

Effect of Water Temperature and Photoperiod on the Oxygen Consumption of Four Different Strains of Red Seabream, *Pagrus major*

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We determined the effects of different water temperatures (15, 20, and 25°C) and photoperiod cycles (24L:0D, 12L:12D, and 0L:24D) on the oxygen consumption of the offspring of a cultured Japanese strain (JJ), a selected Korean strain (KK), and intraspecific hybrid strains (JK and KJ) of red seabream, *Pagrus major*, under starvation conditions. The different fish strains, water temperatures, and photoperiod cycles had effects on the mean oxygen consumption of fish. Oxygen consumption increased with increasing water temperatures for all photoperiod treatments ($p < 0.001$). Fish held in continuous darkness (0L:24D) used consistently less oxygen than fish exposed to continuous light ($p < 0.05$). The oxygen consumption of fish exposed to the light phase in a 12L:12D photoperiod was higher than that of fish in the dark phase of the 12L:12D cycle, and differences were significant in three of the strains: JJ (15°C), KK (15 and 20°C), and KJ (25°C). The oxygen consumption of the inbred (JJ and KK) and intraspecific hybrid (JK and KJ) strains varied with differing water temperatures and photoperiod cycles. The JK strain displayed significantly higher oxygen consumption than the other strains under all experimental conditions except 15°C with a 0L:24D photoperiod. The JK and KJ strains usually showed the highest and lowest oxygen consumption values, respectively, whereas the inbred strains exhibited intermediate values. Oxygen consumption in the JJ and JK strains was usually higher than that of the KK and KJ strains. We propose that differences in the thermal sensitivity and photosensitization properties of the strains contribute to differences in their ability to adapt to changes in water temperature and photoperiod, thus resulting in differences in the amplitude of their metabolic rates.

Keywords: *Pagrus major*; Oxygen consumption; Temperature; Photoperiod; Strain

Introduction

Oxygen consumption is a widely used indicator of metabolic rate. Estimates of oxygen consumption rates are essential for assessing the energy metabolism of fish, as well as developing bioenergy models for production (Kaushik, 1998). Oxygen consumption is influenced by numerous internal and external factors, including water temperature (Lyytikäinen and Jobling, 1998), salinity (Forsberg, 1994), fish size (Wuenschel et al., 2004), feed ration (Brett and Groves, 1979), feed composition (Roberts, 1990), photoperiod

(Withey and Saunders, 1973), activity (Brett, 1964), and season (Beamish, 1964). Among a variety of environmental factors, water temperature exerts a profound influence on the metabolic reactions that affect all physiological processes in aquatic poikilothermic animals, including fish (Brett and Groves, 1979). Photoperiod is also one of the primary Zeitgebers (i.e. cues or synchronizers) that can influence the daily physiological rhythms of fish (Biswas et al., 2002). Temperature is considered to be a rate-controlling factor, whereas light is classified as a directive factor (Brett, 1979) that stimulates the endocrine system (Björnsson, 1997). The extent to which water

temperature and photoperiod combine to influence oxygen consumption appears to be specific to distinct fish species (Jonassen et al., 2000; Biswas et al., 2002; Biswas and Takeuchi, 2002). Although the fisheries literature is replete with studies evaluating environmental effects, including water temperature and photoperiod, far less research has been conducted on the differences in oxygen consumption between inbred and intraspecific hybrid strains of fish.

The red seabream, *Pagrus major*, is a commercially important aquaculture fish cultivated in Korea and Japan. Red seabream has been selectively bred for increased growth for the last 20 years in Korea (Noh et al., 2004) and 35 years in Japan (Murata et al., 1996), resulting in the improved growth of this species. Moreover, in Korea, local governments and Korea Institute of Ocean Science & Technology (KIOST) have initiated breeding program protocols aimed to improve growth rates and tentatively establish optimum breeding strains (Noh et al., 2003). Selective breeding programs designed to improve growth rates via better feed utilization have proved successful for several fish species (Gjedrem 1983, 1997; Ogata et al., 2002). However, little information is available on the effects of such selective breeding on the metabolic parameters that affect growth rates, including oxygen consumption. The main objective of this study was to determine the combined effects of water temperature and photoperiod on the oxygen consumption of offspring of a cultured Japanese strain, a selected Korean strain, and intraspecific hybrid strains of red seabream.

