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Research paper

Effects of water temperature, dissolved oxygen and body mass on the metabolic scope of larvae and juveniles of the nigorobuna carp, *Carassius auratus grandoculis*

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Abstract

The metabolic scope (MS), defined by the difference between active and standard metabolic rates of fish, was modelled as a function of temperature, dissolved oxygen concentration and body mass, as a surrogate for the fitness of the larvae and juveniles of a swamp-dwelling fish, nigorobuna carp (*Carrasius auratus grandoculis*). The active and standard metabolic rates were measured under different conditions of temperature (15, 20, 25, 30°C), dissolved oxygen concentration (> 90, 70, 40, 30, < 20% of saturation), and body mass class of fish (0.01, 0.1, 1, 10 g). The optimal temperature at which the MS took a maximum decreased with body mass, and asymptotically increased with dissolved oxygen concentration. The physiological ability to maintain the MS under hypoxic conditions was greater in a smaller fish. The MS of large fish (10 g) was estimated to decline to be zero under hot (≥25°C) and hypoxic (10% level of saturation) condition. Nigorobuna carp hatches in the inner part of macrophyte zone in spring and moves to offshore deeper habitat in late summer. Size-dependent physiological change in this species may be related to the seasonal migration. The MS models could be a useful tool to estimate the quality of habitat with large spatial scales because they only require environmental data, which can be easily measured in the field.

Key words: nigorobuna carp, metabolic scope, hypoxia, habitat quality

INTRODUCTION

Many freshwater fish use macrophyte zones in lakes as spawning sites, nursery grounds, and refugia during their early life stages, although the environmental conditions greatly fluctuate diurnally and seasonally within the zones (Petr 2002). Utilization of these habitats varies among species, and most fish use the macrophyte zone only during specific developmental stages or specific events such as reproduction (Miura 1966). If the environmental conditions at a habitat do not meet the physiological demands of fish, then the habitat quality for the fish can be reduced (Huey *et al.* 1991). Clarification of the relationship between the physiological condition and ambient environment is a crucial issue for habitat quality assessment to conduct efficient habitat conservation and restoration activities.

In Lake Biwa, the largest lake in Japan, most of the indigenous cyprinid fish are associated with macrophyte zones (Miura 1966). The nigorobuna carp (*Carassius auratus grandoculis*, Temminck and Schlegel 1846) depends profoundly on macrophyte zones from the larval stage (it hatches in spring) to the first half period of the juvenile stage, and moves to offshore habitats in late summer (Miura 1966). Macrophyte zones tend to be hypoxic (Petr 2000) and an increase in

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temperature from spring to summer promotes a decrease in dissolved oxygen concentration (DO). The seasonal decrement may facilitate the migration of nigorobuna carp to offshore in late summer, if DO decreases below the tolerable level for the fish. Recently, some conservation and restoration actions are conducted by a local government in Lake Biwa because of a recent decline in the population size of indigenous fish. However, little is known for the suitable physicochemical conditions of their habitats for the early life stages of the fish to develop effective restoration programs.

Temperature and DO are the primary determinants for the habitat selection of aquatic organisms via their physiological demands. Temperature controls the metabolic rate of fish, whereas DO determines the maximum rate of metabolic activity (Neill *et al.* 1994). The difference between the active metabolic rate (AMR), which is attained by fully active fish, and the standard metabolic rate (SMR), which is a minimum requirement for body maintenance, is defined as the metabolic scope (MS; Fry 1971). The MS is a surrogate for the amount of available energy for all activities other than the body maintenance, so it does not mean the energy usage per unit time, i.e. metabolic rate, but is a total amount of allowable energy expenditure for each individual. The MS is recognized as a physiological indicator which has a positive correlation with food intake (Mallekh and Lagardère 2002) and growth (Jobling 1981). Moreover, the MS is positively correlated with a lower mortality risk due to factors such as predation and disease (Priede 1977). Meanwhile, reduction in the MS causes a loss in fitness and increase mortality (Pörtner and Knust 2007). Thus, the MS can be a surrogate for fitness as a result of condition-dependent physiological status.

