Effect of Temperature on Oxygen Consumption of Juvenile Oval Squid *Sepioteuthis lessoniana*

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The effects of water temperature on oxygen consumption rate of the juvenile oval squid *Sepioteuthis lessoniana* ranging from 0.04 to 4.28 g in body weight were investigated individually by a water bottle method at 10, 15, 20, 25, and 30°C. Oxygen consumption rate in ml oxygen/indiv./h (R) increased linearly with increase of body weight in g (W) and was expressed as $R = aW^b \cdot C^T$ for all temperature conditions (T), where $a = 0.143$, $b = 0.929$, and $C = 1.069$ ($n = 202$). The correlation coefficient between R and T was 0.993, and Q_{10} showed 1.95 within the range of 10 and 30°C. The influence of temperature on the oxygen consumption was relatively constant in the young over 0.48 g up to 4.28 g at temperature levels under the present investigation. However, the effect of temperature upon oxygen consumption rates was larger in the younger squid reared at a temperature higher than 20°C. The metabolism of squid in the early stages before 0.199 g is assumed to be strongly affected by the differences of water temperature within the range of 15–25°C.

Key words: oxygen consumption, oval squid, *Sepioteuthis lessoniana*, water temperature, Q_{10}

Cephalopods are one of the most active animals among marine organisms¹⁾ and the oxygen uptake and environmental condition, such as water temperature, greatly affect their activities.²⁾ The neritic squid *Sepioteuthis lessoniana* has a broad geographical distribution in Japanese waters ranging from Hokkaido to Okinawa.³⁾ Around the coast of mainland Japan, this squid occurs in spring for spawning at about 15–17°C (water temperature) and the newborn generation grows quickly in the warm season at water temperatures up to 28°C.⁴⁾ The water temperature of their natural habitat is estimated to range from about 15°C to nearly 30°C and the basic metabolism may change associated with changes of water temperature. Water temperature has a major influence upon the basic energy budget of the squid, and as a result, it affects their feeding rate, growth and maturation.

In the last several years the culture method of squids has progressed remarkably,⁵⁾ greatly promoting research on the experimental biology and applied science of cephalopods. Especially, the culture technique of *S. lessoniana* has been firmly established in the recent years^{4–6)} and many studies on the feeding, growth and metabolism of this species have been conducted by rearing experiments.^{7–9)} In the present study the effect of temperature, within a range from 10°C to 30°C, on oxygen consumption of the hatchlings and juveniles of *S. lessoniana* was examined in an indoor aquarium.

Materials and Methods

Squids used for the present study were 202 hatchlings and juveniles ranging from 0.04 g to 4.0 g in wet body weight, which were reared from eggs in an indoor aquarium at about 25°C (ranging from 23°C to 26°C). Eggs were collected in the vicinity of the Kominato Marine Biological

Laboratory of the Tokyo University of Fisheries (now of Chiba University) on the west side of Uchiura Bay located in the middle of the Pacific coast of Boso Peninsula, central Honshu, Japan. Experimental animals were classified into 5 different weight classes, namely, 0.05 ± 0.08 , 0.19 ± 0.02 , 0.48 ± 0.05 , 1.53 ± 0.08 and 3.61 ± 0.31 , in mean wet body weight and SD (g), respectively, to estimate the effect of temperature on oxygen consumption in accordance with growth. All animals subjected to the experiment were in a post-digestive condition, in which they had been fed for the last time about 12 hours before each experimental incubation. To confirm the post-digestive condition of the squid, the empty condition of digestive organs such as the stomach and caecum was observed through the mantle, which is almost transparent when alive. The effect of temperature on oxygen consumption of the squid was investigated through a series of measurements. Squids initially reared at about 25°C were acclimated to the experimental temperature of 10, 15, 20, 25 and 30°C by lowering or elevating the temperature by 5°C in 10 hours from the preceding rearing temperature. After settlement of the experimental temperature, squids were kept at the respective experimental temperature for about 24 hours before experimental incubation.

