Plaice and other flatfish can be induced to swim down a slope of about 60° against an upwelling water flow in a water tunnel.

2. A tilting Brett-type tunnel respirometer based on the above principle enabled laboratory experiments on swimming plaice to be carried out.

3. From trials at 5°, 10°, 15 °C, the relationship between specific swimming speed, V (body lengths s^{-1}), oxygen consumption, R (mg^{-1}. kg^{-1} h^{-1}) and temperature, T is: $\log_{10} = 0{\cdot}3318V + \log_{10}(2{\cdot}45T + 26{\cdot}52)$.

4. If the fish is resting (i.e. $V = 0$), the oxygen consumption is lower than predicted by the above equation. At rest:

$$R = 3{\cdot}14T + 2{\cdot}66.$$

5. The cost of swimming in plaice is very similar to that of typical round fish such as haddock but the resting metabolic rate is lower than for haddock.

6. Before swimming, a negatively buoyant fish such as plaice must lift off the bottom. This cost of lift-off or posture effect makes it uneconomical for plaice to swim at speeds below $0{\cdot}6V$.

INTRODUCTION

Since the development of tunnel respirometers by Blažka, Volf & Cepela (1960) and Brett (1964) considerable progress has been made in the understanding of metabolic costs of swimming in fish. The techniques developed by the above authors have been applied in a number of laboratories to a variety of fish. All the fish investigated so far have been 'roundfish' such as the gadoids and salmonids; no similar progress has been made on flatfish.

Recent sonic tracking studies on plaice *Pleuronectes platessa* have obtained continuous measurements of swimming activity of individuals during the course of movements in the North Sea (Greer-Walker, Harden-Jones & Arnold, 1978). The present study was designed as a laboratory investigation on the metabolic cost of swimming in plaice complimentary to the advancing knowledge of the behaviour of the fish at sea.

If a flatfish such as plaice is put into a water flow it adheres to the bottom (Arnold, 1969) and no swimming response is observed. Measurements have been made of

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standard or resting oxygen consumptions in plaice (Edwards, 1971) but since it was impossible to elicit sustained swimming in the laboratory no investigations have been made of metabolism and swimming in flatfish.

A new kind of tilting water tunnel for flatfish respirometry studies is described below. With this apparatus the relationship between oxygen consumption and swimming speed was investigated in plaice acclimated to different temperatures.

METHODS

Principle of the tilting water tunnel

Arnold & Weihs (1978) have described the mechanism of rheotaxis in plaice. The fish lies on the bottom facing upstream and depending on size can remain motionless up to a water velocity of about one body length per second before slipping or displacement occurs.

Plaice are negatively buoyant, having one of the highest densities of all marine fish (Harden-Jones & Marshall, 1953). The underwater weight is an important factor in the mechanism of maintaining station (Arnold & Weihs, 1978). We supposed that if the plaice was put on a sloping surface the component of weight acting normal to the substrate would be reduced. Slip and lift-off velocities would then be correspondingly reduced so that the fish could not maintain station and would be obliged to swim.

This idea was first of all tested in a crude water tunnel made by fitting a cover to the annular flume used by Priede (1974) in previous studies on trout swimming. A temporary scaffolding was erected and the entire assembly could be lifted (whilst running full of water) from the horizontal (0° slope) to vertical (90°). The flow was upwelling in the fish chamber so that the fish swam 'downhill' against the water flow.

It was found that at slopes in the region of 60° the ability of plaice to stick to the bottom was severely impaired and swimming could be induced for periods in excess of 10 min. Although the fish was still capable of sticking to the bottom or sides and avoiding swimming for some of the time, we nevertheless decided to build a proper tilting respirometer.

Respirometer

The design is essentially a Brett (1964) type of tunnel respirometer which is mounted on gimbals so that the whole tunnel and main pump assembly can be tilted at 0–90° from the horizontal (Fig. 1).

The water flow is generated by a stainless steel centrifugal pump of 75 mm nominal outlet bore (Holden and Brook, 75 mm, JTVS/–). The main pump circuit is made from 80 mm uPVC high pressure pipe. The water volume in the respirometer is 40 l. The fish chamber is basically rectangular in cross section, 229 mm wide and 148 mm high. The corners are filled with 45° fillet pieces 30 mm wide giving an octagonal cross section to the actual fish space with no corners where the flow is likely to stagnate. The chamber is 500 mm long and is closed off from the rest of the respirometer circuit by stainless steel meshes. The upstream grid consists of two layers of 3 mm mesh which help produce more or less uniform flow over the cross section of the chamber (Bell & Terhune, 1970; Morgan, 1973). A bowl of stainless steel mesh is also fitted at the upstream end to eliminate corners into which the fish would tend