Here, the MS was measured for various sizes of larvae and juveniles of the nigorobuna carp under four temperature conditions with multiple DO levels to create a mathematical model of the MS as a function of temperature, DO, and body mass of the fish. By examining dependencies of the MS to these factors, optimum temperature, DO effect on the optimum temperature, and hypoxia tolerance were analyzed. Based on these analyses, seasonal changes in quality of the macrophyte zone as a habitat for the nigorobuna carp were discussed referring to the physicochemical conditions in macrophyte zone reported in previous studies.

MATERIALS AND METHODS

Fish examined

The nigorobuna carp used for the experiments were provided from the Shiga Prefectural Fisheries Promotion Association in Kusatsu, Shiga Prefecture, Japan. They were the first filial generation of the wild nigorobuna carp from Lake Biwa. They contained a wide variety of body mass (0.0141-20.2 g in wet mass) and consisted of two developmental stages (post larva and juvenile). The body mass of the examined fish covered the whole size range of the nigorobuna carp in the macrophyte zone in the lake reported by Miura (1966), except for pre-larvae during the endogenous feeding period and unable to be served for SMR measurements without an effect of yolk absorption. The examined fish were divided into 4 size classes as follows: 0.0141-0.0884 g (post larva, size class 1), 0.196-0.316 g (juvenile, size class 2), 1.22-2.23 g (juvenile, size class 3) and 11.4-20.2 g (juvenile, size class 4). All fish were acclimated to each experimental temperature according to size classes: 1-2 days for size class 1, 3-7 days for size classes 2 and 3, and at least 10 days for size class 4. Fish for the SMR measurements were used under a fasting condition for one day. Before the AMR measurements, fish were fed so as to make them active. The individuals for the SMR measurements were different from those for the AMR measurements in size classes 1-3. However, in size class 4, the same individuals were used for both SMR and AMR measurements because of the scarcity of the sample number.

Respirometry

Measurements were conducted using a semi closed respirometry system similar to that described by Oikawa *et al.* (1991; Fig. 1). The system had four chambers, one of which was used as a blank chamber to calibrate the background oxygen consumption by bacteria in water. The other three chambers were used for the measurements of fish oxygen consumption (triplicated data were obtained in each experimental condition). The size of the chambers ranged from 105 to 4650 mL. The number of fish in a chamber was varies depending on the size of the fish (Table 1). Each chamber was equipped with an oxygen electrode (BRM 5, Iijima Electronics, Gamagori, Japan) connected to a DO meter (B-505, Iijima Electronics, Gamagori, Japan). Water temperature was controlled at four levels of 15, 20, 25 and 30°C by submerging the respirometry chambers into a constant temperature bath.

Prior to the measurement of SMR, fish were carefully transferred into chambers under a dark condition for six hours to habituate the experimental condition. To avoid stimulating the fish, a blind was placed around the respirometry system. During this period, oxygenated water was supplied to each chamber through an attached tube. We conducted DO measurements at midnight as follows: the water supply through the tube was stopped with a pinchcock and DO measurement was conducted for 30 minutes; then, oxygenated water was supplied again to the chamber for 30 minutes. This procedure was repeated three times for the estimation of SMR.

AMR measurements were conducted on the next day.

