



The effects of temperature on specific dynamic action and ammonia excretion in pikeperch (*Sander lucioperca*)



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ABSTRACT

The magnitude and kinetics of the postprandial metabolic response are strongly affected by temperature. From an aquaculture perspective, it is of interest to determine the temperature at which the lowest digestive energy expenses occur. We have previously demonstrated that the optimal aerobic scope for pikeperch ranges between 11 °C and 27 °C. The aim of the present study was to investigate the thermal biology of pikeperch, by examining how specific dynamic action (SDA) and total ammonia nitrogen excretion (TAN) are affected by temperature, within this optimal temperature range.

From oxygen consumption rate and TAN excretion measurements, we established nitrogen quotients at 13 °C, 19 °C, and 25 °C. Nitrogen quotients were used to calculate instantaneous protein catabolism at the different temperatures. We found, that protein usage (17%–29%) was unaffected by temperature during fasting, but increased significantly in the course of digestion, where it became the main energy source at all experimental temperatures. Energy spent on digestion and the relationship between excreted and ingested nitrogen were unchanged with temperature. However, SDA was of shorter duration at 19 °C than at 13 °C, and a smaller fraction of metabolic scope was utilized for digestion at 19 °C, compared to at 25 °C. We therefore conclude that 19 °C is a more favorable metabolic temperature for this species.

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1. Introduction

Specific dynamic action (SDA) accounts for the energy expenditure associated with ingestion, digestion, absorption and assimilation of a meal (Jobling, 1994). Within the thermal comfort zone of an ectotherm species, duration and peak of elevated metabolism following a meal are correlated to ambient temperature (McCue, 2006). Since these parameters are important for frequency of feeding and ration, the effects of temperature on SDA have received considerable attention to help determine optimal rearing temperatures in cultured fish (Luo and Xie, 2008, 2009; Pang et al., 2010; Perez-Casanova et al., 2010; Pirozzi and Booth, 2009; Vanella et al., 2010). Increasing temperatures are not only associated with increased standard metabolic rate, it also increases magnitude of postprandial peak and reduces duration of SDA until the point where temperature changes from optimal to an increasingly deleterious range (the “pejus” temperature Schwerdtfeger, 1977). There appears to be inter-specific differences in how temperature affects the amount of energy expended on the SDA response. The energetic costs of SDA decrease with a decline in temperature in southern catfish (*Silurus*

meridionalis) (Luo and Xie, 2008), rockcod (*Paranotothenia magellanica*), southern cod (*Patagonotothen sima*), magellan plunderfish (*Harpagifer bispinis*), and eelpout (*Auroltylus depressiceps*) (Vanella et al., 2010) while no effect of temperature was reported in haddock (*Melanogrammus aeglefinus*), Atlantic cod (*Gadus morhua*) (Perez-Casanova et al., 2010), and mulloway (*Argyrosomus japonicus*) (Pirozzi and Booth, 2009). For aquaculture purposes it is important to fully understand the energetics of SDA, in order to maximize feed conversion efficiency and amount of energy retained (Peres and Oliva-Teles, 2001; Secor, 2009).

By measuring oxygen consumption and ammonia excretion rate, it is possible to provide estimates of protein utilization in fish (Van Den Thillart and Kesbeke, 1978). Ammonia excretion rates are generally low during fasting and are primarily linked to food retention and growth (Lyytikäinen and Jobling, 1998), thus making it an important measure of energy utilization at a given time point.

Pikeperch (*Sander lucioperca*) is of interest as a novel high value species for intensive aquaculture (FAO, 2010), yet knowledge about the effect of temperature on SDA is lacking, as is information on how nitrogen excretion is affected by temperature and feeding in this species. Previously, we documented that pikeperch are thermal generalists, with a broad thermal optimum (for aerobic scope) ranging from 11 °C to 27 °C (Frisk et al., 2012). To improve our understanding of optimal rearing conditions for this species, it was decided to investigate temperature effects on metabolism and ammonia excretion during fasting and following food ingestion in pikeperch.