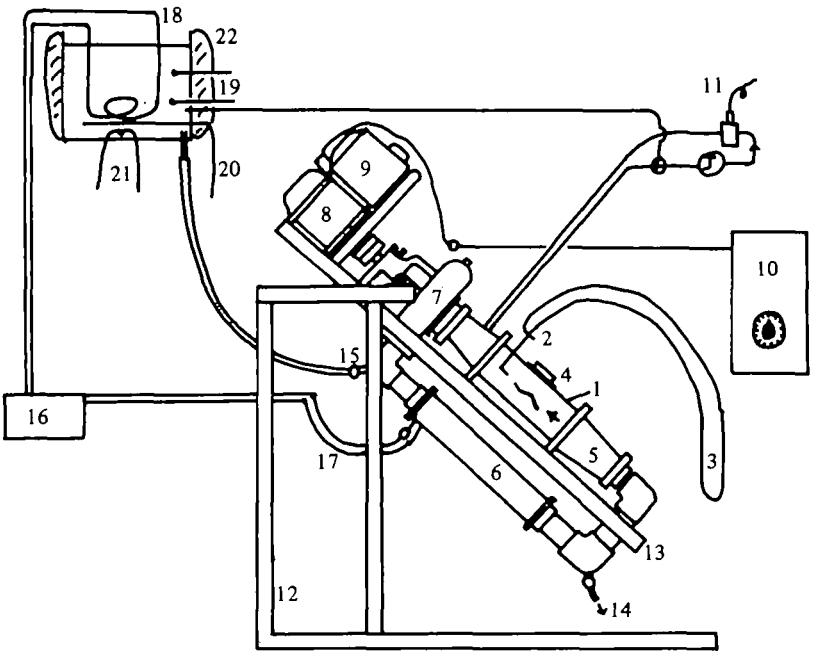

Fig. 1. Schematic diagram of the respirometer. The tunnel assembly including the main pump and motor are tilted by a tackle which is omitted from the diagram. 1, Fish chamber; 2, Pitot tube; 3, manometer; 4, access hatch; 5, expansion cone with anti-gyration vanes; 6, main heat exchanger; 7, main pump; 8, Heenan VHO21 variable speed drive; 9, motor; 10, Heenan 70/3C excitation unit (speed control); 11, P_{O_2} electrode in secondary circulation; 12, main frame; 13, pivoting bed; 14, drain valve; 15, inlet valve; 16, refrigeration condensor compressors in adjacent plant room; 17, flexible refrigerant hoses; 18, header tank cooling coil; 19, contact thermometers for temperature control; 20, air supply; 21, heater; 22, insulated header tank.

to push its snout so as to avoid swimming. The fish as it swims downhill is therefore guided into the centre of the water flow by a concave mesh bowl around its head. A 151 mm diameter circular hatch sealed with an 'O' ring is provided for access. Ports spaced at 25 mm intervals across the top of the test section enable velocity profiles to be measured with pitot–static tube.

Expansion and contraction cones connect the chamber to the pump and the rest of the respirometer circuit. The upstream one has longitudinal 'egg box' baffles to straighten the flow in particular to eliminate torsion after the bends immediately upstream.

The pump is driven by a 3 h.p. electric motor via a Heenan VHO21 electromagnetic variable speed drive unit. This provides continuous variation of speed from 0 to 1500 rev/min. A calibrated control dial on the Heenan 70/3C excitation unit allows reproduction of speed settings once the respirometer is calibrated. The relationship between control dial setting and water velocity is linear.

Velocity profiles were determined from 40 measurements across the cross section of the test chamber. At a mean velocity of 13·42 cm s^{-1} the standard deviation was 2·34 and at 31·90 the standard deviation was 4·93 across the cross-section. Velocity

was measured using a pitot tube in conjunction with sloping water manometers as described in detail by Priede (1973).

A heat exchanger is fitted to cool the respirometer. This consists of a stainless steel section in the main water circuit with 10 mm diameter copper pipe closely wrapped round it through which refrigerant is circulated. This copper evaporator is connected by flexible hoses to a Frigidaire FG75.22 refrigeration compressor in an adjacent plant room. The compressor is controlled by a contact thermometer in the main respirometer circuit which gives temperature control to 0·1 °C.

Water is supplied to the respirometer via flexible hoses from a header tank. This is cooled by a stainless steel (ASTM type 316) refrigerated coil. A heater is also fitted and the temperature is controlled by contact thermometers and relays. An aerator ensures stirring of the water as well as saturation with oxygen. A tapping from this tank provides the 100% calibration for the oxygen electrode.

Oxygen tension in the respirometer is measured in a sample flow driven by an Eheim (381) pump. A Beckman 39553 oxygen electrode is used in conjunction with a Beckman (1008) Field-Lab oxygen analyser. The electrode has to be removed from its cuvette for zero calibration.

Determination of oxygen consumption is achieved by closing off the respirometer and measuring the decline in P_{O_2} over a period of time. The P_{O_2} was never allowed to fall below 80% saturation before flushing out with fresh aerated sea water from the header tank.