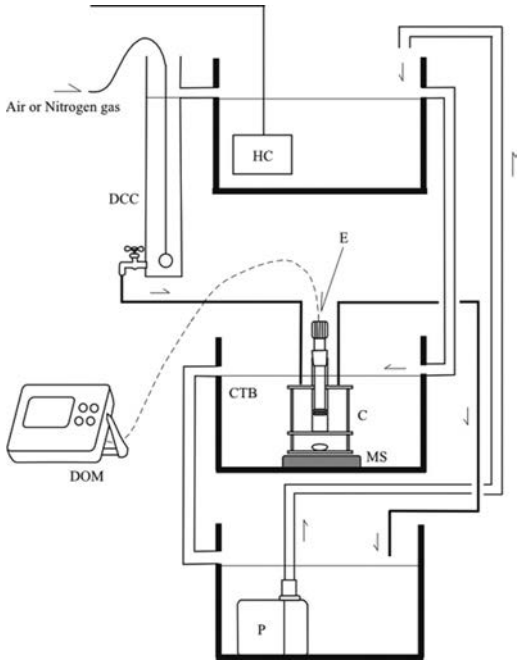

Fig. 1. Schematic image of the respirometry system. Fish were placed in a respiration chamber (C) equipped with an oxygen electrode (E). The chamber has two rooms, the upper room is for fish, and the other is for a magnetic spinbar. These two rooms are connected each other through small holes to homogenize the water in the chamber. For the large fish in size class 4, different type of chamber was installed to the system and used. E, oxygen electrode (BRM5, Iijima Electronics); C, respiration chamber; CTB, constant temperature bath; MS, magnetic stirrer; DOM, DO meter (B-505, Iijima Electronics); DCC, DO controlling column; HC, heater and cooler; P, pump.

Fish were forced to swim under a normoxic condition to increase their oxygen consumption to the maximum level. In size classes 1 and 2, fish were transferred into a 1000 mL beaker with 500 mL water and forced to swim against water flow artificially created using a 10-mL pipette. In size classes 3 and 4, fish were forced to swim in a 1000 mL plastic tank equipped with a small water pump. After the fish was exhausted (i.e. when the fish was not able to swim against the flow any more), it was transferred into a respirometry chamber and a 30-minute measurement of oxygen consumption was conducted immediately. This procedure was repeated under five different DO conditions (> 90, 70, 40, 30, < 20% of DO saturation) using the same fish. The procedure (i.e. swimming and measurement) was repeated in the order from high to low DO conditions. The DO level was controlled by nitrogen gas bubbling.

DO in respiration chambers were recorded at intervals of one minute in the measurements of SMR and AMR. The difference in DO between one-minute intervals was interpreted as the rate of oxygen consumption of the fish per minute. Therefore, 29 data were obtained from each 30-minute measurement of DO. Then, the data were converted into 20 data by calculating 10 period moving averages and used to calculate the mass specific oxygen consumption (mg O_2 g^{-1} h^{-1}) at each time period (one-minute intervals). Detailed experimental settings such as the number of fish in a chamber, fish body mass, and chamber size for each temperature condition are summarized in Table 1.

Data modeling

Because SMR is difficult to measure due to spontaneous

Table 1. Detailed experimental settings for each measurement. Number of fish and mean wet body mass of fish are shown separately for each of standard metabolic rate (SMR) and active metabolic rate (AMR). Body masses of fish are indicated as mean ± SD. Asterisks (*) indicate fish used twice for SMR and AMR measurements in size class 4.

			number of fish in a chamber		mean wet body mass (mg)	
size class	temperature (°C)	volume of chamber (ml)	SMR	AMR	SMR	AMR
1	15	105	6	4	54.6 ±13.9	48.3±16.0
	20	105	5	4	28.2±4.3	27.6±10.5
	25	105	3	2	52.1±9.2	71.2±14.3
	30	105	3	2	60.9±11.5	81.8±17.9
2	15	105	3	2	220±30.0	253±26.7
	20	105	2	2	227±30.2	271±40.0
	25	105	2	1	269±31.4	239±33.6
	30	105	2	1	207±11.5	226±27.0
3	15	105	2	1	1360±190	1420±130
	20	420	1	1	1930±260	2630±190
	25	420	1	1	1560±40	1520±180
	30	420	1	1	1680±300	1350±170
4	15	4650	1*	1*	14270±320	14270±320
	20	4650	1*	1*	14090±2140	14090±2140
	25	4650	1*	1*	19220±1020	19220±1020
	30	4650	1*	1*	13160±1560	13160±156

