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Thermal optimum for pikeperch (*Sander lucioperca*) and the use of ventilation frequency as a predictor of metabolic rate

Michael Frisk [a,b,*], Peter Vilhelm Skov [b], John Fleng Steffensen [a,b]

[a] Marine Biological Laboratory, University of Copenhagen, Strandpromenaden 5, DK-3000 Helsingør, Denmark
[b] Technical University of Denmark, DTU Aqua, Section for Aquaculture, The North Sea Research Centre, PO Box 101, DK-9850 Hirtshals, Denmark

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ABSTRACT

Pikeperch is of increasing interest to the aquaculture industry, as a novel high value species. To our knowledge there is currently no information available on the metabolic rates of adult pikeperch. The present study determined the standard and maximum metabolic rates and ventilation frequency at six temperatures, ranging from 13 to 28 °C, in order to identify the temperature where pikeperch has the largest metabolic scope (MS). Between 13 and 25 °C, standard metabolic rates (SMR) increased as expected with a $Q_{10} = 1.8$ in response to increasing temperatures, while maximum metabolic rate (MMR) did not change significantly within this temperature range. As a result, MS was not significantly affected by acclimation temperature between 13 and 25 °C. Above 25 °C, SMR increased significantly with a $Q_{10} = 2.5$ while MMR declined, resulting in a decreased MS. In the present study, the maximum MS (MS_{MAX}) was found at 18.8 °C. Defining the optimal temperature as the thermal range where fish can maintain 80% of MS_{MAX}, shows that adult pikeperch have a broad thermal optimum between 10.4 and 26.9 °C. Since earlier studies on juvenile pikeperch have reported an optimal temperature range of 25–30 °C, we show that pikeperch have an ontogenetic shift in their thermal optimum, emphasizing the importance of considering fish size when deciding the temperature in aquaculture facilities.

As a secondary objective we investigated whether gill ventilation frequency (f_V) could be used as an accurate predictor of oxygen consumption rate ($\dot{M}O_2$), during normoxia and progressive hypoxia. A strong correlation was found between f_V and $\dot{M}O_2$ across all temperatures, and f_V could predict $\dot{M}O_2$ with a high degree of accuracy in normoxia.

1. Introduction

Pikeperch (*Sander lucioperca*) is naturally distributed throughout most of continental Europe (Deelder and Willemsen, 1964). Within this geographical range, temperatures vary from about 0.1 °C to 30 °C (Koed, 2000; Willemsen, 1978). The species thrives in nearly all temperate European inland waters (Deelder and Willemsen, 1964), but prefers turbid waters (Ali et al., 1977; Barthelmes, 1988; Dahl, 1982; Lehtonen et al., 1996), and experience seasonal occurrences of moderate and severe hypoxia during summer months and under the ice during winter (Lehtonen et al., 1996). Environmental conditions, such as temperature and oxygen availability, constitute major selection criteria in the habitat selection of fishes. Specific temperatures are selected from a need to maintain bioenergetic costs at a minimum (Dalla Valle et al., 2003). As such, the thermal preference of an ectothermic animal is often close to temperatures where physiological performance is at its optimum (Martin and Huey, 2008) and Darwinian fitness is at its maximum. Bryan et al. (1990) hypothesized that if fish are to maximize energy accessible for growth and reproduction, they must first maximize energy capacity and minimize the amount of energy diverted to other activities.

There is growing interest in pikeperch from the aquaculture industry, as a novel high value species (FAO, 2010). In order to establish successful rearing practices for this species, it is fundamental to obtain information about the metabolism and respiratory physiology under different environmental conditions. Data on metabolism is helpful to evaluate energy requirements, environmental impact assessments, species-specific physiological thresholds and aquaculture system oxygen requirements (Fitzgibbon et al., 2007). Additionally, all activities, such as swimming, growth and reproduction are powered by metabolism (Neill et al., 1994). The difference between maximum metabolic rate (MMR) and standard metabolic rate (SMR) determines the aerobic metabolic scope (MS). MS is an indicator of the available power at a given temperature. Therefore, the bigger metabolic scope, the larger amount of available power, and thus the greater growth potential (Fry, 1971).

It has previously been shown that pikeperch have exceptionally high temperature-preferences (27-28 °C) (Deelder and Willemsen,

* Corresponding author at: Marine Biological Laboratory, University of Copenhagen, Strandpromenaden 5, DK-3000 Helsingør, Denmark. Tel.: +45 51947919.
E-mail address: micf@aqua.dtu.dk (M. Frisk).