Experimental procedure

Plaice were caught by trawling in the North Sea off Aberdeen. The fish were kept in tanks of sea water at the experimental temperature ± 1 °C for at least 30 days prior to respiration measurements. The experimental fish was not fed for 24 h before an experiment and was then allowed 18 h (usually overnight) to settle down in the respirometer.

The test chamber was covered to minimise the possibility of disturbance and the flow in the tunnel was kept at 5 cm s^{-1}. The tunnel was horizontal and the fish usually settled and orientated with the head pointing into the flow. Resting oxygen consumptions were then measured over a 1 or 2 h period. Only when the oxygen consumption had declined to a uniform low level were swimming trials attempted.

For a swimming trial the water velocity was increased and then the tunnel was inclined until the fish could no longer adhere to the bottom and had to swim. That angle of slope was usually between 50 and 70°. If the fish glided without any swimming movement or stuck to the walls of the tunnel this could normally be discouraged by rocking the tunnel to and fro so that no state of equilibrium was possible and continual swimming was maintained.

A swimming trial was only deemed acceptable if the fish had swum steadily without struggling, turning round in the chamber or resting for at least 10 min. Usually trials lasted more than 10 min in order to ensure accuracy of oxygen consumption measurements. Training improved performance of individual fish but many would never perform satisfactorily; some for example always faced the wrong way in the test chamber and merely struggled and flapped about the chamber if the water velocity was increased. Due to these difficulties trials were concentrated on a few

Table 1. *Details of the fish used in the respirometry experiments*

	Length (mm)	Weight (g)
5 °C	317	327·4
	288	251·0
	319	287·5
10 °C	330	394·1
	329	364·0
	330	391·0
15 °C	293	260·4
	313	312·7
	310	259·7
	317	315·0
	297	258·0

Table 2. *Results of respirometry experiments*

(Oxygen consumption mg $O_2.kg^{-1}.h^{-1}$.)

Temperature	Standard	Active	Intercept	Posture effect	Swimming regression	Critical swimming speed
5 °C	19·51 ± 3·85	94·15	33·92	14·41	$\log_{10}O_2 = 0{\cdot}4014V + 1{\cdot}5304$	1·18
					$(\log_{10}O_2 = 0{\cdot}3318V + 1{\cdot}5926)$	
10 °C	31·76 ± 3·65	148·00	50·85	19·09	$\log_{10}O_2 = 0{\cdot}3269V + 1{\cdot}7063$	1·36
					$(\log_{10}O_2 = 0{\cdot}3318V + 1{\cdot}7017)$	
15 °C	50·91 ± 4·56	180·0	65·46	14·55	$\log_{10}O_2 = 0{\cdot}3199V + 1{\cdot}816$	1·53
					$(\log_{10}O_2 = 0{\cdot}3318V + 1{\cdot}8038)$	

Swimming speed (V) is specific speed or body lengths per second. Standard deviations are indicated for standard oxygen consumption. Intercept is the value derived from extrapolation of the oxygen consumption – swimming speed regression to zero (i.e. antilog of the regression constant). Posture effect is intercept minus standard oxygen consumption. Two regression equations are given at each temperature – the first is fitted to the individual set of data and is shown in Fig. 2, the one in parentheses is fitted using a pooled slope estimate for all the data at all three temperatures.

co-operative individuals (Table 1) rather than a large sample which may have been preferable. It has since been found that other species of flatfish, for example the flounder, are better performers than plaice in this apparatus.

Results

Fig. 2. shows the relationship between oxygen consumption and swimming speed for plaice at 5, 10 and 15 °C. Swimming speed is expressed as the specific speed (V) or body lengths per second. Regression lines are fitted to the data. The resting metabolic rates are excluded from the line fitting exercise and are shown separately as the mean and standard deviations.

The regression correlation coefficients are all significant at the 0·1% level. Covariance analysis showed that the regression lines are not significantly different from one another in slope but the elevations are significantly different at the 0·5% level. Pooling all the data for the three regressions gives an overall slope for the relationship between logarithm of oxygen consumption and swimming speed of