activity of fish (Claireaux and Lagardère 1999), the lowest 10% data in each 30-minute measurement were selected as the representative of SMR for each chamber. In the case of AMR measurement, the highest 10% data in each of five DO conditions were selected as AMR for each chamber. The selected data were averaged among three replicated chambers under the same DO and temperature condition. Finally, we obtained 16 data for SMR modeling (4 size classes × 4 temperature conditions) and 80 for AMR (4 size classes × 4 temperature conditions × 5 DO conditions).

Minimal models were made for SMR and AMR based on Fry (1971), Claireaux and Lagardère (1999), and Lefranèois and Claireaux (2003). SMR (mg O_2 g^{-1} h^{-1}) is a function of body mass of fish (allometric) and temperature (exponential):

$$\mathrm{SMR} = a_{\mathrm{smr}} W^{b_{\mathrm{smr}}} e^{cT} \quad (1)$$

where W is the wet body mass of examined fish (g), T is the water temperature (℃), a_{smr} is the oxygen consumption of the fish per 1 g body mass, b_{smr} is the slope of the allometric mass function, and c is the temperature coefficient. AMR (mg O_2 g^{-1} h^{-1}) is a function of body mass (allometric), temperature (unimodal) and DO (asymptotic):

$$\mathrm{AMR} = a_{\mathrm{amr}} W^{b_{\mathrm{amr}}} e^{d(T-f)^2} (1 - e^{g \cdot DO - h}) \quad (2)$$

where W is the wet body mass of examined fish (g), T is the water temperature (℃), DO is the dissolved oxygen concentration (mg O_2 L^{-1}), a_{amr} is the oxygen consumption of the fish per 1 g body mass, b_{amr} is the slope of the allometric mass function, d and f are temperature-associated coefficients, g and h are DO-associated coefficients.

The MS is defined as the difference between AMR and SMR:

$$\mathrm{MS} = a_{\mathrm{amr}} W^{b_{\mathrm{amr}}} e^{d(T-f)^2} (1 - e^{g \cdot DO - h}) - a_{\mathrm{smr}} W^{b_{\mathrm{smr}}} e^{cT} \quad (3)$$

where W is the wet body mass of examined fish (g), T is the water temperature (° C), and DO is the dissolved oxygen concentration (mg O_2 L^{-1}). The MS is a function of temperature, DO, and body mass of fish. In order to estimate the physiological adaptability to hypoxic conditions within the macrophyte zone in lakes where DO fluctuates, we calculated the MS at various DO concentrations under different temperature conditions. Fujiwara *et al.* (2011) reported that DO frequently dropped to less than the half saturation level and sometimes to an anoxic level in the inner part of the macrophyte zone in Lake Biwa. Here we represented the relative MS values at 50%, 25% and 10% DO levels to the MS value at the saturation (100% DO) level as the physiological adaptability. When negative values were obtained by the MS model, they were all regarded as zero.

RESULTS

Model fitting

SMR (mg O_2 g^{-1} h^{-1}) and AMR (mg O_2 g^{-1} h^{-1}) were fitted to respiratory data sets as follows:

$$\mathrm{SMR} = 0.0275 W^{-0.0804} e^{0.0914T} \quad (4)$$

(Fig. 2),

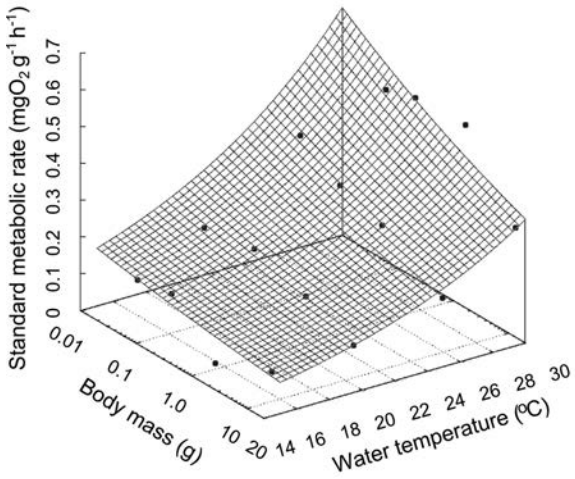

Fig. 2. Relationship between standard metabolic rate (SMR, mg O_2 g^{-1} h^{-1}), body mass (g), and water temperature (℃). Dots indicate measured data in the experiment. Mesh surface indicates fitted model for the measured data. Axis for body mass is indicated in normal log scale.

$$\mathrm{AMR} = 1.09 W^{-0.166} e^{-0.00209(T-39.5)^2} (1 - e^{-0.321DO - 0.285}) \quad (5)$$

(Fig. 3), where W is the wet body mass of examined fish (g), T is the water temperature (℃), and DO is the dissolved oxygen concentration (mg O_2 L^{-1}). All constants were estimated with statistical significance (all constants, $p < 0.05$). The multiple correlation coefficients (r^2) of measured and estimated data were 0.91 and 0.82 for SMR and AMR, respectively. We obtained the MS as:

$$\mathrm{MS} = 1.09 W^{-0.166} e^{-0.00209(T-39.5)^2} (1 - e^{-0.321DO - 0.285}) - 0.0275 W^{-0.0804} e^{0.0914T} \quad (6)$$

where W, T and DO are as above. The MS was a decreasing function of body mass and an increasing function of DO when temperature was fixed at a constant value (Fig. 4).

Temperature and oxygen dependency

The MS was a unimodal function of temperature (Fig. 5). The optimal temperature at which the MS took a maximal value decreased with body weight. The optimal temperature at

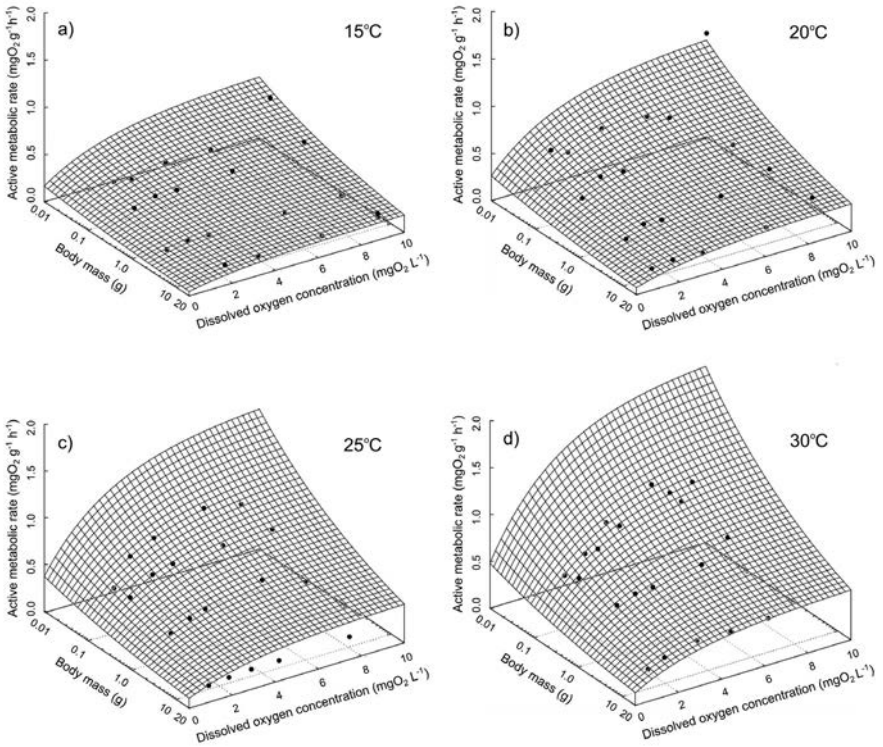

Fig. 3. Relationships between active metabolic rate (AMR, mg O_2 g^{-1} h^{-1}), body mass (g), and dissolved oxygen concentration (mg O_2 L^{-1}) at 15° C (a), 20° C (b), 25° C (c), and 30° C (d). Dots indicate measured data in the experiment. Mesh surface indicates fitted model for the measured data. Axis for body mass is indicated in normal log scale.