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1964; Hokanson, 1977), and maximum growth rates occur at 26-30 °C for fry and fingerlings (Hilge and Steffens, 1996; Kestemont et al., 2003; Wang et al., 2009; Willemsen, 1978), while Ronyai and Csengeri (2008) reported highest growth rate at 25 °C for juveniles. In the adult life stages, growth is impaired, and it is therefore important to gather information on optimal rearing temperatures of adult pikeperch, for the sake of optimizing breeding potential; yet, no studies have investigated this. The optimal temperature for a given fish species, with respect to growth and welfare in aquaculture, corresponds to the temperature range where the fish has its maximum metabolic scope (MS) (Fry and Hart, 1948; Kelsch and Neill, 1990), in accordance with the principle of maximum power (Bryan et al., 1990). The aim of the present study was to investigate whether the relatively high temperatures, previously reported as optimal for fingerlings and juveniles, are also valid for adult individuals. Therefore, measurements of standard and maximum metabolic rates were conducted at intervals from 13 to 31 °C.

Additionally, since hypoxia induces reduced growth rates and may increase mortality rates, knowledge about hypoxia tolerance is important when optimizing culture conditions for aquacultural species (Cruz-Neto and Steffensen, 1997). To establish critical thresholds of the oxygen partial pressure of water in culture, the critical oxygen pressure (P_{CRIT}), was determined at the same temperature intervals as the metabolic rates.

Even though optimizing metabolism is important for aquacultural production, very few facilities are able to determine metabolic scope of the fish at the premises. Although it is relatively simple to determine metabolic scope in an experimental setup, estimation of metabolic rates in the field or in a tank is difficult and prone to errors (Kerr, 1982; Millidine et al., 2008). It would, therefore, be of great value if metabolic rate could be estimated directly in the holding tanks of an aquacultural perimeter. Rather than incurring the errors by extrapolating values from the laboratory, one possibility is to estimate metabolism based on gill ventilation frequency. Several studies (Dalla Valle et al., 2003; Grantner and Taborsky, 1998; Millidine et al., 2008; Rogers and Weatherley, 1983; Van Rooij and Videler, 1996) investigated the relationship between gill ventilation frequency (f_V) and oxygen consumption rate ($\dot{M}O_2$) in order to predict $\dot{M}O_2$ from f_V. To examine whether such correlations exist for pikeperch, we measured f_V at rest, during progressive hypoxia and following exhaustion.

2. Materials and methods

2.1. Experimental animals

Pikeperch, *Sander lucioperca*, (n = 70) were obtained from a commercial rearing facility (Aquapri A/S, Egtved, Denmark) and transported to the experimental aquaculture facility at the Technical University of Denmark in Hirtshals. Fish were distributed in freshwater tanks of 650 L. Each tank was connected to a submerged biofilter containing 25 m^2 of filter media, and water was recirculated at 40 l/min. Oxygen levels in the tanks were maintained above 75% saturation by aeration, and approximately 20% of the water volume was replaced on a daily basis. Each tank was stocked with 10 fish. Fish arrived from a temperature of 23 °C. This temperature was changed at a rate of 1 °C d^{-1} until the desired experimental temperature was reached (i.e. 13, 16, 19, 22, 25, 28, 31 °C). The temperature in each tank was regulated using temperature controllers (T Controller 2001 C, Aqua Medic GmbH, Bissendorf, Germany), and maintained at ± 1 °C. The fish were kept under dim lighting 24 hours a day. Fish were allowed to acclimate to the experimental temperature for a minimum of three weeks prior to experiments. Fish were kept on a maintenance diet of commercial feed pellets (Ecolife 70, 4.5 mm; BioMar Group, Denmark). Feed was delivered using automated belt feeders, with a daily ration corresponding to 1% of their body mass (BM). During the course of the study (6 weeks of ongoing experiments) fish growth was negligible on this ration size.

2.2. $\dot{M}O_2$-measurement

To measure standard oxygen consumption rates, an organism has to be in steady state (i.e. temperature and oxygen level has to be stable, and individual fish need to be in a post-prandial state). In this study fish were kept at a stable temperature in normoxic water for three weeks, and feed was withheld for a minimum of 3 days prior to oxygen consumption rate measurements, to ensure that fish were fasting.

