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Tolerance, behaviour and oxygen consumption in the sand goby, *Pomatoschistus minutus* (Pallas), exposed to hypoxia

J. K. PETERSEN AND G. I. PETERSEN*

Marine Biological Laboratory, Strandpromenaden, DK-3000 Helsingør, Denmark

Behavioural and metabolic reactions of *Pomatoschistus minutus* (Pallas) exposed to various degrees of hypoxia were studied. At 15° C and 20‰ mortality was 50% at 15.2% oxygen saturation. Avoidance and oxygen saturation showed a linear inverse relationship. At levels lower than 60% saturation increased activity occurred; avoidance was significant at 30% saturation. Active, routine and standard MO_2 correlated linearly with weight at 6 and 15° C (salinity = 19‰). During hypoxia at 15° C routine MO_2 rose significantly at 60–50% and 40–30% saturation expressed either as MO_2 during longer periods at night or MO_2 at shorter intervals during the day. Standard MO_2 was unaffected by hypoxia at 15° C. Haemoglobin concentration was significantly increased when *P. minutus* was acclimatized to 35% saturation.

Key words: *Pomatoschistus minutus*; tolerance; avoidance; oxygen consumption; hypoxia.

I. INTRODUCTION

Hypoxia is known to occur locally in shallow waters (Muus, 1967) and can occur nocturnally in tidal pools (Bovbjerb & Glynn, 1960). Recently, an increasing frequency and duration of hypoxia has been reported in shallow waters around Scandinavia, and severe oxygen depletion for longer periods has been reported for larger areas in the Kattegat (Miljøstyrelsen, 1984; Kaas *et al.*, 1987; Pihl, 1989). Concomitant with these occurrences incidences of large-scale escape of fishes have been reported (Pihl, 1986; Petersen & Petersen, 1986).

Besides death caused by severe hypoxia or anoxia, decreased oxygen availability may limit the distribution of fish species by reducing the energy available for locomotion, growth and reproduction (e.g. Brett & Groves, 1979). Recognition of the subtle impact of sublethal hypoxia has generated numerous studies which relate respiration physiology to dissolved oxygen. These studies may, however, be of limited value in predicting effects on fish *in situ* if they are not combined with studies of habitat shifts and the possible use of alternative breathing modes such as aquatic surface breathing (Kramer, 1987). A frequently applied mode to evaluate the behavioural response to hypoxia has been to use avoidance as a measure of the change of habitat induced by reduced oxygen availability (Doudoroff & Shumway, 1970).

The lack of consistency regarding experimental conditions, insufficient acclimatization times and the lack of certainty about which metabolic level has been measured, are problems that emerge from attempting to make comparative studies involving data in the literature (Fry, 1971). In the present work, the definitions of metabolic levels proposed by Brett (1972) have been used. Because the sand goby is

*Present address: Water Quality Institute, Agern Allé 11, DK-2970 Hørsholm, Denmark.

921

a sluggish species, the $\dot{M}O_2$ at burst activity has been used to represent active metabolism (Vahl & Davenport, 1979).

The sand goby, *Pomatoschistus minutus* (Pallas), is an important component of the shallow coastal water food web. During late summer and autumn it can become very abundant on sandy or partly muddy bottoms, particularly in estuaries and coastal areas at depths from 1–20 m. During the winter it migrates to deeper water (Muus, 1967).

The purpose of this investigation was to study the behavioural and metabolic reactions of *P. minutus* when exposed to various degrees of hypoxia. Emphasis was focused on reactions at the routine level of metabolism. Concentrations of haemoglobin in the blood of fish acclimated to hypoxia have been investigated to establish possible acclimation effects at prolonged hypoxia.

II. MATERIALS AND METHODS

Sand gobies, *P. minutus*, (0·41–2·24 g) were caught with beam trawl (trawling for max 20 min) at the boundary between the Isefjord and the Kattegat, N. Sealand, Denmark. The fish were caught at depths of 2–10 m, in January for the 6° C experiments and during spring and summer for the 15° C and hypoxia experiments.

The fish were placed in large tanks at the same temperature and salinity as that of the catch locality. The fish were acclimatized to laboratory conditions for at least 2–3 weeks. During acclimatization the gobies were fed with fish food pellets.

RESISTANCE AND TOLERANCE

Five groups of ($n = 10$) fish were kept in separate glass tanks with an area of $27 \times 30·5$ cm and a volume of 25 l (salinity (S): 18‰; temperature (T): 15° C; L:D = 16:8). The bottoms were covered with a thin layer of sterilized sand.