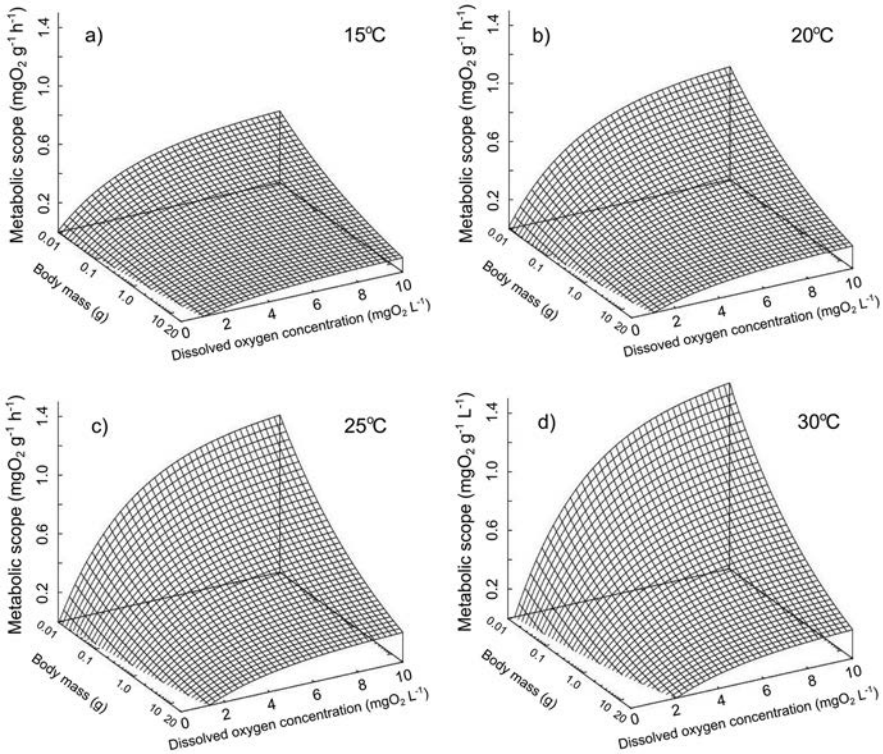

Fig. 4. Estimated values of metabolic scope (mg O_2 g^{-1} h^{-1}) depending on body mass (g) and dissolved oxygen concentration (mg O_2 L^{-1}) at 15°C (a), 20°C (b), 25°C (c), and 30°C (d). Axis for body mass is indicated in normal log scale.

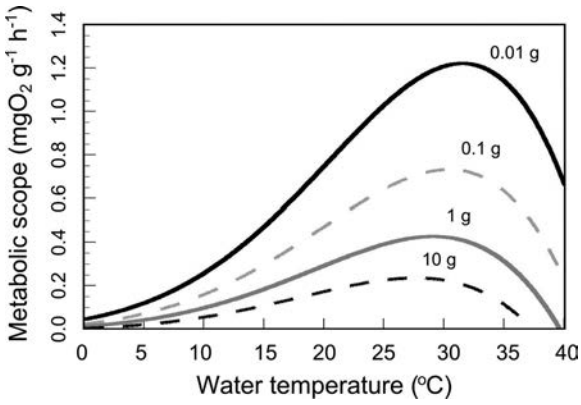

Fig. 5. Metabolic scope (mg O_2 g^{-1} h^{-1}) depending on water temperature (°C). Estimated results at DO concentration of 8 mg O_2 L^{-1} are shown for 0.01 g (black solid line), 0.1 g (gray dotted line), 1 g (gray solid line), and 10 g (black dotted line) fish, respectively.