The experimental setup consisted of two 8.5 L resting respirometers immersed in a 150 L holding tank. The holding tank was supplied by a 600 L reservoir and water was recirculated over a trickle filter. Inlet water was aerated and UV treated (9 W UV-C, Aquacristal GmbH, Neuhofen, Germany), and the experimental temperature was maintained at ± 0.1 °C by a 1600 W heater, controlled by a programmable relay (PR-5714, PR Electronics, Denmark).

Measurement of the oxygen consumption rate ($\dot{M}O_2$) was performed by computerized intermittent flow respirometry (Steffensen, 1989), in loops of 12 min (one loop consisting of a eight minutes flush period followed by a one minute waiting period prior to the 3 min measuring period). Oxygen level was measured every second by fiber optic oxygen sensors (Fibox 3, Precision Sensing GmbH, Regensburg, Germany). Data was collected and stored by Autoresp 4 software (Loligo Systems, Tjele, Denmark). The software determined oxygen consumption rate by linear regression of the decline in oxygen content over time ($\Delta po_2\ \Delta t^{-1}$) within the respirometer, according to the equation given by Steffensen et al. (1984):

$$\dot{M}O_2 = \alpha V_{resp} \beta BM^{-1}$$

where $\dot{M}O_2$ is the oxygen consumption rate (mg O_2 kg^{-1} h^{-1}), α is the slope ($\Delta pO_2\ \Delta t^{-1}$), V_{resp} is the volume of the respirometer minus the volume of the fish (L) where body mass is equal to body volume, β is oxygen solubility at a given temperature and BM is the body mass of the fish (kg). Maximum metabolic rate (MMR) was determined by chasing the fish to exhaustion as described by (Killen et al., 2007). In short, a fish was exercised manually until it was possible to hold the tail without any attempts to escape (usually within 1 min). Following exhaustion, the fish was immediately transferred to the respirometer, where the first subsequent $\dot{M}O_2$-measurement (i.e. within the first 12 min, Fig. 1) was assumed to equal MMR. The correlation between temperature and MMR was fitted to the equation:

$$MMR = a + bT - cT^2$$

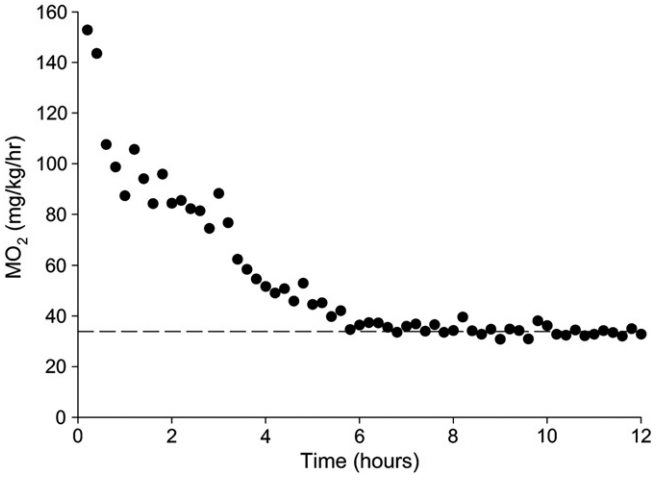

Fig. 1. The typical course of oxygen consumption rate ($\dot{M}O_2$) from first measurement (MMR) to end of protocol (12 h post introduction to respirometer). Dashed line indicates standard metabolic rate of this particular individual at 13 °C.

where T is temperature in °C. The coefficients *a*, *b*, and *c* were estimated from multiple regression analysis. Following MMR-determination $\dot{M}O_2$-measurements were continued throughout the night (for a minimum of 12 hours) to establish standard metabolic rate (SMR, Fig. 1). When determining SMR, $\dot{M}O_2$-measurements were grouped in frequency classes, and SMR was then calculated as described by Steffensen et al. (1994). The correlation between temperature and SMR was described using the equation given by Stewart et al. (1983):

$$SMR = a \times 10^{(bT)}$$

where the coefficients *a* and *b* were estimated by multiple regression analysis on the natural Log transformed data (Stewart et al., 1983). Q_{10}-values were subsequently calculated using the van't Hoff equation:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\left(\frac{10}{T_2 - T_1}\right)}$$

where R_2 is SMR at temperature two, R_1 is SMR at temperature one and T_2 and T_1 is the temperature at R_2 and R_1 respectively.

P_{CRIT} was established following determination of SMR. Water oxygen level was slowly reduced by bubbling nitrogen gas (N_2) through the water column. Whenever three consecutive $\dot{M}O_2$-measurements fell below SMR, a linear regression was fitted, and P_{CRIT} was defined as the PO_2 where the regression line intercepted the horizontal line through the SMR. Following hypoxia, normoxic conditions were re-established and $\dot{M}O_2$-measurements carried on until $\dot{M}O_2$ returned to the initial SMR. The experiment was subsequently terminated and fish were killed by a blow to the head followed by spinal transection.