After 24 h the fish were transferred to identical tanks with oxygen saturations of 5% (range 4–6%), 10% (9–11%), 15% (13·5–16·5%), 20% (18–24·5%) and 100% saturation. Every 24 h surviving fish were transferred to identical tanks with new water of the desired oxygen saturation. The oxygen saturation was lowered by purging with nitrogen gas and checked with an YSI 58 oxygen probe. If the oxygen saturation had changed from the stipulated percentage, this was corrected four times an hour in the 5 and 10% saturation experiment, once every hour in the 15% experiment and every fourth hour in the 20% experiment by either N_2- or air-bubbling. The temperature was checked daily. Controls were kept simultaneously under full oxygen saturation and otherwise identical conditions. Average size of the fish used was $1·38$ wet wt $\pm 0·08$ g (s.e.), which gave a load of $0·55$ g fish l^{-1} water. The fish were starved for 96 h before the start of the experiment.

Mortality, defined as no reaction when touched with a pair of forceps, was recorded four times an hour in the 5 and 10% saturation experiment, every hour in the 15% saturation experiment and after 3, 6, 24, 48, 72 and 96 h in the 20% saturation experiment. Dead fish were removed.

AVOIDANCE

An experimental set-up as shown in Fig. 1 (Miljøstyrelsen *et al.*, 1986) was used for avoidance studies (T: 16° C; S: 20‰). Addition of dye to one of the reservoirs confirmed that the two flows in section C were actually separated. After regulation of the pumps to a stable flow rate of 6 l min^{-1}, 15 fish were placed in section C. The fish were acclimatized to the set-up for approximately 1 h. Avoidance reactions were tested at oxygen saturations ($\pm 2\%$) of 60, 50, 40, 35, 30, 25, 20 and 12%. The desired oxygen saturation was attained by purging with nitrogen gas in the reservoirs and continuously checked with an YSI 58 oxygen probe. Oxygen saturation in the reservoir did not differ from that of the observation area. Each test procedure started with a 10 min observation period with normoxic water on both sides to establish an even distribution of fish. Five minutes after introduction of hypoxic
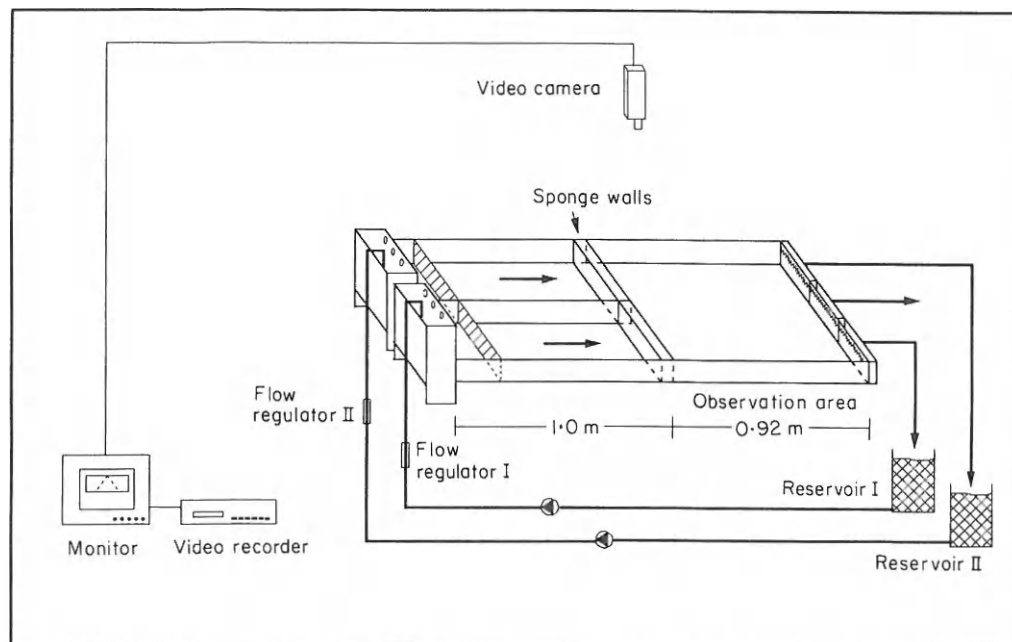
FIG. 1. Experimental set-up for avoidance tests.

water to one of the sides a 20-min observation period followed, after which the flow was reversed via the connecting tubes so that the side that previously had been hypoxic became normoxic and vice versa. This was followed by 5 min reversal time and a new 20-min observation period. During each observation period the number of fish in both parts of the section were counted every 30 sec from the 5th min. A control experiment was made with fully aerated water in both sides of section C.