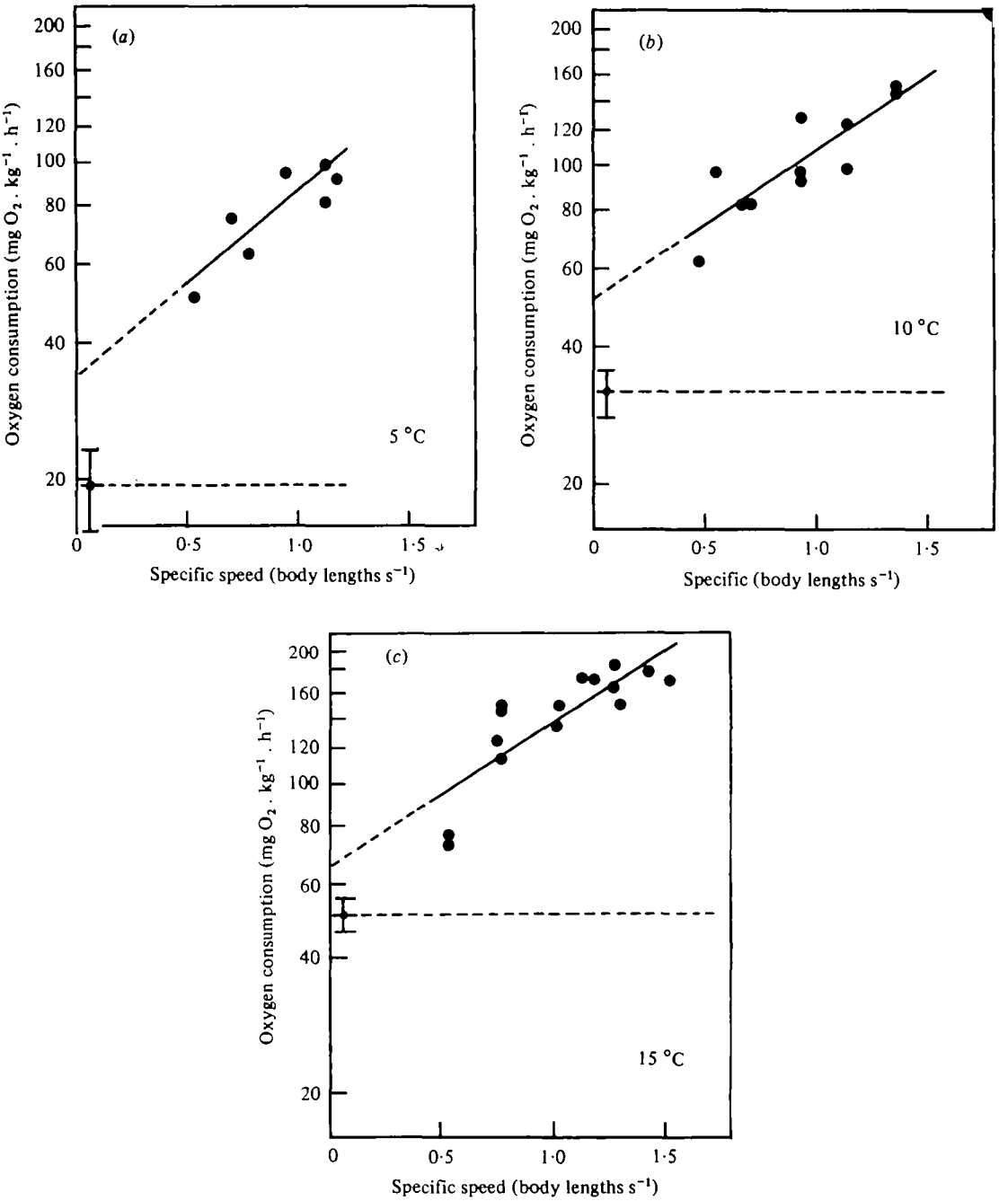

Fig. 2. The relationship between oxygen consumption and specific swimming speed (body lengths per second) at 5, 10 and 15 °C. The dashed horizontal lines are standard or resting oxygen consumptions, the vertical bars indicating the standard deviations. Note that the standard oxygen consumption lies below the intercept of the regression line – this difference is termed the posture effect which is positive in this case.

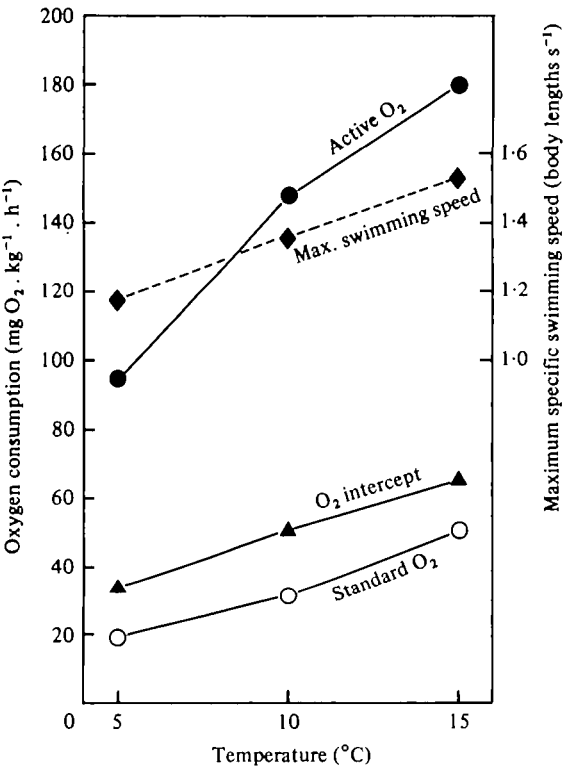

Fig. 3. The effect of temperature on oxygen consumption and critical or maximum sustainable swimming speed.

0·3318. Equations for all the regression lines are given in Table 2 together with corresponding corrected equations using the pooled estimate of slope.