Materials and Methods

1. Fish and rearing conditions

The red seabream used in this study came from two sources. The cultured Japanese broodstock was imported from southeastern Honshu, Japan, and was maintained at a sea farming station operated by Korea Institute of Ocean Science and Technology (KIOST) (Tongyeong, Korea). The parents of the Korean strain were selected for improved growth within a sea cage for four generations. The offspring of the two inbred strains, i.e., a cultured Japanese strain (JPN, JJ) and a selected Korean strain (KIOST-F4, KK) as well as those from two intraspecific hybrid strains (JPN ♀ x KIOST-F4 ♂, JK; and KIOST-F4 ♀ x JPN ♂, KJ) were obtained from the Gyeongsangnamdo Fisheries Resources Research Institute. After 5 months of growth, fingerlings from each strain were transported to the indoor recirculating facilities and were then raised in 110-l rectangular glass tanks for 3 weeks prior to the experiment. During

the conditioning period, the fish were hand-fed a commercial diet (E-hwa Feed Co., Busan, Korea), which contained 46.7% crude protein, at 3% body weight per day. The water temperature and salinity in the system were maintained at $20 \pm 0.2^\circ\text{C}$ and $34.0 \pm 0.5\text{‰}$, respectively, and the water flow was adjusted to maintain an oxygen saturation level $>80\%$. Light was provided by a 32-W fluorescent tube, and the photoperiod was maintained at 12:12 L:D.

2. Measurement of oxygen consumption

To determine the effects of temperature and photoperiod on the oxygen consumption of the four *P. major* strains (JJ, JK, KK, and KJ), we evaluated the effects of different combinations of three water temperatures (15, 20, and 25°C) and three photoperiod cycles (24L:0D, 12L:12D, and 0L:24D).

The water temperature was gradually adjusted, from 20°C to either 15 or 25°C over 3 days, but the light conditions were changed abruptly. Before transfer to a respirometer, the fish were acclimatized to the test water temperature and photoperiod for 7 days. After all of the fish had been acclimatized to the test water temperature and photoperiod, they were starved for 48 hours, then anesthetized with MS-222 (Sigma Chemical Co., USA) and weighed before being placed in the respirometer. The average mean body weights (\pm SEM, $n=5$) were 52.0 ± 0.6 g (JJ), 52.3 ± 0.7 g (JK), 51.7 ± 0.4 g (KK), and 52.1 ± 0.7 g (KJ).

Oxygen consumption rates were determined using an automated flow-through respirometer with three closed 6-l rectangular acrylic chambers, which were designed according to the specifications of Oh and Noh (2006), with minor modifications. To measure metabolic rates, five fish were stocked in each chamber, and the fish were acclimated to the environment of the system for approximately 24 hours before initiating the experiment. The oxygen consumption of the fish was then measured every 10 min for the following 1 days. Oxygen concentrations in the inlets and outlets of all chambers were measured automatically with the OxyGuard system (Denmark), which was connected to a computer. The inlet water was aerated to maintain over 95% oxygen saturation. The water flow rate in each chamber was maintained at 0.96 l min^{-1} throughout the experiment. All experimental combinations were carried out in triplicate.

The specific oxygen consumption was calculated according to the following formula:

$$\text{MO}_2 = (\text{DO}_{\text{in}} - \text{DO}_{\text{out}}) \times Q / B$$

where MO_2 is the specific oxygen consumption rate ($\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$). DO_{in} and DO_{out} are the dissolved oxygen concentrations (mg

l^{-1}) in the inlet and outlet water, respectively. Q is the water flow ($l\ h^{-1}$), and B is the fish biomass (in kg) within the chamber. The mean daily oxygen consumption was calculated as the arithmetic mean of the 144 oxygen consumption measurements taken each day. At the end of each experiment, data were downloaded

from the computer and processed.

3. Statistical analysis

The statistical analysis was performed using MINITAB for Win-

Table 1. Results of ANOVA on the effects of temperature and photoperiod on the oxygen consumption of offspring of a cultured Japanese strain (JJ), a selected Korean strain (KK), and intraspecific hybrid strains (JK and KJ) of *Pagrus major*

Sources of variation	d.f.	SS	MS	F
Strain (S)	3	642156	214052	778.49***
Water temperature (T)	2	6193091	3096545	11000.00***
Photoperiod (P)	2	680990	340495	1238.36***
S x T	6	194642	32440	117.98***
S x P	6	61007	10168	36.98***
T x P	4	94561	23640	85.98***
S x T x P	12	98383	8199	29.82***
Data transformation	None			
Levene's test	$p = 0.903$			