The relative density (D) of fish in normoxic water at a given saturation (s) is

$$D_s = \Sigma_n \, (M/N) \times 100\%$$

where n is the total number of observations, M is the number of fish in normoxic water and N is the total number of fish (15). From the relative density, avoidance (A_s) can be calculated as:

$$A_s = (D_s - 50) \times 2.$$

In the calculations of avoidance the theoretical value 50% for D_{100} has been used; the actual value measured was 50·8%. A χ^2-test was used to determine whether a given avoidance was significant.

OXYGEN CONSUMPTION

Respiration experiments were carried out in winter (6° C) and summer (15° C) on starved fish kept in a small tank of about 6 l supplied with running sea water at the experimental temperature and salinity (19‰) for 20–24 h prior to the experiment. Oxygen consumption rates (MO_2) were measured according to Hagerman & Szaniawska (1986). A relatively small respiration chamber (35 ml), relatively high flow rates (0·12–0·61 h^{-1}) and long acclimation time (see below) were used in order to avoid some of the common errors in respirometry (Steffensen, 1989).

To minimize external stimuli the entire reservoir was covered with black plastic sheet and noise was minimized. When the cover was removed, for instance when bubbling nitrogen, the fish reacted instantly. No diel rhythms of the fish could be observed in the respirometer.

Experiments were started by placing a single fish in the respirometer in the morning. The fish were then taken out in the afternoon the following day so that each experiment had more than 24 hours of continuous recording of oxygen consumption. During the end of the normoxic experiments at 6 and 15° C the fish were activated by removing the cover and turning the chamber sideways in the reservoir. Hypoxic experiments were carried out separately. Hypoxia was gradually induced 5–6 h after the fish had been placed in the respirometer. At each oxygen saturation the fish were allowed to settle down so that a stable MO_2 was recorded for some hours before the oxygen saturation was further lowered. For longer periods—usually night time—the oxygen saturation was kept at a fixed, low level to facilitate comparisons of the MO_2 over a long hypoxic period with that of shorter periods during the day. The various metabolic levels were defined as

Standard MO_2: the lowest reproducible value during a 24-h period. In the hypoxia experiments the standard MO_2 was determined in a similar way, although at shorter intervals. It should be noted that it was not always possible to obtain a value for the standard MO_2.

Routine MO_2: an average of 8 h of measurements, recorded approximately 12 h after the fish had been placed in the respirometer. Normally the MO_2 had fallen from the high consumption rates following introduction of the fish in the respirometer, to the routine level within 3–4 h, similar to findings of Jobling & Davies (1980). During hypoxia the routine MO_2 was determined in two ways: as a mean of the nocturnal MO_2 (*ca.* 8 h) at a constant low oxygen saturation; or as averages of the shorter (*ca.* 2 h) stable periods during the day.

Active MO_2: was determined as the maximum oxygen uptake following initial stress due to introduction of the fish in the respirometer or by turning the chamber sideways numerous times in the reservoir at the end of each experiment. During hypoxia the active MO_2 could not be determined.

Linear regressions (least squares of log respiration on log wet weight) were made for normoxia and hypoxia in the intervals 60–50% ($P_wO_2 = 90–75$ torr) and 40–30% saturation ($P_wO_2 = 60–40$ torr). The oxygen consumption rates (MO_2) in normoxia were compared using analysis of covariance (Sokahl & Rohlf, 1981). Averages of the day time MO_2 were compared using Student's t-test.

HAEMOGLOBIN CONCENTRATION

Fish used for haemoglobin analyses were kept in small tanks with recirculating sea water at oxygen saturations of 36·3 ($\pm 8·1\%$, S.D.) and 58·8 ($\pm 6·5\%$) for 8, 14 and 26 days and were fed *ad libitum* daily. Oxygen saturation was checked daily with an YSI 58 oxygen probe. Blood samples (4 μl) were taken from the caudal vein and analysed according to Assendelft (1970) on an Unicam SP 1800 UV-spectrophotometer. Blood taken from fish acclimatized to full saturation for 26 days were used as controls. Student's t-test was used for comparison of haemoglobin concentrations ([Hb], g Hb 100 ml^{-1}).

