Effects of temperature and hypoxic stress on the oxygen consumption rates of the mudsucker fish *Labeo capensis* (Smith)

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The specific oxygen consumption rate ($\dot{V}O_2/Mb$) of *Labeo capensis*, the freshwater mudsucker, was determined for small and large fish at winter (8°C) and summer (23°C) temperatures. $\dot{V}O_2/Mb$ was also determined during hypoxic conditions of the experimental water. It was found that $\dot{V}O_2/Mb$ does not differ substantially compared with other active fish. The $\dot{V}O_2/Mb$ for a fish with a body mass of 250 g is 0,053 ml O_2 per gram wet body mass per hour for fish acclimated at 8°C and 0,127 ml O_2 per gram per hour for fish acclimated at 23°C. The calculated mass exponent, *b*, is 0,71 at 23°C and 0,68 at 8°C. Hypoxic conditions are relatively well tolerated especially by 23°C-adapted fish.

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Die spesifieke suurstofopnamekoers ($\dot{V}O_2/Mb$) van die moddervis *Labeo capensis* is vir klein en groot vis tydens winter (8°C) en somertoestande (23°C) bepaal. $\dot{V}O_2/Mb$ is ook tydens hipoksiese toestande van die water bepaal. Daar is vasgestel dat $\dot{V}O_2/Mb$ by *L. capensis*, in vergelyking met ander aktiewe vis, nie drasties verskil nie. Die $\dot{V}O_2/Mb$ vir 'n vis met 'n liggaamsmassa van 250 g is 0,053 ml O_2 per gram natweefsel per uur vir vis aangepas by 8°C en 0,127 ml O_2 per gram natweefsel per uur vir vis aangepas by 23°C. Die berekende massaeksponent, *b*, is 0,71 vir 23°C en 0,68 vir 8°C aangepaste temperatuurtoestande. Hipoksiese toestande word veral by 23°C aangepaste visse, goed verdra.

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During the past decades numerous studies have evaluated the relationship between temperature and respiratory metabolic rates in fish (Heath 1973; Dejours 1975; Brett & Groves 1979; Randall 1982). The dramatic effects of temperature on the metabolic rate of ectothermic animals are shown by the approximate doubling of metabolism for each 10°C temperature increase ($Q_{10} = 2$) within normal temperature ranges (Schmidt-Nielsen 1983). Most researchers examining temperature effects have used animals acclimated to constant temperatures in the laboratory prior to oxygen consumption determinations. However, many freshwater organisms exist in thermal environments which cycle on a tidal, diel or seasonal basis (Vondracek, Cech & Longanecker 1982). In addition, many aquatic organisms regularly encounter temperature fluctuations through vertical or horizontal migrations (Neil & Magnuson 1974; Enright 1977).

The effects of changing environmental temperature and fluctuating oxygen tensions in the water on fish metabolism have been rather poorly studied (Hughes 1973; Vondracek, Cech & Longandecker 1982). No such studies on *Labeo capensis* (Smith), an endemic freshwater fish in Southern Africa, have been undertaken. This mudsucker is the dominant fish species in the lower Vaal and Orange River catchment areas. In those rivers *Labeo* spp. are usually abundant in pools isolated during the dry, hot season (Jubb 1967). More than 80% of the fish biomass (286,3 kg ha^{-1}) in the Boskop Dam consists of *L. capensis* (Koch & Schoonbee 1980). This mudsucker is relatively active and feeds mainly on detritus associated with the watergrass *Potamogeton pectinatus* (Schoonbee 1969).

A unique feature of Boskop Dam (storage capacity: 20,8 × 10⁶m³; surface area: 376,9 ha) is the high pH (8,2 – 8,4) and alkalinity (280 p.p.m.) of the water (Van As & Combrinck 1979). The seasonal temperature fluctuates between 8 – 10°C in winter and 23 – 25°C in summer.

The purpose of this study was to measure low routine oxygen consumption rates ($\dot{V}O_2$) (Marais 1978) for fish at two different seasonal temperatures. $\dot{V}O_2$ was also measured during experimentally induced hypoxic stress.