All oxygen consumption rate measurements were made mass independent by normalizing to a 1.0 kg individual according the principles of allometric scaling:

$$\dot{M}O_{2(1)} = \dot{M}O_{2(i)} \times \left(\frac{BM}{1}\right)^{(1-A)}$$

where $\dot{M}O_{2(1)}$ is the oxygen consumption rate for fish corrected to 1 kg, $\dot{M}O_{2(i)}$ is the oxygen consumption rate for fish with the body mass *i*, BM is the body mass (kg) and *A* is the mass exponent. In this study an exponent of $A = 0.79$ was used, as suggested for fish by Clarke and Johnston (1999).

2.3. Gill ventilation frequency

To determine gill ventilation frequency (f_V) fish were monitored using a light sensitive camera (DCS-2121, D-Link). Recordings were made every hour from the onset of MMR measurements until SMR was reached, and following hypoxiauntil fish returned to their SMR. For analysis of f_V, one minute of recordings were analyzed manually, and correlated with the corresponding $\dot{M}O_2$-measurement. Correlations between temperature and f_V were described by the same equations as for $\dot{M}O_2$.

2.4. Statistics and analysis

All curve fittings and extrapolations were performed using TableCurve 2D version 5.01 (Systat Software Inc., Chicago, Illinois, USA). The intercept between the extrapolated curves for resting and maximum metabolic rate corresponds to the lower and upper critical temperature beyond which there is no metabolic scope (Frederich and Portner, 2000; Portner and Knust, 2007; Sommer et al., 1997; Van Dijk et al., 1999). When correlating $\dot{M}O_2$ and f_V, each value of f_V depicted corresponds to the mean of all oxygen consumption rate rates coinciding with that particular f_V.

Statistical significance is denoted by superscripts and unless otherwise stated, ANOVA followed by the Holm-Sidak method was applied as an indicator of statistical significance. $P<0.05$ was considered significant. All values are means ± standard error (SE).

3. Results

Fish were able to survive and feed at all temperatures, but the two highest temperatures selected (28 °C and 31 °C) proved to be near-critical. The stress of handling fish when transferring them to the experimental setup caused many to lose equilibrium and die within a few hours in the experimental setup. At 31 °C ($n = 6$) no animals survived the entire experimental protocol, whereas we were able to obtain data from 3 individuals in the 28 °C group ($n = 8$). There were no mortalities at the lower temperatures.

3.1. Oxygen consumption rate

Values for SMR and MMR are given in Fig. 2 and Table 1. At 13 °C, SMR was significantly lower than for temperatures between 19 °C and 28 °C. There were no significant differences in SMR between 16 °C, 19 °C and 22 °C. At 25 °C and 28 °C SMR was significantly higher than for all other temperatures. Q_{10} was calculated between all temperatures, for example: between 13 °C and 16, 19, 22, 25, 28 °C and between 16 °C and 19, 22, 25, 28 °C and so forth. Between all temperatures Q_{10} was 1.96 ± 0.14. When excluding 28 °C, Q_{10} was 1.77 ± 0.12, whereas Q_{10} equaled 2.49 ± 0.26 between 28 °C and all other temperatures, which was significantly higher than between the residual temperatures ($P<0.017$ with *t*-test). The correlation between temperature and SMR was described as:

$$SMR = 1.151 \times 10^{(0.0292T)} \quad (1)$$

where T is temperature (°C). The coefficient of determination (R^2) was 0.9557.

MMR at 13 °C was significantly different from 25 °C and 28 °C, whereas no other significant differences were present. The correlation between temperature and MMR could be described as:

$$MMR = 21.78 + 13.36T - 0.265T^2 \quad (2)$$

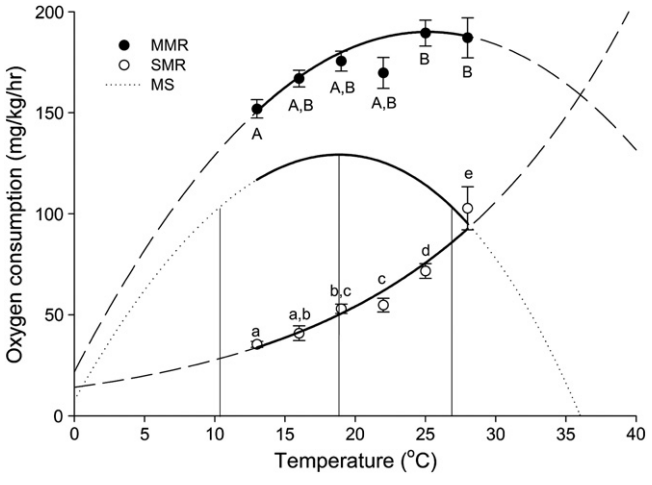

Fig.2. The relationship between oxygen consumption rate ($\dot{M}O_2$) and temperature at six different temperatures (13–28 °C). Error bars represent ± SE. Black dashed lines describe the relationship between temperature and; SMR ($=1.151\times10^{(0.0292T)}$, $R^2 = 0.9557$) and MMR ($=21.78+13.36\,T-0.265\,T^2$, $R^2 = 0.9598$) (T equals the ambient temperature in °C) respectively. Dotted line demonstrates the metabolic scope (MS) as calculated from the equations of SMR subtracted from MMR. Vertical lines reveal the temperature of maximum MS (MS_{MAX}) at 18.8 °C and the range of 80% of MS_{MAX} (10.4 and 26.9 °C). Superscripts that differ indicate significant differences ($P<0.05$).

Table 1

	13 °C	16 °C	19 °C	22 °C	25 °C	28 °C
SMR (mg O_2/kg/h)	35.37 ± 1.49^{a}	$40.87 \pm 3.62^{a,b}$	$52.97 \pm 2.32^{b,c}$	54.79 ± 3.38^{c}	71.65 ± 3.61^{d}	102.70 ± 10.67^{e}
MMR (mg O_2/kg/h)	151.90 ± 4.56^{a}	$166.90 \pm 4.13^{a,b}$	$175.52 \pm 4.91^{a,b}$	$169.71 \pm 7.62^{a,b}$	189.46 ± 6.42^{b}	187.09 ± 9.90^{b}
MS (mg O_2/kg/h)	116.53 ± 5.12^{a}	126.03 ± 7.05^{a}	122.55 ± 4.95^{a}	$114.92 \pm 6.18^{a,b}$	117.80 ± 5.20^{a}	84.38 ± 13.47^{b}
P_{CRIT} (kPa)	2.34 ± 0.14^{a}	$3.42 \pm 0.47^{a,b}$	$3.67 \pm 0.31^{a,b}$	$3.81 \pm 0.15^{a,b}$	$5.06 \pm 0.44^{b,c}$	5.98 ± 1.22^{c}
f_{VSMR} (BPM)	7.5 ± 0.8^{a}	$10.0 \pm 2.8^{a,b}$	$12.4 \pm 1.3^{a,b}$	15.0 ± 1.6^{b}	16.2 ± 1.0^{b}	31.0 ± 5.1^{c}
f_{VMMR} (BPM)	26.8 ± 1.1^{a}	32.5 ± 2.3^{a}	44.7 ± 1.1^{b}	44.6 ± 1.2^{b}	$46.4 \pm 3.1^{b,c}$	54.8 ± 3.0^{c}
VS (BPM)	19.40 ± 1.08^{a}	$21.60 \pm 2.37^{a,b}$	32.29 ± 1.16^{c}	$28.35 \pm 1.37^{b,c}$	30.20 ± 3.40^{c}	$28.67 \pm 1.89^{b,c}$
Mean weight (g)	984 ± 40	833 ± 113	848 ± 89	938 ± 88	691 ± 58	586 ± 82
N	8	8	8	8	8	3

The effect of temperature on: standard metabolic rate (SMR), maximum metabolic rate (MMR), metabolic scope (MS), critical oxygen saturation (P_{CRIT}), gill ventilation frequency at resting rate (f_{VSMR}), gill ventilation freqeuncy at maximum rate (f_{VMMR}) and scope of gill ventilation frequency (VS). All values except P_{CRIT} were obtained in normoxic water (oxygen partial pressures >17 kPa). Different superscripts in each row indicate significant differences among temperature treatments ($P<0.05$). Values are presented as mean ± standard error of means.

R^2 of Eq. (2) was 0.9598. The influence of temperature on metabolic scope was assessed by subtracting Eqs. (1) from (2).