III. RESULTS

TOLERANCE AND RESISTANCE

Resistance and tolerance to hypoxia is shown in Figs 2 and 3. In the control group no mortalities occurred. The oxygen saturation interval between no mortality and full mortality is very narrow with a mean mortality at 15·2%. When exposed to severe hypoxia the fish tried to reach the surface and if this was unsuccessful they remained inactive at the bottom. A similar hypoxic mortality pattern has previously been noticed (Shephard, 1955; Hagerman & Szaniawska, 1986).

AVOIDANCE

Normally the sand goby is sluggish, remaining inactive except when feeding (Fonds & Veldhuis, 1973). At oxygen saturations below 40% the gobies became
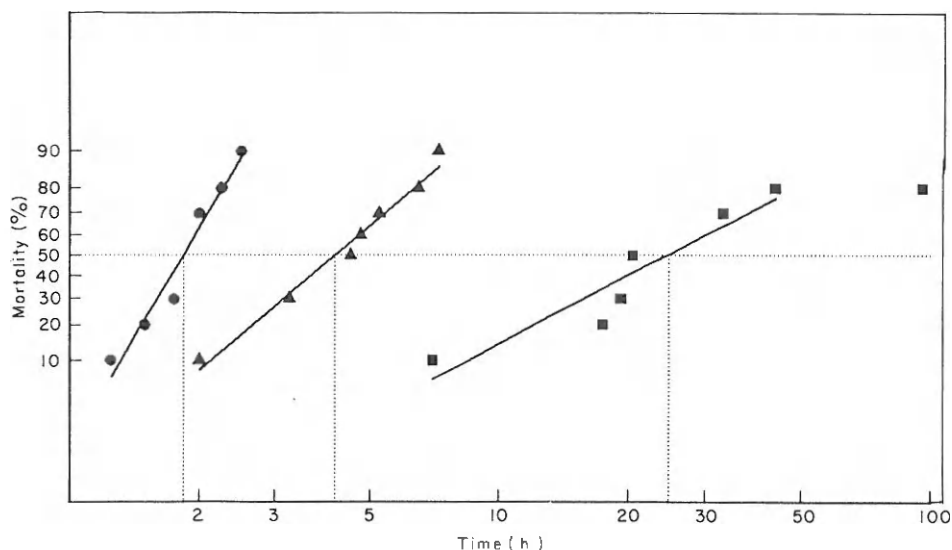
FIG. 2. Resistance to hypoxia. Mortality at 5 (●), 10 (▲) and 15 (■) % oxygen saturation (T: 15° C. S: 18‰) plotted on logarithmic probability paper according to Litchfield (1949).
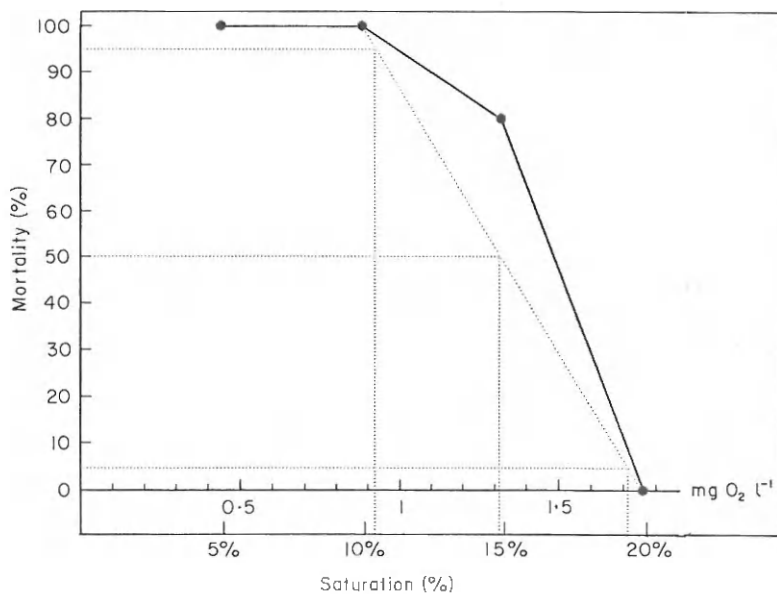

FIG. 3. Tolerance to hypoxia. Oxygen concentrations and saturations (T: 15 C, S: 18‰) for 95, 50 and 5% mortality within 96 h calculated according to Litchfield & Wilcoxon (1949).