*** $p < 0.001$

Table 2. The exponential model ($M = ae^{bt}$) for oxygen consumption with increasing water temperature (T; 15, 20, and 25°C) of offspring of a cultured Japanese strain (JJ), a selected Korean strain (KK), and intraspecific strains (JK and KK) of *Pagrus major* under different photoperiods

Strain	Photoperiod	Regression parameters		Regression statistics	
		a-value Mean \pm s.e.	b-value Mean \pm s.e.	r^2	p
JJ	24L : 0D	104.50 \pm 33.01	0.06 \pm 0.01	0.88	<0.001
	12L : 12D	77.05 \pm 9.60	0.06 \pm 0.01	0.96	<0.001
	0L : 24D	56.94 \pm 4.16	0.07 \pm 0.01	0.93	<0.001
JK	24L : 0D	87.87 \pm 35.90	0.07 \pm 0.02	0.90	<0.001
	12L : 12D	108.94 \pm 0.72	0.06 \pm 0.01	0.97	<0.001
	0L : 24D	43.61 \pm 13.78	0.09 \pm 0.01	0.93	<0.001
KK	24L : 0D	78.90 \pm 14.31	0.07 \pm 0.01	0.94	<0.001
	12L : 12D	79.63 \pm 7.13	0.06 \pm 0.01	0.85	<0.001
	0L : 24D	84.40 \pm 31.13	0.05 \pm 0.02	0.85	<0.001
KJ	24L : 0D	64.54 \pm 19.29	0.08 \pm 0.01	0.93	<0.001
	12L : 12D	43.91 \pm 1.79	0.09 \pm 0.01	0.98	<0.001
	0L : 24D	39.70 \pm 2.19	0.09 \pm 0.01	0.97	<0.001

dows (MINITAB Statistical Software, USA, r 13.20). An ANOVA was conducted to identify differences in oxygen consumption among the triplicate experiments and the various treatments. The effects of water temperature on oxygen consumption throughout the experiment were determined by fitting an exponential equation to the data:

$$M = ae^{bT}$$

where M is the average metabolic rate ($\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$), T is the water temperature ($^{\circ}\text{C}$), and a and b are constants.

A one-way ANOVA was used to determine the effects on each strain for all combined treatments. Data were then subjected to Tukey's test at a 95% significance level to compare the means when differences occurred. Prior to the ANOVA, a Kolmogorov-Smirnov test was used to assess the normality of the distributions, and the homogeneity of variances was assessed using Levene's test.

Results

Oxygen consumption among the different fish strains was significantly affected by water temperature and photoperiod cycles (Table 1). The mean oxygen consumption of all fish strains increased exponentially with increasing water temperature for all photoperiod treatments ($p < 0.001$; Table 2).

The oxygen consumption of the fish ranged from 156.0 to 279.5 $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ at 15 $^{\circ}\text{C}$, from 236.8 to 342.7 $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ at 20 $^{\circ}\text{C}$ and from 302.2 to 529.8 $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ at 25 $^{\circ}\text{C}$ (Fig. 1). The amplitude of the oxygen consumption values of each strain varied with different water temperatures and photoperiod cycles. When the water temperature was increased from 15 to 25 $^{\circ}\text{C}$, the mean daily oxygen consumption values of the JJ, JK, KK, and KJ strains increased 1.2~2.0, 1.2~2.8, 1.3~1.8, and 1.3~2.4 times, respectively, depending on the photoperiod. When the photoperiod