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2. Materials and Methods

2.1. Experimental animals

Pikeperch ($n = 45$) were obtained from a commercial supplier (Aquapri Denmark A/S, Egtved, Denmark) and transported to the Technical University of Denmark in Hirtshals. Fish were kept in three freshwater tanks of 650 L. Each tank was connected to a submerged biofilter containing 25 m² 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 contained 15 fish (mean mass = 966 ± 38 g SE). Upon arrival fish were acclimated to 23 °C. This temperature was gradually changed by 1 °C per day to reach a desired experimental temperature of 13 °C, 19 °C or 25 °C. Temperature in each tank was regulated by temperature controllers (T Controller 2001C, Aqua Medic GMBH, Bissendorf, Germany), and maintained at ± 1 °C. Fish were allowed to acclimate to a given temperature for at least 3 weeks prior to experiments.

Fish were kept under dim lighting 24 h a day, and fed a daily ration of commercial feed pellets (Ecolife 70, 4.5 mm; BioMar Group, Denmark) using automated belt feeders. Due to the fairly small stomach size of cultured pikeperch, feed rations corresponded to 1% of estimated body mass.

2.2. $\dot{M}O_2$ measurements

To ensure that fish were fasting upon initiation of experiments, feed was withheld for 3 days prior to oxygen consumption rate measurements. The experimental setup consisted of 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 treated with UV light (9 W UV-C, Aquacristal GmbH, Neuhofen, Germany). The temperature was maintained (± 0.1 °C) by a 1000 W heater, controlled by a programmable relay (PR-5714, PR Electronics, Denmark). Measurements of oxygen consumption rate ($\dot{M}O_2$) were performed by computerized intermittent flow respirometry (Steffensen, 1989), in loops of 11 to 13 min (i.e. one loop consisting of a 8 min flush period followed by a 1 min waiting period prior to a measuring period). Depending on temperature, the measurement period ranged from 2 to 4 min in order to avoid hypoxic conditions at high temperatures. The oxygen partial pressure was registered every second by fiber optic oxygen sensors (Fibox 3, Precision Sensing GmbH, Regensburg, Germany). Data were stored by Autorep 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 (mmol O₂ 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 (BM) in kilograms is equal to body volume, and β is oxygen solubility at a given temperature. Maximum metabolic rate (MMR) was determined by chasing fish to exhaustion as previously described (Frisk et al., 2012). Following exhaustion a fish was swiftly transferred to the respirometer, where the first $\dot{M}O_2$ -measurement was assumed to equal MMR. Following MMR-determination $\dot{M}O_2$ -measurements continued (typically 12 h) to establish standard metabolic rate (SMR), which was calculated as described by Skov et al. (2011). In brief, $\dot{M}O_2$ -measurements were grouped in frequency classes to create a frequency distribution, then SMR was calculated from the most frequently occurring $\dot{M}O_2$ s and their relative contribution. Standard errors (SE) of SMR were calculated

from the $\dot{M}O_2$ -values falling within the most frequently occurring bins, after replacing true $\dot{M}O_2$ -values with bin center values.

Following SMR, the fish was gently removed from the respirometer and lightly sedated in 2-phenoxyethanol (250 mg L⁻¹). When equilibrium was lost; the fish was removed from the sedative solution, and force fed with commercial feed pellets (Ecolife 70, 4.5 mm; BioMar Group, Denmark; nutritional content: 19.3 MJ/kg; 54% protein, 18% lipid, 10% carbohydrate), using a 50 ml syringe connected to a piece of silicone tubing (Ø 8 mm). The feed pellets, 1% (dry weight) of fish BM, had been pre-soaked in water to soften them (feed to water mass ratio ≈ 2:3), which allowed them to be pushed through the silicon tube. Following feeding, the fish was reintroduced into the respirometer and $\dot{M}O_2$ -measurements were resumed and continued until $\dot{M}O_2$ had decreased to SMR plus 1 SE (standard error of mean). SDA was defined as the integral of $\dot{M}O_2$ from time 0 post feeding, to the time when SMR plus 1 SE was reached. Upon return to SMR, the fish was anesthetized again, as described above, only this time without feeding. The trajectory of the fasting post-anesthetic $\dot{M}O_2$ was subtracted from the trajectory of the post-feeding $\dot{M}O_2$, to determine the true SDA response. All oxygen consumption measurements were normalized to a 1.0 kg individual according to the principles of allometric scaling:

$$\dot{M}O_{2(1)} = \dot{M}O_{2(i)} (BM/1)^{(1-A)}$$

where $\dot{M}O_{2(1)}$ is the oxygen consumption rate for fish corrected to a BM of 1.0 kg, $\dot{M}O_{2(i)}$ is the oxygen consumption rate for fish with the BM i , and A is the mass exponent. In this study an exponent of $A = 0.79$ was applied (Clarke and Johnston, 1999).

2.3. TAN measurements

During fasting, a 5 ml water sample was retrieved from the respirometer immediately before the waiting period started, and again immediately before the measuring period ended, at MMR and once SMR was established. This procedure was repeated 2, 10, 20, and 35 h post feeding, and when oxygen consumption rate had returned to SMR plus 1 SE. Samples were stored at -18 °C for later analysis.

The total nitrogen concentration in water was determined as specified by the International Standard (ISO 11905-1:1997(E)) using spectrophotometric analysis at 340 nm. Since ammonia-N is considered to be the major constituent of nitrogen excretion in freshwater fish (80% to 99%; Brett and Groves, 1979; Mommsen and Walsh, 1991; Wood, 1993) the contribution of other nitrogenous compounds was not considered. TAN excretion was calculated by adapting the equation for oxygen consumption rate:

$$TAN = \frac{V_{resp} \times \Delta[N]}{\Delta t \times BM}$$

where V_{resp} is the volume of the respirometer in liters (L) excluding the fish, $\Delta[N]$ is the change in N-concentration (mmol/L) over the time course, and Δt is the time period in hours. TAN excretion was normalized to a 1.0 kg individual as described for $\dot{M}O_2$.

2.4. Statistics and data analysis

Integrals of area under curve (AUC) and curve fittings were performed using TableCurve 2D version 5.01 (Systat Software Inc., Chicago, Illinois, USA). We quantified and analyzed the following parameters from the oxygen consumption rate measurements: SMR (mmol O₂/kg/h), MMR (mmol O₂/kg/h), postprandial metabolic peak (mmol O₂/kg/h), factorial scope of that peak (postprandial peak divided by SMR), time to peak (TTP) (hours), duration of the SDA response (hours), SDA (calculated as integrated oxygen cost (mmol O₂/kg) in excess of SMR for the duration of SDA), and the SDA coefficient (%). The latter was calculated by dividing the energy spent on SDA by the

energy of the meal, as described by Jobling (1981). In order to convert SDA (mmol O₂/kg/h) into energy spent on SDA, a conversion factor of 442.88 J/mmol O₂ was applied (Brafeld and Llewellyn, 1982).

From the TAN profile we quantified and analyzed standard TAN excretion rate (STR) (mmol N/kg/h), maximum fasting TAN excretion rate (MTR) (mmol N/kg/h), postprandial peak (mmol N/kg/h), factorial postprandial scope (postprandial peak divided by STR), TTP (hours), duration (hours), total N-excreted (mmol N/kg), N-intake (mmol N), and N-excreted/N-intake. N-intake was assumed to equal 16% of the protein content of a meal (Luo and Xie, 2009).

The nitrogen quotient (NQ) was calculated as TAN excretion rate divided by $\dot{M}O_2$ for a given period. Protein metabolism can be calculated as NQ divided by 0.27, where 0.27 is NQ when protein is the only fuel being metabolized (Van Den Thillart and Kesbeke, 1978).

Statistical significance is depicted by * or superscripts. Student's *t*-test was applied to indicate statistical significance between resting and maximal rates during fasting, and postprandial peak rates, as well as to test for differences between $\dot{M}O_2$, TAN excretion, and TTP of the SDA response. For all other purposes, a one-way ANOVA followed by the Holm–Sidak method was applied. *P* < 0.05 was considered statistically significant. All results are presented as mean values ± SE.