' restless ' showing obviously increased ventilation and random swimming activity, which could lead them to the normoxic section. A linear relationship between avoidance and oxygen concentration was obtained (Fig. 4), as also shown by Whitmore *et al.* (1960). Avoidance was significant at 30% and highest at 20%
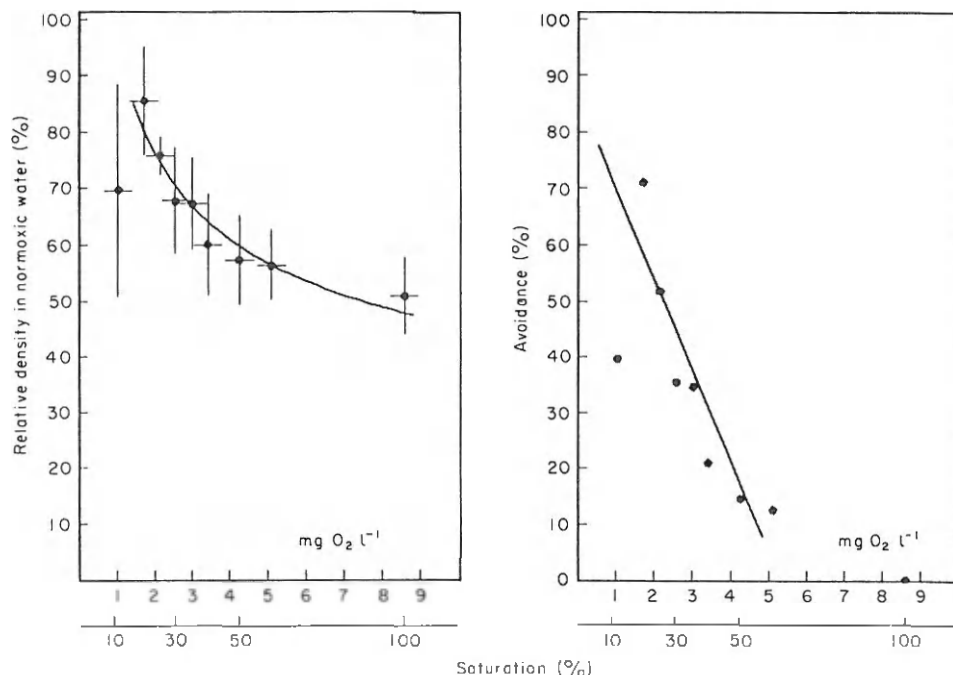
J. K. PETERSEN AND G. I. PETERSEN

FIG. 4. Relative abundance and avoidance. Values are calculated as described in the text and given as means ± S.E. at different oxygen saturations (T: 16° C, S: 20‰). The regression line is given by $A = 65\cdot3\% - 9\cdot1 \times$ saturation ($r^2 = 0\cdot73$) and is calculated on all saturations except 12%, where the fish were immobilized and therefore did not avoid the hypoxia.

saturation. At 12% saturation (i.e. below the tolerance limit) the data were inconsistent showing great differences between the separate runs; these data were not included in the linear regression. At 12% saturation the fish were immobilized and if they did swim this was towards the surface, possibly leading the fish to the normoxic section. If failing to reach the normoxic section the fish remained inactive in the hypoxic section before again attempting to reach the surface. Schooling could not be observed at all.