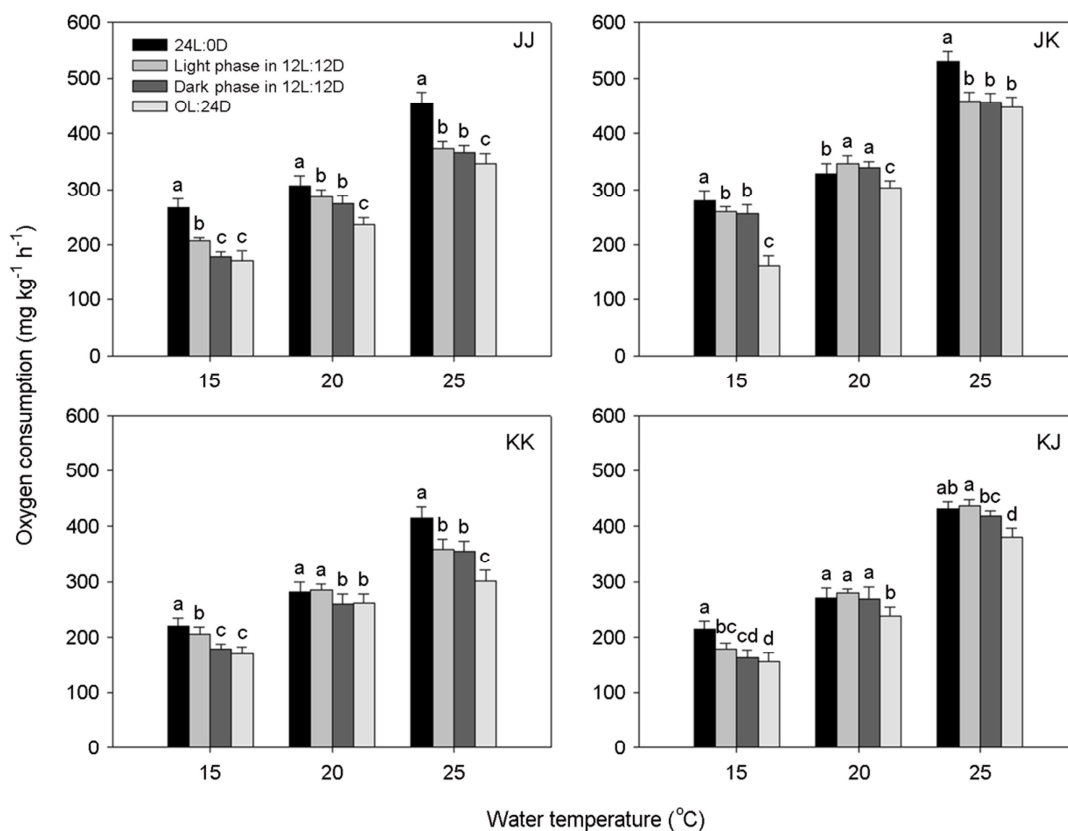


Fig. 1. Mean daily oxygen consumption rates of the offspring of a cultured Japanese strain (JJ), a selected Korean strain (KK), and intraspecific hybrid strains (JK and KJ) of *Pagrus major* at different water temperatures and photoperiod cycles. Vertical bars indicate the standard error of the mean (SEM). Different letters indicate statistical differences ($p < 0.05$).

Table 3. Results of a one-way ANOVA on the effects of photoperiod on the mean daily oxygen consumption rates of offspring from a cultured Japanese strain (JJ), a selected Korean strain (KK), and intraspecific hybrid strains (JK and KJ) of *Pagrus major* in different water temperatures

Strain	Sources of variation	15°C				20°C				25°C			
		d.f	S.S	M.S	F	d.f	S.S	M.S	F	d.f	S.S	M.S	F
JJ	Photoperiod	2	120849	60424	207.01***	2	60266	30133	134.60***	2	155875	77937	267.58***
	Levene's test	$p = 0.614$				$p = 0.253$				$p = 0.237$			
	Tukey's test*	24L:0D>12L:12D>0L:24D				24L:0D>12L:12D>0L:24D				24L:0D>12L:12D>0L:24D			
JK	Photoperiod	2	187870	93935	301.65***	2	18814	9407	38.37***	2	97267	48633	159.06***
	Levene's test	$p = 0.818$				$p = 0.707$				$p = 0.436$			
	Tukey's test*	24L:0D>12L:12D>0L:24D				12L:12D>24L:0D>0L:24D				24L:0D>12L:12D=0L:24D			
KK	Photoperiod	2	31177	15589	73.24***	2	5096	2548	8.18**	2	154599	77300	218.61***
	Levene's test	$p = 0.302$				$p = 0.534$				$p = 0.994$			
	Tukey's test*	24L:0D>12L:12D>0L:24D				24L:0D>0L:24D 24L:0D=12L:12D, 12L:12D=0L:24D				24L:0D>12L:12D>0L:24D			
KJ	Photoperiod	2	44540	22270	95.48***	2	19190	9595	32.57***	2	39399	19699	87.47***
	Levene's test	$p = 0.946$				$p = 0.719$				$p = 0.201$			
	Tukey's test*	24L:0D>12L:12D>0L:24D				24L:0D=12L:12D >0L:24D				24L:0D= 12L:12D>0L:24D			

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, =: not significant

cycle was changed from 0L:24D to 24L:0D, the amplitude of oxygen consumption by the JJ, JK, KK, and KJ strains increased 1.1~1.6, 1.0~1.7, 1.0~1.4 and 1.1~1.4 times, respectively, at different water temperatures.