3. Results

3.1. $\dot{M}O_2$

Increasing temperature from 13 °C to 25 °C increased standard metabolic rate (SMR) from 1.28 to 2.94 mmol/kg/h, corresponding to a *Q*₁₀ of 2.0 while maximum metabolic rate (MMR) increased by less than 30% (from 4.94 to 6.28 mmol/kg/h, Table 1).

Although temperature affected the kinetics of SDA, pikeperch displayed a typical response at all temperatures; $\dot{M}O_2$ increased rapidly followed by a slow decline (Fig. 1). Postprandial peak of $\dot{M}O_2$ was significantly higher at 25 °C than at 13 °C and 19 °C (Table 1). As a result of higher SMR at 25 °C, the factorial postprandial scope at 13 °C was larger than at 25 °C (Table 1). Despite relatively large numerical differences in maximum investment into SDA (postprandial scope), it did not differ significantly between temperatures (Table 1). TTP was significantly different between all temperatures, the value at 13 °C being longest (11.5 h). Duration of SDA at 13 °C (72.0 h) was significantly longer than at 19 °C and 25 °C (49.5 h and 45.0 h, respectively; Table 1). No differences in total metabolic expenditure on SDA were observed between temperatures (Table 1), nor were differences between SDA coefficients significant (Table 1).

3.2. Nitrogen excretion

STR was smaller at 13 °C than at 19 °C, but no statistical difference was seen between 13 °C and 25 °C (Table 1). There were also no significant differences in MTR. Postprandial course of TAN excretion was essentially in line with the course of $\dot{M}O_2$ with an initial steep increase followed by a slow decline (Fig. 2). The postprandial peak of TAN excretion at 25 °C was significantly higher, than at the two other temperatures. However, when comparing postprandial scopes no differences were apparent (Table 1). At 13 °C, TTP of TAN excretion was significantly longer than at 25 °C. Despite tendencies towards shorter TAN duration at high temperatures, none were significantly different due to variation within temperature groups (Table 1). No differences in total N-excretion or N-excreted/N-intake, during SDA, were observed between temperatures (Table 1).

TTP differed between $\dot{M}O_2$ and TAN excretion, where TAN excretion peaked first. Similarly, the duration of elevated TAN excretion was shorter than the duration of SDA at 13 °C.

NQ at fasting (SMR and MMR) was similar between the three temperatures, and so was protein utilization which at fasting was estimated to lie between 17% and 30% (Table 1). During SDA, NQ was significantly

Table 1

Measurements of oxygen consumption ($\dot{M}O_2$) and ammonia excretion (TAN) variables in pikeperch held at three temperatures.