Table 2 also gives the maximum sustained swimming speeds and oxygen consumptions. In previous work on round fish (Brett, 1964; Webb, 1971*a*), criteria for critical speed could be adopted related to exhaustion in a series of increasing velocity tests. In this study the maximum values recorded over at least a 10 min period are recorded. It was not possible consistently to force these fish to swim to exhaustion. These maximum values are plotted against temperature in Fig. 3. The swimming speed regression line intercept values are also indicated. The difference between this intercept and the resting rate can be considered as the power requirement for lift-off which will be termed the 'posture effect'. There is no significant change in the posture effect with temperature.

The values of intercepts of the corrected swimming speed regressions correspond closely to the following linear relationship:

$$R = 2{\cdot}45T + 26{\cdot}52,$$

where T is the temperature in degrees centigrade. Combining this with the pooled swimming speed regression gives a relationship between oxygen consumption, swimming speed and temperature:

$$\log_{10} R = 0{\cdot}3318V + \log_{10}(2{\cdot}45T + 26{\cdot}52).$$

This equation can be used to predict the oxygen consumption at any velocity (except zero) for this size of plaice in the whole temperature range investigated. R is in mg $O_2.kg^{-1}.h^{-1}$. If $V = 0$ then for a resting fish the standard oxygen consumption conforms closely to the relationship: $R = 3{\cdot}14T + 2{\cdot}66$.

The difference between maximum and resting oxygen consumption, the metabolic scope (Fry, 1947), increases with increase in temperature.

Correction for respirometer tilt

The purpose of this experiment is to determine the metabolic cost of horizontal swimming. Plaice are negatively buoyant with an underwater weight W and therefore in the tilted respirometer tunnel experience a force in the direction of swimming:

$$W_c = \sin \alpha W,$$

where α is the angle of the respirometer measured from the horizontal. This component of weight helps the fish and would reduce the power requirement for swimming; this needs to be corrected for.

Plaice will glide against the water flow in the respirometer. 90° tilt (vertically downwards) gives the highest glide velocity and the body is held rigid and straight. In swimming trials the typical respirometer tilt was 60° and the observed glide speed at this angle is 0·52 body lengths s^{-1}. Drag (D) is approximately proportional to the square of velocity.

$$D = kV_g^2.$$

V_g is glide velocity. But in swimming fish the drag coefficient of the oscillating body is 3–4 times that of a rigid straight body (Webb, 1971*a*; Weihs, 1974). Therefore for the swimming fish:

$$D = 3kV_s^2.$$

In the gliding experiment $D = W_c$ therefore:

$$W_c = D = kV_g^2 = 3kV_s^2,$$

if

$$V_g = 0{\cdot}52,$$

then

$$V_s = (0{\cdot}52/3)^{\frac{1}{2}},$$

$$V_s = 0{\cdot}3.$$

Thus a fish with an oscillating body will travel at 0·3 body lengths per second down the slope without doing any external work. The oxygen consumption data therefore underestimates requirements for horizontal swimming and an amount equal to the cost of swimming at $0{\cdot}3V$ should be added to the data. If the relationship between oxygen consumption and swimming speed is:

$$\log_{10} R = mV + \log_{10} R_i.$$

R_i is the 'intercept' value of oxygen consumption (see Table 2) taking antilogarithms:

$$R = R_i (\text{antilog}_{10} V)^m.$$

Correction

$$R_{0\cdot3} = R_i\,(\text{antilog}_{10}\,V)^m - R_i,$$

which is the apparent O_2 consumption used for swimming alone at 0·3 body lengths s^{-1}.

This is an over simplification since it assumes that the oscillating fish gliding at $0\cdot3V$ is not doing any work. It does not do any useful external work but it is doing internal work in oscillating the body. The oscillations would consist of passing neutral waves down the body which generate no thrust, i.e. the wave velocity along the body is equal to the velocity of motion through the water. From Webb (1971*b*) the muscular efficiency of normal swimming is about 20% and the propellor efficiency about 50%. This means that only about 10% of energy consumed by the fish for swimming results in useful thrust. The fish producing neutral swimming movements at $0\cdot3V$ would be doing everything necessary for swimming; muscles contracting, bending the body, etc., except for producing useful thrust. A reasonable conservative estimate of the cost of internal work would be 80% of the cost of proper swimming movements. This amount, $0\cdot8R_{0\cdot3}$ should therefore be subtracted from $R_{0\cdot3}$ to provide the correction for external work avoided by swimming 'downhill'. Then the correction for respirometer slope becomes:

$$\text{correction} = R_{0\cdot3} - 0\cdot8R_{0\cdot3}.$$

The actual corrections are 2·17, 2·58 and 3·24 mg kg^{-1} h^{-1} for the data at 5, 10 and 15 °C respectively. The relationships between oxygen consumption and swimming speed corrected for respirometer slope are then

$$\begin{aligned} 5\ ^\circ\text{C} \quad & \log_{10} R = 0\cdot4014V + 1\cdot574, \\ 10\ ^\circ\text{C} \quad & \log_{10} R = 0\cdot3269V + 1\cdot7277, \\ 15\ ^\circ\text{C} \quad & \log_{10} R = 0\cdot3199V + 1\cdot8369. \end{aligned}$$

These corrections are small, well within the range of error in the data and can be regarded as negligible.