The length of the photoperiod (Table 3) also had a significant effect, with continuous light (24L:0D) resulting in the highest levels of oxygen consumption, except for the JK, KK and KJ strains at 20°C and KJ strain at 25°C. Significantly high oxygen consumption for the JK strain at 20°C occurred in a 12L:12D photoperiod. The mean daily oxygen consumption of the fish kept in darkness (0L:24D) was consistently lower than that of fish exposed to continuous light ($p < 0.05$).

All fish strains displayed a diurnal variation in oxygen consumption, associated with light variation, under a 12L:12D photoperiod (Fig. 1). The oxygen consumption of fish exposed to the light phase of the 12L:12D photoperiod was consistently higher than that of fish exposed to the dark phase. The JJ (15°C), KK (15 and 20°C), and KJ (25°C) strains (Fig. 1) displayed significant differences in oxygen consumption based on their exposure to the light or dark phase.

The oxygen consumption of the inbred (JJ and KK) and the

intraspecific hybrid strains (JK and KJ) varied with the water temperature and photoperiod cycle (Table 4). The oxygen consumption of the JK strain, except in the 15°C, 0L:24D treatment, was significantly higher than that of the other strains in all tested treatments. At 25°C under continuous darkness and 12L:12D photoperiod, the inbred strains exhibited significantly lower oxygen consumption than did the intraspecific hybrid strains ($p < 0.05$). Under other experimental combinations, however, the JK and KJ strains usually showed the highest and lowest oxygen consumption, respectively, and the inbred strains were intermediate in consumption. The high oxygen consumption tendency of the JJ and JK strains was observed compared to that of the KK and KJ strains (Table 4).

Discussion

The influence of water temperature on the oxygen consumption of fish in our study was consistent with previous reports that suggested that water temperature exerts a general rate-controlling effect on oxygen consumption of the red seabream (Mitsunaga et al., 1999; Kim et al., 1995) and other fish species (Fonds et al., 1992; Imsland et al., 1995; Oh et al., 2012). Kim et al. (1995) reported

Table 4. Results of a one-way ANOVA evaluating the effects of strain on the mean daily oxygen consumption rates of offspring from a cultured Japanese strain (JJ), a selected Korean strain (KK), and intraspecific hybrid strains (JK and KJ) of *Pagrus major* at different water temperatures and photoperiod cycles

Photo-period	Sources of variation	15°C				20°C				25°C				
		d.f	S.S	M.S	F	d.f	S.S	M.S	F	d.f	S.S	M.S	F	
24L:0D	Strain	3	76059	25353	96.18***	3	46764	15588	48.60***	3	184427	61476	189.50***	
	Levene's test		$p = 0.271$				$p = 0.954$				$p = 0.445$			
	Tukey's test*		JK>JJ>KK=KJ				JK>JJ>KK=KJ				JK>JJ>KJ>KK			
12L:12D	Strain	3	103152	34384	133.28***	3	81552	27184	98.80***	3	162865	54288	247.25***	
	Levene's test		$p = 0.922$				$p = 0.430$				$p = 0.322$			
	Tukey's test*		JK>JJ=KK>KJ				JK>JJ=KK=KJ				JK>KJ>JJ>KK			
0D:24D	Strain	3	3614	1205	4.54**	3	69587	23196	110.27***	3	268168	89389	264.96***	
	Levene's test		$p = 0.804$				$p = 0.313$				$p = 0.956$			
	Tukey's test*		JJ=KK>KJ JJ=KK=KJ, JK=KJ				JK>KK>JJ=KJ				JK>KJ>JJ>KK			

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, =: not significant

that oxygen consumption in the red sea bream increased from 172.0 to 774.3 ml O₂ kg⁻¹ h⁻¹ when water temperature was increased from 15.2°C to 24.0°C. The differences in our results can be attributed primarily to differences in water temperature, fish size, fish strain, photoperiod, and fasting periods. The respirometer technique we employed also may have influenced our results. The exponential relationship between water temperature and metabolic rate (Table 2) appears to be consistent with previous observations in other fish species (Lyytikäinen and Jobling, 1998).