Temperature	13 °C	19 °C	25 °C
$\dot{M}O_2$			
SMR (mmol/kg/h)	1.28 ± 0.08 ^{a,x}	1.66 ± 0.09 ^{b,x}	2.94 ± 0.20 ^{c,x}
MMR (mmol/kg/h)	4.94 ± 0.14 ^{a,y}	5.14 ± 0.14 ^{a,y}	6.28 ± 0.14 ^{b,y}
Metabolic scope (mmol/kg/h)	3.67 ± 0.46 ^x	3.48 ± 0.26 ^x	3.35 ± 0.25 ^x
Postprandial peak (mmol/kg/h)	2.74 ± 0.35 ^{a,z}	3.00 ± 0.18 ^{a,z}	4.64 ± 0.24 ^{b,z}
Postprandial scope (mmol/kg/h)	1.47 ± 0.27 ^y	1.34 ± 0.09 ^y	1.71 ± 0.04 ^y
Factorial postprandial scope	2.15 ± 0.13 ^a	1.83 ± 0.09 ^{a,b}	1.55 ± 0.07 ^b
Time to peak (TTP, h)	11.47 ± 0.07 ^{a*}	9.50 ± 0.07 ^{b*}	7.70 ± 0.07 ^{c*}
Duration (h)	72.00 ± 4.70 ^{a*}	49.50 ± 1.25 ^b	45.03 ± 6.23 ^b
SDA (mmol/kg)	32.17 ± 10.79	28.81 ± 6.94	29.18 ± 10.69
Meal energy (J)	591.61 ± 7.80 ^a	548.59 ± 9.48 ^b	557.64 ± 7.82 ^b
SDA coefficient (%)	6.47 ± 2.17	6.24 ± 1.50	6.22 ± 2.28
TAN			
STR (mmol/kg/h)	0.06 ± 0.02 ^{a,x}	0.13 ± 0.01 ^{b,x}	0.14 ± 0.05 ^{a,b,x}
MTR (mmol/kg/h)	0.30 ± 0.03 ^y	0.41 ± 0.06 ^y	0.40 ± 0.05 ^y
Scope (mmol/kg/h)	0.23 ± 0.01	0.29 ± 0.04	0.26 ± 0.05 ^x
Postprandial peak (mmol/kg/h)	0.32 ± 0.02 ^{a,y}	0.53 ± 0.05 ^{a,y}	0.94 ± 0.18 ^{b,z}
Postprandial scope (mmol/kg/h)	0.27 ± 0.02 ^a	0.39 ± 0.08 ^a	0.86 ± 0.20 ^{b,y}
Factorial postprandial scope	5.05 ± 0.32	4.15 ± 0.59	6.83 ± 1.42
Time to peak (TTP, h)	7.06 ± 0.11 ^a	5.32 ± 1.30 ^{a,b}	2.55 ± 0.77 ^b
Duration (h)	40.81 ± 3.15	34.58 ± 9.64	23.70 ± 11.16
Total N-excretion (mmol/kg)	5.58 ± 1.50	6.06 ± 1.93	6.09 ± 2.72
N-intake (mmol/kg)	57.92 ± 0.76 ^a	53.71 ± 0.93 ^b	54.60 ± 0.77 ^b
N-exc./N-intake (%)	9.63 ± 2.45	11.28 ± 3.40	11.15 ± 4.82
NQ			
Fasting NQSMR	0.05 ± 0.01	0.08 ± 0.00	0.05 ± 0.01
% protein metabolized at SMR	18.39 ± 5.21	28.48 ± 1.33	17.36 ± 4.76
Fasting NQMMR	0.06 ± 0.00	0.08 ± 0.01	0.06 ± 0.01
% protein metabolized at MMR	22.49 ± 1.61	29.54 ± 3.52	23.59 ± 2.42
NQ during SDA	0.17 ± 0.01	0.21 ± 0.02	0.21 ± 0.02
% protein metabolized during SDA	64.24 ± 4.88	77.90 ± 6.41	77.30 ± 7.09
Sample size (n)	6	6	5

Data are presented as mean ± SE.

TAN: ammonia-N excretion. $\dot{M}O_2$: oxygen consumption. N-exc./N-intake: the ratio of ammonia-N excretion during SDA to total N intake.

NQ nitrogen quotient.

^{a,b,c,d}Different superscripts in each row indicate significant differences among temperature treatments (*P* < 0.05).

^{x,y,z}Different superscripts indicate significant differences between standard rate, maximal rate and postprandial peak rate in TAN or $\dot{M}O_2$ (*P* < 0.05).

* Significant time-differences between $\dot{M}O_2$ and TAN (*P* < 0.05).

higher than at fasting, at all temperatures. However, NQ did not change significantly with temperature. Protein utilization following feeding was estimated to be 64%–78% (Table 1).