Materials and Methods

Mudsucker fish (body mass range: 15 – 410 g) were randomly collected below Boskop Dam, using a thrownet. They were transferred to the laboratory in aerated 500 ℓ polyethylene containers. Prior to experimentation the fish were kept for 24 h in large aerated asbestos tanks outside the laboratory where the dechlorinated tap-water was replenished at a rate of 1,2 ℓ/min. Oxygen consumption rates ($\dot{V}O_2$) were deter-

mined for 20 mudsuckers during the winter season (end July) and 20 individuals during summer (end January) at 8 and 23°C respectively. The respirometer used was an 'open system' constant flow type described by Van Aardt & Steyn (1984). It consists essentially of a reservoir tank (30 ℓ), open to the atmosphere, a thermostatically controlled respiration chamber (1,5 ℓ capacity) and two Clark PO_2 electrodes (Radiometer, E5046/0). One electrode monitors the oxygen tension (PO_2) of the water before entering the respiration chamber while the other monitors the PO_2 of the water after leaving the respiration chamber. Utmost care was taken to reduce handling during the determinations (Cameron 1976). The $\dot{V}O_2$ was determined as low routine metabolism since the fish stay immobilized in the elongated and darkened respiration chamber. At intervals the opercular frequency was visually observed through an opening in the lid of the chamber and the frequency determined with the help of a stopwatch. Usually between 40 – 60 min after a specimen was placed in the respiration chamber a constant difference between the PO_2 values from the in- and outlet water (PO_2) was obtained. Then the PO_2 was noted and the oxygen consumption rate calculated (Van Aardt & Steyn 1984).

To determine the $\dot{V}O_2$ at six fixed values (130, 120, 92, 73, 53 and 37 mmHg), lower than the normal saturated PO_2 level, a Wösthof gas mixing pump (Bochum, West Germany) was used to maintain the desired PO_2 in the reservoir and circulating water during $\dot{V}O_2$ determinations. For this experiment individual fish at each 8°C and 23°C temperature were kept between $3\frac{1}{2}$ and 4 h in the respiration chamber while the $\dot{V}O_2$ determinations at the six chosen oxygen tensions in the circulating water were done.

To determine the capacity of individual fish to deplete oxygen from the water in a closed-off respirometer system (total volume 1,5 ℓ) at 8°C and 23°C the reservoir was disconnected from the system and the inlet and outlet tubes from the respiration chamber connected directly to each other. The water in the respirometer chamber, with a mudsucker in place, was aerated for 40 – 60 min, then the lid was secured and the PO_2 monitored (Van Aardt & Steyn 1984). At the end of the experiment the $WPCO_2$ (the carbon dioxide partial pressure of the water) was determined using a Radiometer PCO_2 electrode (E5036/0) in the place of one of the PO_2 electrodes used for $\dot{V}O_2$ measurements (Van Aardt & Steyn 1984). All experiments were executed between 08h00 and 13h00.

Results and Discussion

The effects of handling of the mudsucker on the $\dot{V}O_2$, after the initial 40 – 60 min adaptation period are not noticeable. This is so because the $\dot{V}O_2$ does not change during the 2 h after the first $\dot{V}O_2$ measurements are made nor does the depletion rate of oxygen change (Figure 3). For the same period the initial high gill frequency subsided after 15 – 30 min and remained the same throughout the experimental period of 2 to 3 h (Figure 2).

In Table 1 the specific oxygen consumption rate, $\dot{V}O_2/Mb$, for L. capensis is compared with other fish weighing 250 g. The values compared favourably with those obtained for the more active fish such as the speckled trout, Salvelinus fontinalis, the common trout, Salmo gairdnerii and the round herring Gilchristella aestuaris. The $\dot{V}O_2/Mb$ for Cyprinus carpio at 20°C is four times lower than the same values found for the mudsucker at 23°C. Compared to the specific oxygen consumption rate tabulated by Prosser (1973) for other poikilothermic vertebrates, L. capensis consumes on the average about twice as much oxygen. This could be an

indication of an active existence. It is interesting to note, however, that the oxygen consumption rate of L. capensis at 23°C is nearly half the value found for the parasitic lamprey species P. marinus at 22°C (Table 1).