The extrapolated curves for SMR and MMR intercepted at −0.6 °C and 36.0 °C, corresponding to the lower and upper critical temperature beyond which there is no metabolic scope (MS). Accordingly, maximum MS (MS_{MAX}) was found at 18.8 °C (Fig. 2). MS did not differ significantly in the temperature range between 13 °C and 25 °C (Table 1). The thermal range of 80% MS_{MAX}, was between 10.4 and 26.9 °C (Fig. 2).

There were no statistical differences between the critical oxygen levels (P_{CRIT}) between 13 and 22 °C (2.34-3.81kPa; Table 1). At 25 °C, P_{CRIT} (5.06 ± 0.44kPa) differed from that at 13 °C (2.34 ± 0.14kPa) and P_{CRIT} at 28 °C (5.98 ± 1.22kPa) differed from those between 13 and 22 °C.

3.2. Gill ventilation frequency

Gill ventilation frequency at SMR (f_{VSMR}) at 13 °C differed significantly from f_V at 22–28 °C (Table 1). There were no significant differences between the values at 16 °C to 25 °C. f_V at 28 °C was significantly higher than at all other temperatures. Q_{10} in the temperature range between 13 °C and 25 °C for f_{VSMR} was 1.93 ± 0.12, whereas Q_{10} between 28 °C and the residual temperatures was 4.01 ± 1.18, which was significantly higher ($P<0.025$ with *t*-test).

As to f_V at MMR (f_{VMMR}), the values at 13 °C and 16 °C were significantly lower than all other values, whereas the values at 19 °C and 22 °C differed significantly from that at 28 °C (Table 1). The correlations between f_V and temperature were best described as:

$$f_{VSMR} = 0.401 \times 10^{(0.0361T)} \quad (3)$$

($R^2 = 0.93$) and:

$$f_{VMMR} = -15.7016 + 4.0101T - 0.0557T^2 \quad (4)$$

(R^2 for $f_{VMMR} = 0.93$). Gill ventilatory scope (VS) was determined by subtracting Eqs. (3) from (4). VS was not significantly different between 19 °C and 28 °C (Table 1). At 13 °C, VS was significantly lower than it was between 19 °C and 28 °C, whereas at 16 °C, VS was different from that at 19 °C and 25 °C.

3.3. Correlation between $\dot{M}O_2$ and f_V

The correlations ($P = <0.0001$, Spearman ranking and Pearson's correlation) between $\dot{M}O_2$ and f_V, in normoxia, is shown in Fig. 3. The equations of best fit across all temperatures were:

$$\mathrm{SMR} = 2.8901 f_V + 15.355 \quad \left(R^2 = 0.96\right) \quad (5)$$

$$\mathrm{MMR} = 1.218 f_V + 122.717 \quad \left(R^2 = 0.79\right) \quad (6)$$

and

$$\dot{M}O_2 = 3.011 f_V + 25.922 \quad \left(R^2 = 0.93\right). \quad (7)$$

The exponents between Eqs. (5) and (7) differed significantly from the exponent in Eq. (6).

4. Discussion

4.1. Resting rates

Most biochemical and physiological reactions have strong thermal dependencies. Therefore, body temperature in ectothermic animals, has major effects on physical performance and general fitness (Bennett, 1980). The natural spatial distribution of pikeperch suggest that they are eurythermal, or thermal generalists (Deelder and Willemsen, 1964; Koed, 2000). We showed that an increase in temperature from 13 °C to 25 °C was associated with a small increase in standard

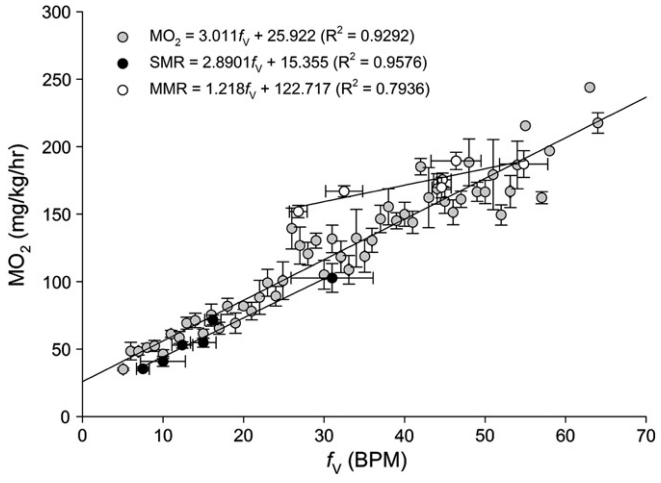

Fig. 3. Oxygen consumption rate ($\dot{M}O_2$) versus gill ventilation frequency (f_V) at six temperatures in normoxia. The correlations are significant ($P = 0.0001$) when applying both Pearson and Spearman ranking. Lines represent best fit for standard metabolic rates (SMR), maximum metabolic rates (MMR), and oxygen consumption rate ($\dot{M}O_2$) in general. Each point equals the mean of $\dot{M}O_2$ at a given f_V. Error bars represent ± SE ($n = 43$).