4. Discussion

4.1. Fasting rates

We aimed at determining the effect of temperature on metabolism and ammonia excretion at fasting and following food ingestion in adult pikeperch. In agreement with earlier findings on pikeperch, SMR was affected by temperature in an exponential manner with *Q*₁₀ values of 1.5, 2.0, and 2.6 at temperatures 13 °C–19 °C, 13 °C–25 °C, and 19 °C–25 °C, respectively. TAN excretion and $\dot{M}O_2$ generally increase with temperature; STR should therefore change similar to SMR when temperature is changed (Luo and Xie, 2009). Indeed, STR of pikeperch did increase with temperature, although this was only significant between 13 °C and 19 °C. NQ_{SMR} was not affected by temperature (Table 1), which is consistent with studies on rainbow trout (*Oncorhynchus mykiss*) (Alsop and Wood, 1997; Kieffer et al., 1998; Lauff and Wood, 1996) and southern catfish (*Silurus meridionalis*) (Luo and Xie, 2009). We calculated instantaneous protein use during fasting to lie between 17% and 29%, which is considerably higher than findings in the closely related Eurasian perch (*Perca fluviatilis*), where fasting

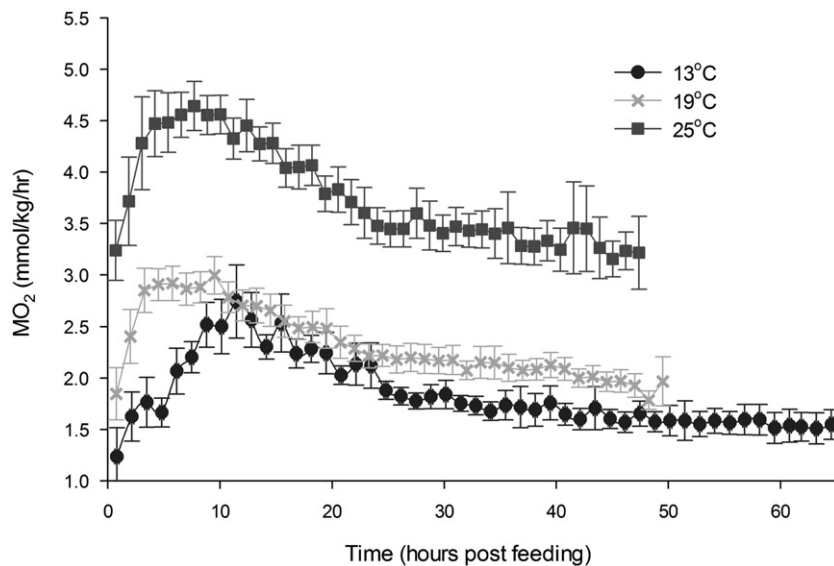


Fig. 1. The effect of temperature on oxygen consumption rate (MO_2) during SDA and standard metabolic rate (SMR) and maximum metabolic rate (MMR). Values are corrected to a body weight of 1 kg. Error bars equal \pm SE.

protein usage was between 7% and 10% at 20 °C and 23 °C (Zakes et al., 2003). However, our findings are within the range of other species (3.3%–33%) (Alsop et al., 1999; Forsberg, 1997; Lauff and Wood, 1996; Luo and Xie, 2009; Lyttikainen and Jobling, 1998).

Maximum oxygen consumption rate (MMR) and maximum fasting TAN excretion rate (MTR) changed similarly with temperature. As a result, NQ_{MMR} was comparable to NQ_{SMR} , suggesting that the fraction of protein used to fuel metabolism was unaffected by exercise, regardless of temperature. This is in accordance with findings in rainbow trout, where instantaneous protein use remained unchanged during rest and exercise (Alsop and Wood, 1997; Kieffer et al., 1998; Lauff and Wood, 1996).

4.2. Specific dynamic action

Oxygen consumption rate ($\dot{M}O_2$) followed the typical SDA response, i.e. a rapid increase followed by a slow return to SMR. A similar pattern was observed for TAN excretion in the present and earlier studies (Leung et al., 1999; Wood, 1993).