Table 1 A comparison of the specific oxygen consumption rate ($\dot{V}O_2/Mb$) of L. capensis with a wet body mass of 250 g and other species with similar body masses except for [a] where the $\dot{V}O_2$ is based on a 1-g fish ($n = 8$)

Species	Temperature (°C)	$\dot{V}O_2/Mb$ ($mlO_2g^{-1}h^{-1}$)	References
Labeo capensis	8	0,053	This study
	23	0,127	This study
Cyprinus carpio	10	0,011	Beamish, 1964
	20	0,030	Beamish, 1964
	25	0,066	Fontes Zuim & Macari, 1985
Salmo gairdnerii	8,8	0,030	Smith & Jones, 1982
	30	0,060	Beamish, 1964
Salvelinus fontinalis	10	0,040	Beamish, 1964
	20	0,120	Beamish, 1964
Platichthys flesus	10	0,022	Duthie, 1982
Entosphenus tridentatus	20	0,090	Johansen et al., 1973
Petromyson marinus	22	0,230	Winberg, 1956
Gilchristella aestuaris[a]	10	0,074	Derived from Talbot & Baird, 1985
	23	0,283	

The relationship between the rate of the oxygen consumption and body mass of L. capensis fitted the general equation

$$\dot{V}O_2 = aM^b$$

or in its linear form

$$\text{Log } \dot{V}O_2 = \text{Log } a + b \text{ Log } M,$$

where $\dot{V}O_2$ is the metabolic rate measured as ml O_2 h^{-1} and M the wet body mass measured in grams. Regression analysis on this allometric relationship was performed using the procedure described by Bailey (1969). At 23°C the regression line Log $\dot{V}O_2$ = Log 0,672 + 0,686 Log M and at 8°C it is Log $\dot{V}O_2$ = Log 0,672 + 0,714 Log M. A one way analysis of covariance on Log $\dot{V}O_2$ with Log M, a covariate, was performed (BMDP1v-computer program, Dixon 1983). The analysis shows no statistically significant difference between the slopes of the regression lines obtained ($P = 0,627$). From this it does not seem as if the mass exponent, b, is influenced by temperature (Figure 1). Furthermore, the levels of the two regression lines differ significantly statistically ($P < 0,001$) (Figure 1).

The value of the respiratory variable, b, for L. capensis does not approach 0,8, which is a typical value found for fish (Winberg 1956; Mann 1965; Talbot & Baird 1985), but is about 0,1 unit lower in value, e.g. 0,686 at 23°C and 0,714 at 8°C. In two interesting papers Heusner (1982a, b) suggested that the mass exponent, 0,75, relating Log metabolism and Log body mass was a statistical artifact and that the true value approximates 0,66. This issue was clarified by Wieser (1984) who argued that a distinction should be made between ontogeny and phylogeny when considering metabolism – weight relationships. Thus the intraspecific mass exponent
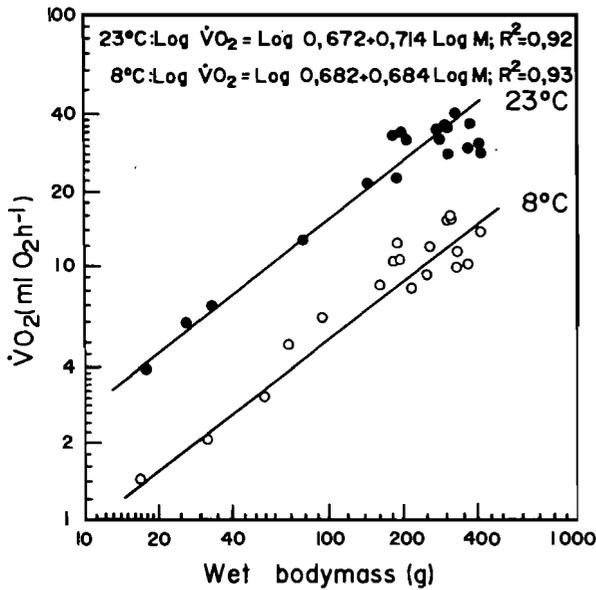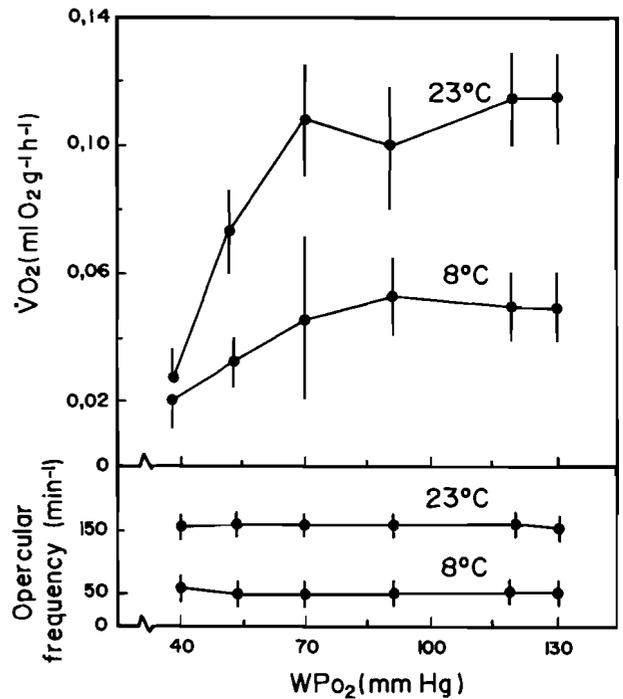
Figure 1 Oxygen consumption rate ($\dot{V}O_2$) of the mudsucker in relation to body size at 23°C (●) and 8°C (○) acclimatized temperatures. R^2 = coefficient of determination.