The effects of photoperiod on oxygen consumption are consistent with the findings of Oh and Noh (2006). The higher rates of metabolic activity during the light phase (Table 3, Fig. 1) are probably attributable to the behavioral interactions of the fish when exposed to light, with their greater activity levels resulting in increased metabolic rates. These biorhythms are probably endogenous and are influenced by light levels and photoperiod. This finding is also consistent with previous results for the other fishes (Ross and McKinney, 1988; Biswas et al., 2002; Oh and Noh, 2006). We found that the metabolic rates of the JK strain in a 12L:12D photoperiod (20°C) were higher than those in the 24L:0D photoperiod cycle (Table 3). This phenomenon is similar to that observed in other fish (Kim, 1999). One possible explanation is that the alternation of light and dark phases during a 12L:12D photoperiod may accelerate physiological activities. Behavioral interactions or the stimulatory effects of Zeitgebers, including photoperiod, in

synchronizing an endogenous rhythm to the external environment may also require more energy in a 12L:12D photoperiod than under continuous light. However, Biswas et al. (2002) suggested that the effects of other variables, including possible alterations in hormone rhythm or locomotor activity by different photoperiods, require further study.

Diurnal variations in oxygen consumption appear similar to those recorded previously for the other fishes (Chakraborty et al., 1992; Biswas et al., 2002; Oh and Noh, 2006). Fish exposed to the 12L:12D photoperiod exhibited daily rhythms, while those exposed to continuous light or darkness exhibited less diurnal variation in oxygen consumption (Fig. 1). In our study, respiration was cyclic for fish acclimated to longer or shorter light periods, whereas for the common carp, continuous light or darkness results in the suppression of respiratory rhythms (Chakraborty et al., 1992). The metabolic rhythmicity seen under a 12L:12D photoperiod tended to decrease with increased water temperature. The metabolic rates of the fish probably increased incrementally more with changes in the water temperature than with the alternations between the light and dark phases in the 12L:12D photoperiod.

Water temperature and photoperiod had marked effects on the oxygen consumption of offspring of the JJ, JK, KK, and KJ strains, but their thermal sensitivity and photosensitization with regard to the metabolic rate varied (Tables 1, 2, 3, 4). The variations in the thermal sensitivity and photosensitization of fish from each

strain indicated their differing adaptive abilities to changes in water temperature and photoperiod and resulted in different metabolic rate amplitude changes. Mitchell and Cech (1994) investigated the metabolic rates of striped bass, white bass, and their hybrids at selected water temperatures (15, 20, 25, and 30°C). They reported that the metabolic rate of each species increased as the water temperature rose, but different thermal sensitivities were only observed at 30°C. They also related some problems, including difficulties in handling the fish, the inability of some individuals to adapt to the cramped conditions of the respirometer, and difficulty in making direct comparisons owing to the differences in the average weight of each fish. Our results appear to differ because of differences in fish sizes, species, and respirometer system.

We found that the metabolic rates induced by the combined effects of water temperature and photoperiod differed by fish strain (Table 4). This suggests that the differences in the metabolic rates of the fish strains may contribute to the variation in growth rates among the JJ, JK, KK, and KJ strains. Jonassen et al. (2000) reported that the metabolic rates induced by changes in the photoperiod varied with water temperatures for the Atlantic halibut. They also suggested that the growth rates of halibut may be affected by metabolic rate changes due to the combined effects of water temperature and photoperiod. Peck et al. (2004) reported that differences in routine (non-feeding) metabolic rates contributed to differences in the growth rates among individual juvenile Atlantic cod and demonstrated that the daily rate of routine energy loss decreased with an increasing growth rate. Danzmann et al. (1987) also reported observed lower rates of routine energy loss (O₂ consumption) in juvenile rainbow trout, *Oncorhynchus mykiss* (Walbaum), in a fast-growing strain than in a slower-growing strain. According to our results, the JK strain exhibited the highest metabolic rates in our tests and has the possibility of a lower growth rate than the other strains. However, to confirm this, other variables including food consumption, assimilation efficiency, swimming activity, and genetic diversity, and whether or not they can be altered by differences in water temperatures and photoperiod cycles, require further study. Our results indicated that differences in metabolic rate can exist among individuals produced by selective breeding and intraspecific hybrids, due to the influences of environmental factors, including water temperature and photoperiod. Differences in fish produced by selection and breeding programs, with regard to physiological traits that influence energy acquisition, will probably have the most profound consequences on differences in growth rate, and should be addressed in future investigations.

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