metabolic rate (Fig. 2), providing evidence that this is a metabolic generalization which partially equips pikeperch to live and thrive at a broad temperature range. This is further supported by the marginal changes in f_V in the same temperature range (Table 1). Nilsson (2010) proposed that ectothermic animals who are in their thermal comfort zone display Q_{10}-values around 2. In the current study, Q_{10} was between 1.8 and 2 for both SMR and f_{VSMR}, in the temperature range between 13 °C and 25 °C. Collectively, these findings partially explain why pikeperch thrive at a broad temperature range.

4.2. Optimal temperature

We aimed at determining temperature optimum for pikeperch, by means of metabolic scope. There was no significant change in metabolic scope (MS) between 13 °C and 25 °C (Table 1). A physiological thermal optimum of 18.8 °C was determined from aerobic scope, based on extrapolation of SMR and MMR, as suggested by Huey and Stevenson (1979). However, according to Huey and Stevenson (1979) it is not necessarily suitable to determine one single optimal temperature point. If no statistical difference between two scopes at two adjacent temperatures exists, there is subsequently no single optimal temperature, but instead an optimal temperature range. Huey and Stevenson suggested that the optimal temperature range of ectotherms can be evaluated on the basis of their level of thermal specialization. This can be calculated by comparing the temperature range over which a species can sustain a rate corresponding to 80% of the maximal scope. Accordingly, in the current study, the optimal temperature range for MS was between 10 and 27 °C (Fig. 2). Additionally, since, the Q_{10}-values increased to 2.5 for $\dot{M}O_2$ and 4 for f_V when approaching 28 °C, it is likely that the fishes are outside of their thermal comfort zone at 28 °C, and possibly approach the upper critical temperature. Thus we propose that the optimal temperature range of pikeperch lie between 10 °C and 27 °C.

The broad temperature optimum may be related to certain behaviors of pikeperch. During day they dwell at the bottom, but at night they seek towards warmer shallow waters to actively hunt for prey (Koed, 2000). Thus, the broad beneficial temperature range established for the species is compatible to meet the demands of diurnal behavioral routines.

A number of growth studies performed on juvenile pikeperch (Hilge and Steffens, 1996; Kestemont et al., 2003; Ronyai and Csengeri, 2008; Wang et al., 2009; Willemsen, 1978) demonstrated that the optimal temperature is 25-30 °C. According to our findings, the results from earlier studies lie in the upper range of the optimal temperature range. However, as we used larger individuals, our results support the recent findings of Morita et al. (2010), who in a simple model demonstrated that lower temperatures are required to induce maximal growth rates in bigger fish, and that bigger fish prefer cooler water. Additionally, the current findings correlate well to the life history of the species. Eggs are spawned during the spring in shallow water, and the progeny depends on warm waters to develop through summer. In autumn they seek towards colder deeper waters where they spend the winter (Lehtonen et al., 1996). Furthermore, older individuals have been reported to dwell in deeper cold waters during day, only seeking towards warmer shallow waters at dusk and night to forage (Koed, 2000). Alternatively, the lower optimal temperature found in this study, compared to former studies, is simply a result of co-variation between populations.

4.3. Critical temperature

The critical temperature of an organism is the temperature at which aerobic scope vanishes (Frederich and Portner, 2000; Portner and Knust, 2007; Sommer et al., 1997; Van Dijk et al., 1999). From extrapolations of the obtained SMR and MMR values, we found that the theoretical lower critical temperature of pikeperch is −0.6 °C, whereas the upper critical temperature is 36.0 °C. Willemsen (1978) monitored extremely high abundancies of pikeperch at 30–31 °C in a natural setting (Lake Ijssel, Holland), whereas Horoszewicz (1973) documented disturbance temperatures (i.e. beginning loss of equilibrium) at 33 °C and lethal temperatures around 36 °C. In the present study, pikeperch could be successfully reared at 28 and 31 °C, but stressful conditions caused large mortalities. According to Portner (2001), the limiting factor of whole animal aerobic scope, when approaching high temperatures, is insufficient oxygen delivery caused by inadequate blood circulation or oxygen extraction at the gills. Although we did not measure blood oxygenation in the present study, we found no significant differences in ventilatory scope (VS, Table 1) between 28 °C and that of the lower temperatures in the thermal comfort zone. As such, we expect that the observed mortality was caused by limitations to oxygen delivery, i.e. the cardiovascular system. High temperatures increase the oxygen demand of the heart (Farrell et al., 2009). In sockeye salmon (*Oncorhynchus nerka*), it has been shown that insufficient cardiac performance is a major contributor to reduced somatic oxygen supply when approaching critical temperatures (Steinhausen et al., 2008). We therefore suspect that high temperatures (i.e. 28 and 31 °C) lead to insufficient oxygen supply to the myocardium and thus mortality.