Most publications, investigating effects of acclimation temperature on SDA, demonstrated that factorial postprandial $\dot{M}O_2$ scope is independent of temperature (Luo and Xie, 2009; Pang et al., 2010; Perez-Casanova et al., 2010; Vanella et al., 2010), and one study (Pirozzi and Booth, 2009) reported that it increases with temperature. We observed a decreasing factorial postprandial scope with increasing temperature and an unchanged absolute postprandial scope (Table 1). The factorial postprandial scope usually reaches 2–3 (Jobling, 1993). In the present study factorial postprandial scope (1.55–2.15) was below or in the lower end of this range, although within the overall range between 1.4 and 4.1, reported by McCue (2006). There are at least two possible explanations for the relatively low postprandial scope we observed. First, the magnitude of postprandial scope is highly dependent on meal size (Boyce and Clarke, 1997; Fu et al., 2005; Hamada and Maeda, 1983). Cultured pikeperch have a fairly small stomach size, so in the present study it was not possible to feed rations higher than 1% of body mass, whereas most other studies on other species applied larger feed rations. Second, formulated feed pellets generally induce a smaller SDA response than natural diets (Secor, 2009). The maximum proportion of MS invested into SDA was 0.40, 0.39 and 0.51 $mmol O_2/kg/h$ at 13 °C, 19 °C and 25 °C. Thus a greater proportion of the scope was invested into SDA at 25 °C than at the other temperatures.

While SDA duration was similar between 19 °C and 25 °C, it was significantly longer at 13 °C (Table 1). The observed duration of SDA was between 45 and 72 h which is within the range of 39 to 120 h reported for Perciformes at these temperatures (Secor, 2009). From an aquaculture perspective it is desirable that postprandial processes have a duration as short as possible to allow more frequent feeding and thereby faster growth (Wang et al., 2009). The long duration of SDA at 13 °C is therefore deemed disadvantageous for aquaculture production.

In agreement with previous reports, time to postprandial peak (TTP) and duration of SDA, decreased with increasing temperature (Jobling, 1982; Luo and Xie, 2008; Pang et al., 2010; Pirozzi and Booth, 2009; Vanella et al., 2010). Similarly, TTP and duration of elevated TAN excretion decreased with increasing temperature. In contrast to most other studies, TAN excretion peaked and terminated earlier than MO_2 (Alsop and Wood, 1997; Owen et al., 1998; Peck et al., 2003). The work on channel catfish (*Ictalurus punctatus*) by Brown and Cameron (1991), demonstrated that in addition to ammonia production, the main components of the SDA response are amino acid transport and protein synthesis. Ammonia production is a result of deamination of amino acids, and therefore it is perhaps not surprising that the peak of ammonia excretion occurs prior to the peak of oxygen consumption from amino acid transport and anabolic processes.

4.3. SDA coefficient

In line with earlier studies, the energetic costs of SDA (the SDA coefficient) were unaffected by temperature (Luo and Xie, 2009; Perez-Casanova et al., 2010; Pirozzi and Booth, 2009; Vanella et al., 2010). Further, no effect of temperature was observed on the N-excretion/N-intake relationship, which is in accordance with earlier studies on pikeperch (Zakes and Karpinski, 1999) and rainbow trout (Medale et al., 1991). We found N-excretion/N-intake relationship to lie between 10% and 11%, which is close to the reported values for juvenile pikeperch (13%–15%) (Zakes and Karpinski, 1999). Postprandial NQ was markedly increased compared to fasting NQ at all temperatures. In all likelihood this reflects an increased protein catabolism during SDA, and agrees well with the finding that a shift in fuel utilization occurs following feeding of fish (Alsop and Wood, 1997; Lyttikainen and Jobling, 1998).