It seems somewhat surprising that the advantage of swimming 'downhill' is so small. We observed that a plaice can glide down vertically at speeds in excess of $1V$ if the body is straight. If it tries to swim actively downwards it is often not capable of sustaining the same velocity. It is evident from such observations that the drag coefficient of the swimming body is much higher than that of the rigid body.

There remains a paradox in the gliding data which should be pointed out. These fish weigh approximately 10 g under water so the force due to gravity in the thrust direction in the respirometer experiments would be about 0·085 N. Arnold & Weihs (1979) estimate that the frontal drag coefficient of a plaice is of the order of 0·08 to 0·16. Taking 0·1 as a round figure using their data for frontal area of plaice the drag at a speed of $0\cdot52V$ (16·3 cm s^{-1}) is 3×10^{-3} N. The drag of the gliding fish is therefore about 27 times higher than might be expected from what we know of the shape of the fish. This discrepancy may be at least partially accounted for by the fact that a fish gliding down a slope must be producing lift. The drag coefficient may be then higher than the simple frontal drag coefficient. Using the figures given by Arnold &

Weihs (1979) a fish gliding vertically down should travel at $3V$ but the highest vertical glide speeds we found were about $1{\cdot}4V$.

The centres of gravity and buoyancy are very close together in plaice so the fish would not be very stable in the gliding mode. Movement of fins and the body in order to orientate may produce an anomalously high drag.

These anomalies cannot be resolved until we know more about flatfish swimming movements, generation of lift and gliding. In the rest of the paper we use the uncorrected respirometery data but in the light of further knowledge some revision of the figures may become necessary.

DISCUSSION

The oxygen consumption measurements in this study can be compared with those of Edwards (1971) on the same species. He measured resting (standard) rates and observed active rates following exercise; he could not exercise the fish in the respirometer. At 10 °C the standard rate was 39 mg kg^{-1} h^{-1} and the active rate 204 mg kg^{-1} h^{-1} for 120 g fish. These results can be corrected to the fish weight used in this study by the formula:

$$R_1 = aW^{0{\cdot}8},$$

where R_1 = oxygen consumption and W is the fish weight. Then the resting rate is 30·96 as compared with 31·76 mg kg^{-1} h^{-1} in this study. The active rate is 161·55 compared with 148·00 mg kg^{-1} h^{-1}. The figures correspond quite closely but the active rate in the present study is somewhat low.

The metabolic rates recorded for plaice are lower than for other fish. The maximum rate of oxygen uptake must be related to gill area (Hughes, 1972) and De Jager *et al.* (1977) show that the gill area of plaice is smaller than for other fish. In their sample there was found to be considerable individual variation in gill area of plaice which may explain discrepancies between metabolic rate determinations. Wood, McMahon & McDonald (1979) compare data for a number of flatfish species with data for roundfish and confirm that in flatfish metabolic rates are low.

The critical swimming speeds are also low when compared with data for other species. Fig. 4 shows the total cost of swimming (including resting) per kilometer at different velocities calculated from the oxygen consumption versus swimming speed relationships.

If R_v is the rate of oxygen consumption at velocity V then the cost per unit distance at velocity V is:

$$C_v = R_v/V.$$

In the figures it can be seen that the critical speed is closely correlated with the optimum swimming velocity. It seems therefore that the aerobic scope of the plaice allows the fish to swim continuously at its most economical velocity and no faster. Greer-Walker *et al.* (1978) tracked individual plaice at sea by means of sonic tags. In one case the speed of the fish through the water was determined by correcting speeds over the ground using current meter data to give the real swimming speed through the water. This fish swam at $0{\cdot}9$–$2{\cdot}0V$. The higher speeds in the work at

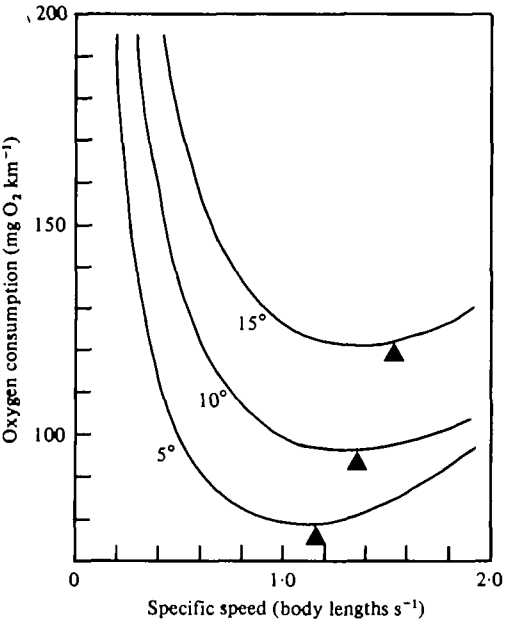

Fig. 4. Total cost of swimming per kilometre at different specific speeds at 5, 10 and 15 °C. The minima of the curves are the optimum swimming speeds. The triangles indicate the maximum sustained swimming speeds observed in the respirometer.

sea may be attributable to differences between fish or represent use of anaerobic metabolism.