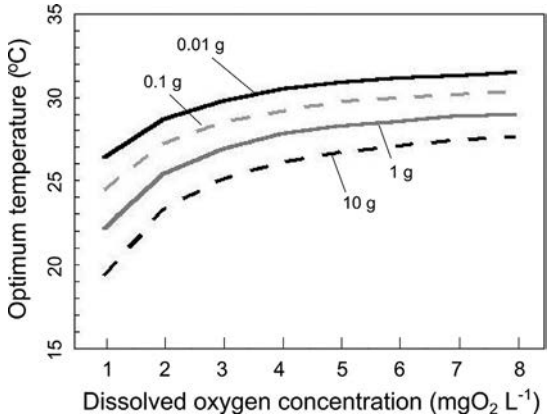

Fig. 6. The optimal temperature at which the metabolic scope (mg O_2 g^{-1} h^{-1}) took a maximal value. Estimated results at various DO concentrations (mg O_2 L^{-1}) in each size of fish (black solid line, 0.01 g; gray dotted line, 0.1 g; gray solid line, 1 g; black dotted line, 10 g) are shown.

the DO level of 8 mg O_2 L^{-1}, for example, was 31.5, 30.3, 29.0, and 27.6 ˚C for 0.01, 0.1, 1, and 10 g fish, respectively. The optimum temperature monotonically increased with DO (Fig. 6). This increasing trend was observed regardless of the fish size.

Physiological adaptability to hypoxic conditions

Physiological ability to maintain the MS under hypoxic conditions was generally greater in a smaller fish at lower temperature (Fig. 7). The decreasing trend of the MS with increased temperature was marked in larger fish. While 0.01 g and 0.1 g fish took a positive value of the MS in all conditions examined, the MS of 1 g and 10 g fish dropped to zero in 10% saturation level of DO under high temperature conditions (Fig. 7c).

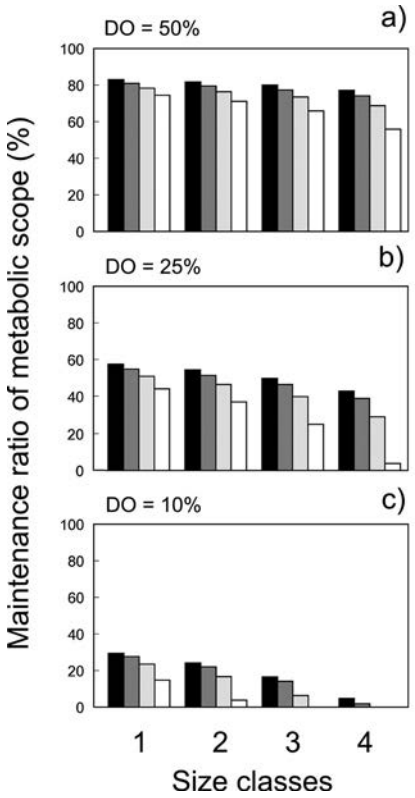

Fig. 7. Maintenance ratio of the metabolic scope (MS; mg O_2 g^{-1} h^{-1}) at 50% (a), 25% (b) and 10% (c) saturation level of DO compared to the MS at saturated condition (100% DO). The ratio was compared between four different temperature conditions: 15°C (black bar), 20°C (dark gray bar), 25°C (light gray bar) and 30°C (white bar).