OXYGEN CONSUMPTION

To establish the magnitude of the different metabolic levels, a series of experiments were carried out at 6° C (Fig. 5). MO_2 varies linearly with wet weight and the slopes of the regression lines ($0\cdot66-0\cdot78$) are not significantly different. A similar picture emerged at 15° C (Fig. 6). At all three levels the MO_2 at 15° C was significantly greater ($P < 0\cdot005$). As a consequence the metabolic scope is greatest at 15° C. The gobies reacted to hypoxia by increasing their routine MO_2 (Table I). This is shown here either as a comparison of regression on oxygen consumption v. wet weight at the stable night levels of 60–50% and 40–30% saturation; or by comparison of averages of weight standardized MO_2 obtained during day time ($P < 0\cdot005$ and $P < 0\cdot01$, respectively). In contrast standard MO_2 seemed unaffected by oxygen depletion (Table I). For technical reasons standard MO_2 could be obtained only during the stable hypoxic night periods. This resulted in few data and large regression variability. No valid weight standardization could
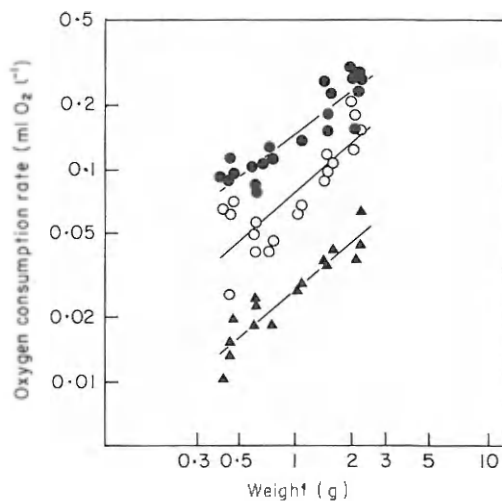
FIG. 5. Weight dependent oxygen consumption rate at 6° C. Active oxygen consumption: A ($\bullet$) = $0.143 \times W^{0.66}$ ($r^2 = 0.82$, $n = 21$), routine oxygen consumption: R ($\bigcirc$) = $0.076 \times W^{0.78}$ ($r^2 = 0.7$, $n = 19$), standard oxygen consumption: S ($\blacktriangle$) = $0.027 \times W^{0.75}$ ($r^2 = 0.88$, $n = 16$); all tests were performed at 19‰.
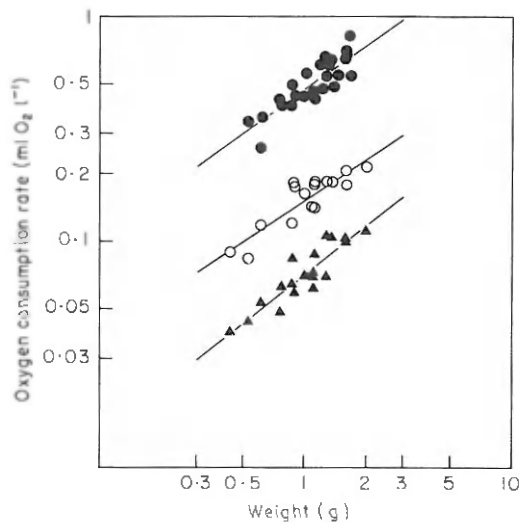

FIG. 6. Weight dependent oxygen consumption rate at 15° C. Active oxygen consumption: A ($\bullet$) = $0.476 \times W^{0.65}$ ($r^2 = 0.73$, $n = 29$), routine oxygen consumption: R ($\bigcirc$) = $0.151 \times W^{0.61}$ ($r^2 = 0.79$, $n = 16$), standard oxygen consumption: S ($\blacktriangle$) = $0.071 \times W^{0.72}$ ($r^2 = 0.82$, $n = 19$); all tests were performed at 19‰.

be established. Standard $\dot{M}O_2$ showed no differences between normoxic and hypoxic conditions, indicating no significant extra cost of ventilating at increased ventilation volumes.

TABLE 1. Oxygen consumption rates during hypoxia. Routine oxygen consumption rates are given as linear regressions of log oxygen consumption on log wet weight of stable night time oxygen uptake and as means $\pm$ s.E. of weight standardized day time rates. Standard oxygen consumption rates are given as linear regressions and means $\pm$ s.E. of weight specific oxygen consumption rates of stable night time oxygen uptake. Intercepts and means are compared as described in text. All rates are in ml O_2 h^{-1} g^{-1} at 15°C and 19‰.

P_wO_2 saturation	$\approx$156 torr 100%	124–108 torr 80–70%	109–93 torr 70–60%	93–79 torr 60–50%	78–62 torr 50–40%	62–48 torr 40–30%	47–39 torr 30–25%
Routine oxygen consumption							
Linear regression (night)	$R = 0.151 \times W^{0.61}$ $r^2 = 0.79$ $n = 16$			$R = 0.265 \times W^{0.72}$ $r^2 = 0.81$ $n = 15$ $P < 0.001$		$R = 0.242 \times W^{0.88}$ $r^2 = 0.74$ $n = 7$ $P < 0.005$	
Mean $\pm$ s.E. (day)	0.164 ± 0.009 $n = 13$	0.147 ± 0.007 $n = 5$	0.244 ± 0.009 $n = 4$	0.225 ± 0.016 $n = 10$ $P < 0.011$	0.043 ± 0.018 $n = 9$	0.234 ± 0.014 $n = 9$ $P < 0.008$	0.234 ± 0.016 $n = 7$
Standard oxygen consumption							
Linear regression (night)	$S = 0.071 \times W^{0.72}$ $r^2 = 0.82$ $n = 19$			$S = 0.082 \times W^{0.65}$ $r^2 = 0.29$ $n = 5$ NS		$S = 0.072 \times W^{0.64}$ $r^2 = 0.41$ $n = 6$ NS	
Mean $\pm$ s.E. (night)	0.09 ± 0.011 $n = 16$			0.074 ± 0.012 $n = 5$ NS		0.088 ± 0.017 $n = 6$ NS	