Anaerobic swimming would involve metabolism of muscle glycogen to lactic acid which releases 558 $J.g^{-1}$ glycogen. Fish white muscle contains about 1 g glycogen per 100 g muscle (Wardle, 1975).

The weight of muscle can be determined by dissection aided by loosening the muscles with boiling water. We have found that excluding the marginal fin muscles the myotomal muscles occupy about 43% of body weight. Taking 40% as a round figure gives a total glycogen store of about 4 g per kg or 2232 J energy store.

Considering a fish at 10 °C the oxygen consumption required to swim at $2V$ would be 229 mg kg^{-1} h^{-1} (from Fig. 2*b*). Since the maximum rate of oxygen uptake is 148 mg kg^{-1} h^{-1} this leaves a deficit of 81 mg kg^{-1} h^{-1}.

Aerobic metabolism releases 22·5 J per mg oxygen so this deficit represents a power requirement of 1822·5 J kg^{-1} h^{-1}. If anaerobic metabolism of muscle glycogen was used for this deficit the fish could swim at $2{\cdot}0V$ for 2232/1822 = 1·23 h before exhausting the reserves. The fish studied by Greer-Walker *et al.* (1978) only spent about 0·5 h at the highest speeds and rested for long intervals so there would be plenty of time for repayment of the oxygen debt. Wood *et al.* (1979) also point out that in the starry flounder (*Platichthys stellatus*) there is a considerable oxygen reserve in the venous blood; this may also be true in the plaice.

The small gill area of plaice would minimize osmoregulatory energy requirements but only permits swimming aerobically up to the optimum swimming speed. Movement in plaice is characterized by periods of swimming, alternating with resting

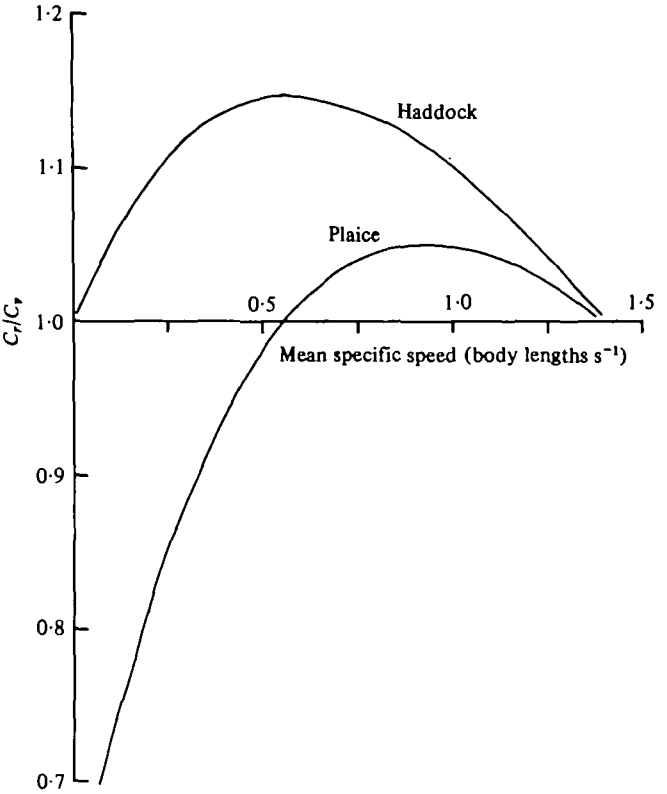

Fig. 5. Curves for haddock and plaice at 10 °C comparing the cost of swimming at a uniform speed (C_s) with swimming intermittently at the optimum speed with rests if there is time (C_r). The curves show how the two strategies compare at different mean swimming speeds. Below 0·6 it is best for plaice to adopt the swim and rest strategy (see text).

periods (Greer-Walker *et al.* 1978), so use of super critical speeds with associated build up of oxygen debts is a plausible strategy.

Plaice use a selective tidal transport system (Weihs, 1978; Greer-Walker *et al.* 1978) swimming with favourable tides and resting during the adverse part of the tidal cycle. If plaice do build up oxygen debts during the swimming phase they may be particularly vulnerable to capture by predators or fishing gear at the end of the swimming period.