Figure 2 Effects of experimentally induced hypoxic stress on the oxygen consumption rate ($\dot{V}O_2$) and opercular frequency in *Labeo capensis* with an average body mass of 230 g. Vertical bars denote 2 × standard deviation.

approximates 0,66 while the interspecific mass exponent approaches 0,75. The former value suggests a close relationship between metabolism and body surface area as was pointed out by Rubner more than one hundred years ago (Wieser 1984). Reasons why the mass exponent values from fish found by Marais (1978) and Talbot & Baird (1985) are much higher than the comparable values found in this study could be attributed to the respiration chambers and the size of fish used. Marais (1978) and Talbot & Baird (1985) used a relatively large respiratory chamber of 2,5 ℓ with fish weighing mostly 20 – 30 g. The situation in their respiration chamber was such that the fish could actively swim around during their specific oxygen consumption determinations. For *L. capensis* the respiration chamber was 1,5 ℓ in volume and the fish were on average three times larger. No active free swimming was allowed for *L. capensis* in the rather narrowly constructed chamber. It is known that, for animals at rest, the efficiency of oxygen uptake decreases with mass (Depledge 1985). During activity this situation no longer pertains as oxygen uptake increases while the ventilatory requirements, such as operculum frequency, decrease. This explanation is supported by the higher value of the mass exponent when active metabolic rate is plotted against body mass (Depledge 1985).

The Q_{10} value for *L. capensis* between 8°C and 23°C is 1,78 (Table 1). For *S. fontinalis* and *C. carpio* between 10 – 20°C it is 2,75 and 2,5 respectively (Beamish 1964) and 1,3 for *Micropterus salmoides* between 10 – 20°C (Beamish 1970). Thus, from the above data, the increase in Q_{10} is lower for *L. capensis* suggesting that this species is less responsive, physiologically, to increases in environmental temperatures.

The opercular frequency per minute is 47,0 (*S.D.* ± 15) at 8°C and 162 (*S.D.* ± 21) at 23°C for *L. capensis*. Opercular frequency does not change at these two experimental temperatures when oxygen consumption decreases during hypoxic stress conditions (Figure 2). Unfortunately ventilation volume was not measured in *L. capensis*. It is known in fish that, while opercular frequency and $\dot{V}O_2$ do not increase during hypoxia, the ventilation volume increases substantially by enlarging the opercular stroke volume (Dejours 1973; Randall & Jones 1973; Smith & Jones 1982). The $\dot{V}O_2/Mb$ for *L. capensis* kept for 40 – 60 min at a particular oxygen

partial pressure (WPO$_2$) stays the same up to a WPO$_2$ of 70 mmHg (Figure 2). This was found for both winter (8°C) and summer (23°C) adapted fish. For both groups no statistically significant difference ($P < 0,001$) was found for the $\dot{V}O_2/Mb$ values between partial oxygen pressures of 73, 92, 120 and 130 mmHg of the respirometer water. The specific oxygen consumption rates, $\dot{V}O_2/Mb$, however, differ mutually significantly when measured at a PO$_2$ of either 53 or 37 mmHg of the water. This is true for fish adapted to both winter and summer temperatures (Figure 2).