DISCUSSION

The optimum temperature at which the MS took a maximum was higher in smaller individuals (Fig. 5). The dependence of optimum temperature on body size is likely to affect the habitat quality of the macrophyte zone for various life stages of the nigorobuna carp in the course of seasons. According to a previous study on the life history of the species, they hatch in the macrophyte zone in spring and stay until they migrate to offshore areas in late summer (Miura 1966). The migration of larger individuals to open waters, where seem to be cooler and richer in oxygen content, may be associated with the decline in the MS caused by decreased DO in the macrophyte zone and the decline in the optimal temperature caused by increased body mass (Fig. 5). The physiological basis for this stage-dependent habitat change was confirmed by our results that small individuals were able to retain higher maintenance ratios of the MS under hypoxic conditions (Fig. 7). Within the macrophyte zone, the inner part

of the macrophyte zone close to the shore edge was hypoxia and DO increased toward the offshore area (Fujiwara *et al.* 2011, Yamanaka 2013). The DO gradient from shore edge to offshore area was observed over time in the spring to summer seasons, and overall DO in the macrophyte zone decreased seasonally (Yamanaka, unpublished data). Though these are not cases in macrophyte zone, Nozaki *et al.* (1998) and Nozaki *et al.* (2011) reported that the DO in communities of filamentous green algae showed large diurnal fluctuation in a pool in an inlet river of Lake Biwa and littoral zone of the lake. These previous researches suggest that the intensive diurnal fluctuation of DO in the water system of Lake Biwa including macrophyte zones are not so rare and have some generality. To live in such environmental condition, the physiological basis of nigorobuna carp revealed in this study should be advantageous for the young individuals, intensifying their ability to use the inner part of the macrophyte zone as refugia.

Seasonal and diurnal changes of temperature and DO in the natural habitat do not always meet the optimal conditions for fish. Our results showed that the MS took a greater value at higher DO regardless of temperature, on the other hand, the optimal temperature at which the MS took a maximum value was affected by DO level. Smale and Rabeni (1995) reported DO as a stronger determinant of fish distribution over temperature in river. The interactive effect of DO and temperature on MS should be taken into consideration when we estimate the habitat suitability for fish. At the same time, body mass-dependent change in the hypoxia tolerance (Chapman and Mckenzie 2009, Nilsson and Östlund-Nilsson 2008) has to be taken into account for more practical simulation of habitat suitability. Fish have some physiological and behavioural adaptations to hypoxia, because aquatic ecosystems frequently suffer from hypoxia. Fish may be able to avoid hypoxic areas and seek an oxygen-rich habitat (Hochachka 1980), reduce their activity level to decrease oxygen demand (Hughes 1973, Chapman *et al.* 1995), use an oxygen-rich boundary surface between air and water by aquatic surface respiration (e.g., Gee *et al.* 1978, Kramer and McClure 1982), and switch their metabolism from the aerobic to anaerobic system under sever hypoxic or anoxic conditions (Nilsson and Renshaw 2004). The way of choosing one out of these alternative strategies vary between species and even among individuals (Killen *et al.* 2011). However, these compensations seem to be short term strategies to avoid mortality under episodic hypoxia, because the strategies cannot provide sufficient energy to conduct essential activities such as capturing foods and growth.

In aquaculture studies, the MS has been focused on as an indicator to estimate the optimal rearing condition under which fish growth is maximized (Mallekh and Lagardère 2002). There are a number of ecological studies in which the MS is used as a surrogate for fish feeding rate and growth (Jobling 1981), and an energetic standard to evaluate energy expenditure for feeding or swimming under environmental influences (Fu *et al.* 2009, Lefrançois *et al.* 1998). Moreover, MS is used to evaluate environmental suitability for species or population (Farrell *et al.* 2008, Pörtner *et al.* 2001). Temperature and DO greatly fluctuate over time in the macrophyte zone in lakes (e.g. Petr 2000, Miranda *et al.* 2000, Miranda and Hodges 2000, Petry *et al.* 2003); therefore, a model of the MS, which can estimate the habitat suitability using environmental condition data, can provide a useful tool which allows us to quantitatively assess how much activities would be carried out by the fish of interest in a specific environmental condition. Accumulation of such MS models would help to conduct easy estimation of the habitat quality for aquatic animals in spatially extensive, temporally fluctuating lake environments by just substituting environmental variables into the models.

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