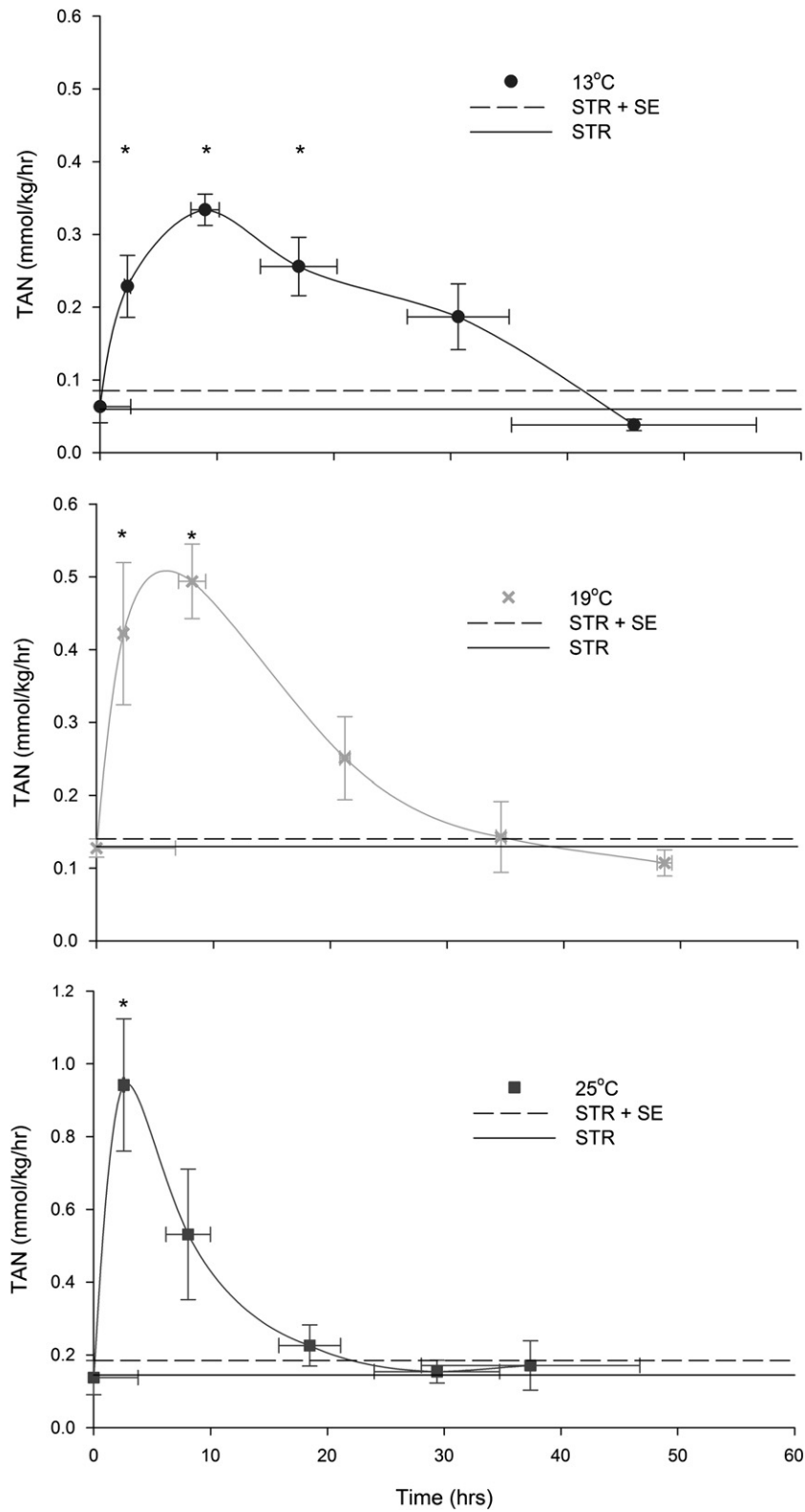


Fig. 2. The effect of temperature on total ammonia-N excretion (TAN) during SDA. Values are corrected to a body weight of 1 kg. Note the different y-axis scale in the lower panel (25 °C). * depicts significant difference from STR (ANOVA, $P < 0.05$). Error bars equal \pm SE.

5. Conclusion

From an aquaculture perspective, frequent feeding with large rations is favorable to achieve maximal growth. It may therefore be tempting to conclude that the quicker SDA peaks and begins to decline,

the more frequently the feed can be administered. Following that paradigm 25 °C would be the optimal temperature for adult pikeperch; however, with the same food consumption, fish have to sustain a much larger SMR at 25 °C than at 13 °C and 19 °C, and the surplus energy available for growth is therefore smaller. Contrarily, a rearing

temperature of 13 °C is prohibitive due to long duration of SDA. In conclusion the present study indicates that the temperature for optimal growth of large pikeperch is close to 19 °C.

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