TABLE II. Haemoglobin concentration. [Hb] is given as means $\pm$ s.e. in g Hb 100 ml^{-1} after 8, 14 and 26 days of acclimation to different oxygen saturations

Saturation (%)	8 days	14 days	26 days
35	4.87 ± 0.24 $n = 6$ $P < 0.01$	4.12 ± 0.38 $n = 10$ NS	4.72 ± 0.55 $n = 17$ $P < 0.05$
60	3.44 ± 0.40 $n = 6$ NS	3.64 ± 0.30 $n = 8$ NS	3.76 ± 0.25 $n = 12$ NS
100			3.53 ± 0.13 $n = 45$

HAEMOGLOBIN CONCENTRATION

P. minutus is able to increase the haemoglobin concentration when acclimatized to 35% saturation (Table II). At this oxygen saturation the rise in [Hb] is significant after 8 and 26 days of acclimation (14 days not significant). No significant effect of moderate hypoxia (60% saturation) could be detected.

IV. DISCUSSION

The estimated weight-specific oxygen consumption rates of *P. minutus* at 6° C is much lower than those reported for *Gobiusculus flavescens* (Fabricius) (Hanson, 1985) and lower than values for very young *Zoarces viviparus* (Linnaeus) (Broberg & Kristoffersen, 1983). The estimates at 15° C are generally in agreement with other findings in ecologically, closely related gobies (Healey, 1972; Fonds & Veldhuis, 1973; Congleton, 1974; Tolksdorf, 1978; von Oertzen, 1983). Our findings on standard and routine MO_2 are generally lower and on active MO_2 generally higher than those found in the studies mentioned above. At both temperatures for *P. minutus*, active MO_2 is five to six times and routine MO_2 two to three times standard MO_2; this is a normal difference between metabolic levels (see e.g. Brett, 1972). What comprises 'routine' MO_2 in the various studies quoted above is not always easy to deduce. For the present studies we have elected to use the mean rate derived from 8 h of continuous recording which included periods of active movement and period of quiescence. In the hypoxic 'day' experiments we derived the mean values from 2 h of continuous recordings.

That fish are able to avoid hypoxic water is well known (Doudoroff & Shumway, 1970; Kramer, 1987) but there has been some discussion with regard to the mode of their response. Jones (1952) and Höglund (1961) concluded that escape movements were accidental and induced by respiratory stress, thus they did not reflect an immediate detection of hypoxic water. Responses to hypoxia before the initiation of respiratory stress were noted by Whitmore *et al.* (1960), Deubler & Posner (1963) and Ogilvie (1982). Though the present findings resemble those of Jones (1952) it cannot be concluded that the sand goby responds just as a consequence of respiratory stress, since the gobies often reacted within a very short time after their introduction into hypoxic water. A possible mode of reaction could be that the

changes in circulation and ventilation induced by hypoxia exert swimming activity, here interpreted as escape movements.

Respiratory stress, as increased routine $\dot{M}O_2$ was found at water oxygen saturations that were much higher than those which induced avoidance. In the majority of earlier investigations, routine $\dot{M}O_2$ has been reported to decrease with progressive hypoxia. Thus Kerstens *et al.* (1979) and Jensen & Weber (1985) both found very reduced routine $\dot{M}O_2$ on exposure to acute severe hypoxia, while Watters & Smith (1973) found only minor reductions in oxygen uptake at declining oxygen tension. Lomholt & Johansen (1979) found only a slightly reduced routine $\dot{M}O_2$ when P_wO_2 was gradually lowered to 40 torr, but large reductions in $\dot{M}O_2$ at P_wO_2 below that. Few investigations have confirmed the opposite trend. For lingcod, *Ophiodon elongatus*, Farrell & Daxboeck (1981) showed increasing routine $\dot{M}O_2$ with decreasing oxygen tension to c. $P_wO_2 = 60$–50 torr, at lower P_wO_2 values the $\dot{M}O_2$ fell. Cech & Wohlslag (1973) and Cech *et al.* (1979) found no consistent response of $\dot{M}O_2$ at moderate hypoxia but at temperatures of c. 15° C, the routine $\dot{M}O_2$ was generally found to be elevated under hypoxic conditions.