The constant oxygen consumption rate of *L. capensis* up to a WPO$_2$ of 70 mmHg (Figure 2) and a constant depletion rate of the oxygen in the water (Figure 3) to about 20 mmHg indicates that the mudsucker fish does regulates his oxygen consumption rate down to some critical pressure, Pc, below which the oxygen consumption declines rapidly (Figure 2). Whether the Pc for *L. capensis* should be taken as 20 mmHg or 70 mmHg is not clear. According to the literature (Prosser 1973; Pörtner, Heisler & Grieshaber 1985) Pc is about 30 mmHg for most aquatic vertebrates and may be influenced by the size of the animal, its state of metabolic activity and temperature. The method used to measure $\dot{V}O_2$ e.g. by way of oxygen depletion in a sealed-off respirometer or by open respirometry at a particular WPO$_2$ could have an influence on Pc values. The open respirometry method applied by us, necessitates more time to determine $\dot{V}O_2$. This is more so when an animal's $\dot{V}O_2$ is measured against a stepwise decrease of the WPO$_2$. The PCO$_2$ accumulation in a sealed-off respirometer may change the freshwater animal's Pc values because PCO$_2$ accumulation usually increases the ventilation volume (Peters 1938; Basu 1959; Prosser 1973).

The ability of *L. capensis* to deplete the oxygen content in a closed-off respirometer is not much better developed compared to the findings of Fry & Hart (1948) on goldfish. Goldfish have a critical partial oxygen pressure (Pc) of 20 mmHg at 5°C and 40 mmHg at 25°C. At a water temperature
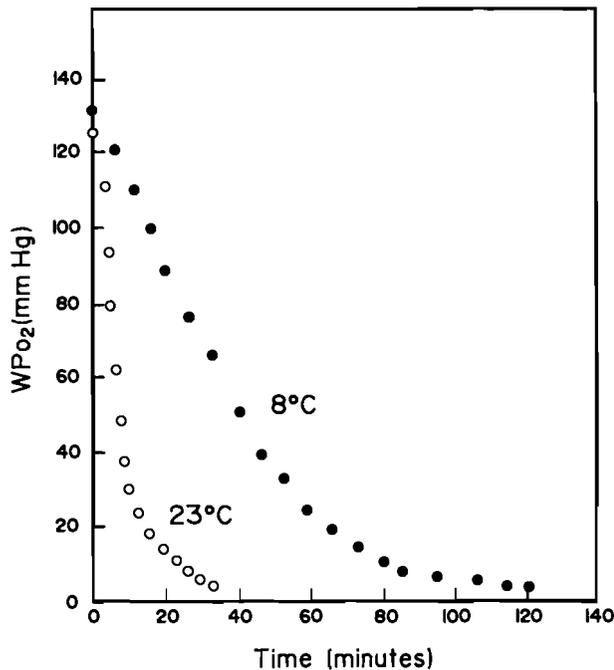
Figure 3 The oxygen depletion rate of the mudsucker, *Labeo capensis*, placed in a sealed-off water volume (1,5 ℓ) saturated with oxygen. Each curve (●: winter-adapted fish; ○: summer-adapted fish) represents the measurements made on six fish with an average wet body mass of 278 g (range: 256–291 g).

of 8°C it takes *L. capensis* five times longer to reach the Pc. Below this value it was found that the gill frequencies become irregular. Oxygen uptake and opercular frequencies cease at a WPO_2 of 7 mmHg at both 8°C and 23°C. At this WPO_2 all fish from both experimental temperatures were found to lie on their sides. When individual fish were immediately placed in oxygen saturated water, all specimens from the 8°C experiment died. Contrary to this all specimens kept at 23°C and at a Pc of 7 mmHg survived the hypoxic ordeal. No doubt the very short exposure time for fish to the hypoxic water at 23°C compared to long exposure time for fish at the 8°C water was responsible for the complete recovery of the specimens. No dissolved CO_2 was found to accumulate in the closed-off respirometer. Presumably this gas binds chemically with the bicarbonates in the alkaline water (pH 8,4) of Boskop Dam from where the water supply to the laboratory originates.

From the data presented here it is evident that the specific oxygen consumption rate of *L. capensis* is typical of the values found for the more active fish such as trout. However the Pc value for *L. capensis* is much lower than that found for trout and compares favourably with Pc values for the more hardy fish such as goldfish and, presumably, carp. The good oxyregulatory capability of *L. capensis* could be an advantage in the extreme oxygen and temperature fluctuations encountered in the habitat of this fish. Furthermore, knowledge of the hemoglobin – oxygen affinity of this species should be of great value in understanding the mudsucker's oxygen dependence in water with low oxygen partial pressures together with its active existence in these waters. In a preliminary report (Van Aardt & Frey, in press) the results indicate that blood with a high oxygen affinity does occur in *L. capensis* which can change into low oxygen affinity blood at high seasonal temperatures thus providing the necessary oxygen supply to the tissues for supporting an active life.

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