Why did the plaice not use this aerobic capacity in the respirometer in order to sustain faster swimming speeds? Bursts of fast swimming were observed in the experiments. They consisted of very fast tail beats which quickly accelerated the fish to the front of the chamber. There was not enough space in the chamber to allow for these bursts of acceleration and the fish ended up either pushing against the grids or struggling ineffectually and the trial had to be curtailed. It seems that the plaice white muscle is a fast muscle and can only work at high speeds. It is therefore used for burst and glide locomotion (Weihs, 1978) for which there is no facility in the uniform velocity environment of the tunnel respirometer. Greer-Walker & Pull (1973) have however shown that in *Gadus virens* white muscle is used at ordinary

cruising at speeds below 1·0 body lengths s^{-1}, but this may reflect differences in muscle innervation (Bone, 1978).

In the only previous studies on marine fish, Tytler (1969) measured oxygen consumption of haddock (*Melanogrammus aeglifinius*) swimming in a water tunnel. The relationship between oxygen consumption and swimming speed in his study was

$$\log_{10} R = 0{\cdot}33V + 1{\cdot}77 \quad (10\ ^{\circ}\mathrm{C}).$$

It is immediately apparent that the constant 0·33 is almost identical to that found for plaice and if appropriate weight corrections are applied the plaice and haddock swimming data are indistinguishable. The main difference is that the resting metabolic rate for haddock lies on the intercept of the swimming speed regression line, whereas for plaice it lies below this line. Extrapolation of metabolism-activity relationships to zero activity is the usual method of determining the standard (resting) metabolic rate.

Plaice differs from roundfish in that the resting metabolic rate lies below this extrapolated standard rate. This is attributable to the posture effect. Plaice are negatively buoyant and must lift off the bottom before horizontal progression can begin; thereafter at higher velocities normal hydrodynamic laws apply. Neutrally buoyant fish such as haddock can float at rest in mid-water and begin moving at slow speeds without any cost of take-off; the posture effect is zero. In practice, fin movements are required to remain stationary so in respiration studies elevated oxygen consumptions can be observed at low swimming speeds (Brett, 1964; Smit, 1965; Tytler, 1978), which gives an apparently negative posture effect.

In summary it seems that the cost of locomotion in flatfish is similar to that in neutrally buoyant fish roundfish but the resting rates are considerably lower than in the roundfish. This has important consequences for locomotion strategies.

In order to cover a given distance in still water in a given time, fish can adopt two different strategies:

(*a*) swim uniformly at the appropriate velocity;

(*b*) swim at the optimum velocity and rest for any spare time if ahead of schedule.

The total cost of swimming in strategy (*a*) is given by the equation:

$$C_u = R_v/V.$$

Cost in strategy (*b*) is

$$C_r = R_{vo}/V_o + T_r R_r/V_r,$$

where R_{vo} is the rate of oxygen consumption at the optimum swimming velocity, V_o is the optimum swimming velocity, T_r is the proportion of time spent resting which takes values from 0 to 1, and R_r is the resting rate of oxygen consumption. V_r is the mean velocity resulting from strategy (*b*):

$$V_r = V_o(1 - T_r)$$

substituting in the above equation gives:

$$C_r = R_{vo}/V_o + R_r(1/V_r - 1/V_o).$$

(In calculating C_u and C_r velocities and rates of oxygen consumption should be expressed in terms of the same time units, for example per second or per hour.)

These two strategies can then be compared by the ratio C_r/C_u. If $C_r/C_u > 1$ then strategy (*a*) uses less energy and if $C_r/C_u < 1$ strategy (*b*) is preferable.

Fig. 5 shows the relationship between C_r/C_u and mean velocity for fish with positive posture effect (plaice) and one with a zero posture effect such as haddock. These curves were calculated using the 10 °C plaice data:

$$\log_{10} R = 0{\cdot}33V + 1{\cdot}7063.$$

For plaice R_r is taken as 31·76 mg kg^{-1} h^{-1} and for haddock R_r is taken as 50·85 mg kg^{-1} h^{-1}. The optimum velocity is taken as 1·4 body lengths s^{-1}.

It can be seen that for the haddock the swim and rest strategy always costs more than uniform swimming at the appropriate velocity. For plaice this is true at velocities above 0·6 but below that speed it is better to adopt the swim and rest strategy. It is therefore uneconomical for plaice to swim at low velocities and they should always swim at velocities above $0{\cdot}6V$. Greer-Walker *et al.* (1978) found that plaice at sea always swim at velocities above $0{\cdot}9V$.

CONCLUSIONS

The new tilting respirometer has opened up possibilities of studying flatfish locomotion in the laboratory.

It is clear from these experiments that the metabolic scope of plaice is small and the critical swimming speeds are correspondingly low. The standard or resting metabolic rate is lower than that predicted from extrapolation of the metabolism/swimming speed regression to zero activity. This difference represents the cost of take-off or posture effect and means that it is uneconomical for plaice to swim at low speeds.

It was observed that plaice are good at gliding in the respirometer and whilst this was not examined in detail it is likely that this is an important aspect of the normal behaviour in this species. It seems that intermittent use of the fast white myotomal muscle is the usual mode of locomotion in plaice and steady aerobic cruising may be rather unusual. This would explain the difficulties experienced in inducing uniform swimming in the respirometer.

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