Besides variation attributable to differences in definition of routine metabolism, the opposing trends mentioned above can be a result of different experimental conditions. Thus Hughes *et al.* (1983) found that carp, *Cyprinus carpio* (Linnaeus), acclimatized to the experimental setup showed increased routine $\dot{M}O_2$ with progressive hypoxia, whereas the converse could be seen for less acclimatized fish. Lomholt & Johansen (1979) stated similarly, that the decreasing $\dot{M}O_2$ at moderate hypoxia could reflect acclimation since the fish were introduced into the respirometer shortly before the measurements started. In the present investigation the gobies were allowed to settle in the respirometer until a stable routine $\dot{M}O_2$ was obtained and this may be the reason for the response observed.

Reduced oxygen availability will affect metabolism broadly, including both activities like ventilation and swimming and more subtle activities such as assimilation and growth. Attention has been paid especially therefore to studies of effects of hypoxia on the ' borders ' of activity, namely standard and active metabolism. For both it has been shown that hypoxia will decrease the metabolic rate. For standard $\dot{M}O_2$ it has been generally agreed that the oxygen uptake is unaffected by hypoxia until an ' incipient lethal level ' (van Dam, 1938; Shephard, 1955), as also shown here for sand gobies.

Routine metabolic rate is vaguely defined and poorly established experimentally. Thus, one cannot expect that this metabolic rate will show the same course during progressive hypoxia as at the metabolic limits (i.e. standard and active metabolism). Routine $\dot{M}O_2$ can be considered as a crude expression of the costs of ' normal activity ' (Brett, 1972) including spontaneous activity and feeding. Consequently this gives much variation which can complicate comparisons. For this reason routine $\dot{M}O_2$ should perhaps be regarded as a wider zone instead of a fixed level, but is nevertheless still representative of ' normal life ' in the ecological state. Under normal conditions, acute hypoxia can be seen as stress and the ensuing elevation of the routine $\dot{M}O_2$ as the costs of a stress-induced rise in (mainly locomotory) activity. Other authors have described increased activity during hypoxia. Jones (1952) found increased activity before avoidance was fulfilled, Dandy (1970) showed increased locomotory activity of *Salvelinus fontinalis* at lower oxygen concentrations. Weber & Kramer (1983) noted that guppies,

Poecilia reticulata, increase both their horizontal and vertical activity (swimming) during progressive hypoxia. Hagerman & Szaniawska (1986) showed for the brown shrimp, *Crangon crangon,* that increased routine oxygen uptake rate at 40–50% saturation was due to increased pleopod beating. It thus seems reasonable to conclude that the routine metabolism is not strictly comparable to the metabolic limits in its response to hypoxia and that at least some aquatic animals will increase their routine metabolism when exposed to hypoxia. Probably, the increased activity is mainly of locomotory nature and may be achieved by allocation of energy from feeding, digestion and growth. Therefore this results in only minor changes in oxygen consumption rate. The gobies in this study had not been fed 20 h before introduction into the respirometer, which renders a low routine $\dot{M}O_2$. This can be the explanation for the rather great elevation found in the routine $\dot{M}O_2$.

Increased activity was seen in three different tests. Bursts of activity could be noted at oxygen saturations lower than those tested in the oxygen consumption experiment. It is however obvious that during hypoxia routine oxygen uptake can rise only to a threshold. Lower oxygen concentrations will result in reduction in oxygen uptake. The kind of activity causing the elevated oxygen consumption during moderate hypoxia is not clear from this study since activity sensors were not used and visual observation impossible.

In summary, *P. minutus* reacts to acute, moderate hypoxia by increasing its activity. At sufficiently low oxygen saturation the goby tries to escape the hypoxic area or attempts aquatic surface respiration as also seen in other species (Congleton, 1980). The level where active escape movements/swimming are induced seems to be at 30–40% saturation and may be this low because of the hazards of escape (e.g. increased risk of predation, changed food availability) and/or may be seen as a consequence of the costs of active swimming. At normoxia, active oxygen consumption is substantially higher than routine oxygen consumption. At lower temperatures where the metabolic scope is smaller, the response to acute hypoxia is somewhat different. At prolonged hypoxia the stress element will diminish through acclimation and metabolic activity will be channelled into adaptations like haemoglobin synthesis or other ways of increasing the carrying capacity of the blood (Tetens & Lykkeboe, 1981). In effect, less energy will be available for growth and reproduction.

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B 1315