4.4. Correlation between $\dot{M}O_2$ and f_V

As, it would be of great value for the aquaculture industry to be able to determine $\dot{M}O_2$ in an easy way, we investigated f_V as a tool for predicting $\dot{M}O_2$ at SMR, MMR, and following stress and hypoxia (Fig. 3). For f_V to be a useful predictor of $\dot{M}O_2$, there has to be a strong correlation between the two, across a wide range of activities and temperatures, and it must be possible to describe this correlation by a general mathematical equation. Additionally, the relationship between f_V and $\dot{M}O_2$ should be applicable for all fish sizes so there is no need for individual calibration (Millidine et al., 2008). We found a strong correlation between f_V and $\dot{M}O_2$ following activity and following hypoxia at any given temperature and individual body mass, which is comparable to the findings of others (Dalla Valle et al., 2003; Millidine et al., 2008). Especially when predicting SMR from f_V, we demonstrated a remarkably good correlation, and SMR was also well predicted by the general equation (Eq. 7). However, when applying Eq. (7); MMR tend to be underestimated. Due to the decreasing oxygen availability and blood oxygen affinity with increasing temperatures (Cerezo and Garcia, 2004; Riggs, 1970), an increased f_{VMMR} will not necessarily reflect an increased MMR. Accordingly, even though f_V is a very good indicator of $\dot{M}O_2$ in general, it is not exact enough to predict the metabolic scope of pikeperch. Supplementary to f_V, other factors can contribute to regulation of $\dot{M}O_2$ (i.e. gill ventilation volume, oxygen extraction, and gill perfusion (Brauner and Randall, 1996). Hence, it can be argued that f_V is not the single predictor of $\dot{M}O_2$. The percent contribution of f_V to changes in $\dot{M}O_2$ at a certain temperature can be described using the equation:

$(\mathrm{Log}(f_{VMMR})\text{-}\mathrm{Log}(f_{VSMR})) / (\mathrm{Log}(\mathrm{MMR})\text{-}\mathrm{Log}(\mathrm{SMR})) \times 100$ (Millidine et al., 2008). The percent contribution of f_V to changes in $\dot{M}O_2$ for pikeperch across all temperatures was 95%. Therefore, it appears that f_V is the main regulatory mechanism of $\dot{M}O_2$ in pikeperch, and that $\dot{M}O_2$ can be estimated directly as a function of f_V independent of temperature and activity. However, caution should be made when applying this method in natural settings. When pikeperch were exposed to a continuous decline in oxygen level, an increase in f_V was seen, without a corresponding increase in $\dot{M}O_2$ (Table 1). This pattern corresponds well to other findings (Nilsson, 2010; Steffensen et al., 1982). Consequently, knowledge about the oxygen level is important when estimating $\dot{M}O_2$ from f_V. In addition, the oxygen level at which f_V begins to increase depends on the temperature. Accordingly, if hypoxic conditions are suspected it is crucial to monitor gill ventilation frequency along with water oxygen level and temperature since the correlation is merely present in normoxia.

5. Conclusion

The present study reveals a broad beneficial temperature range for pikeperch. All metabolic indicators suggest that there is no single point of optimality. However, it seems reasonable to conclude that the optimal temperature for pikeperch is in the range between 10 and 27 °C. This is lower than what previous studies have shown for juveniles. Our finding thus emphasizes the importance of considering fish size when optimizing temperature in aquaculture premises. The implications of the present findings for aquaculture practices should be verified through further studies on growth rates and feed conversion efficiency within this temperature range.

In addition, it can be concluded that oxygen consumption rate and gill ventilation frequency is highly correlated in normoxic water, at temperatures between 13 and 28 °C. Given this, it is possible to perform precise estimates of oxygen consumption rate based on information from opercular movements in pikeperch.

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