Oxygen consumption of the squid was measured at each temperature class with a salinity of 32 in dark conditions, using the water bottle method^{7,10)} with an initial flow-through period of about 1 h for acclimation before the measurement. The animals were individually put into bottles of 100–1500 ml, depending on the size of squid. The incubation medium was the same sea water as the initial rearing, and was filtered (glassfibre filter Whatman GF/C) before use for the measurement. Experimental periods ranged from 1 to 4 hours to maintain an oxygen concentration of not less than about 2.5 ml/l at the end of the experi-

ment. The basis of this oxygen concentration was the value of dyspneic level of the dissolved oxygen concentration for the young oval squid (20 mm in mantle length) at 30°C, which is estimated to be 1.6 ml O₂/l (Segawa, unpublished). Bottles were settled in an incubator to keep the experimental temperature bias within $\pm 0.3^\circ\text{C}$. Dissolved oxygen was analyzed by Winkler's titration method.¹¹⁾ Immediately after each incubation, the dorsal mantle length (L) in mm and wet body weight (W) in g were measured on living animals.

Results

Oxygen consumption rates of individual *Sepioteuthis lessoniana* in ml O₂/indiv./h (R) increased linearly with an increase in wet body weight in g (W). They were expressed as $R = aW^b$, with the correlation coefficient, r , being over 0.994 in every temperature class (Table 1). The value of a was influenced by the change of temperature and increased linearly with increasing water temperature (T in $^\circ\text{C}$), and was expressed by the equation $a = 0.108 + 0.036T$, ($r = 0.979$). While b was nearly constant at 0.85 to 1.02 (Table 1), it showed a slightly decreasing tendency with increase of water temperature as expressed by the equation $b = 1.097 - 0.0075T$ ($r = -0.807$). This indicates that b is independent of temperature.

Concerning the effect of temperature in general, the oxygen consumption rate of the individual squid in each body weight class increased with increasing water temperature (Fig. 1, Table 2). Since the oxygen consumption rate (R) rose linearly with increases in both body weight (W) and temperature (T), R is expressed as follows: $R = 0.143W^{0.929} \cdot 1.069^T$ ($n = 202$, $r = 0.993$). Within the range from 10°C to 30°C, the value of Q_{10} is calculated as 1.95 from this equation.

An analysis of the effect of temperature on oxygen consumption according to squid growth revealed that the tem-

perature effect varied among different body weights (Fig. 1, Table 2). The oxygen consumption of the squid over 0.5 g in body weight increased linearly with increasing temperature from 10°C to 30°C. The influence of temperature was relatively great in the young reared at temperatures higher than 20°C (Fig. 1, Table 2), and the relationships between R and T were expressed as $R = 0.156 \cdot 1.0721^T$ ($r = 0.993$), $R = 0.176 \cdot 1.058^T$ ($r = 0.997$) and $R = 0.204 \cdot 1.048^T$ ($r = 0.995$) for 0.48 g, 1.53 g and 3.60 g mean body weight, respectively. Q_{10} calculated from these equations was 2.01, 1.76 and 1.60 for each weight class mentioned above.

Younger squid, 0.19 g in mean body weight, had a high temperature sensitivity which was shown as a relatively high Q_{10} (2.85–4.47) within the range from 15°C to 25°C (Table 3). This temperature range corresponds to the temperature in their natural habitat for the season. On the contrary, their sensitivity to temperature was shown as a low Q_{10} at lower and higher ranges of 10–15°C and 25–30°C (Fig. 1, Table 2). Especially, for animals of 0.2 g in body weight, the oxygen consumptions at 10 and 15°C were lower than those of any other weight class (Fig. 1, Table 2).

Fig. 1. Relationship between water temperature and oxygen consumption rate of oval squid *Sepioteuthis lessoniana*.

Table 1. The a and b values of the regression line in oxygen consumption rate (R , ml O₂/g wet body weight/h) to wet body weight (W , g), $R = aW^b$, for oval squid *Sepioteuthis lessoniana*

Temperature (°C)	W (g)	N	a	b	r
10	0.04–4.28	35	0.320	0.991	0.996
15	0.04–3.59	31	0.397	1.023	0.996
20	0.05–3.50	35	0.550	0.980	0.994
25	0.04–4.13	66	0.772	0.848	0.996
30	0.05–3.82	35	1.036	0.890	0.996

Table 2. Oxygen consumption rate of oval squid *Sepioteuthis lessoniana* measured at 5 different temperatures for 5 different weight classes

Wet body weight (mean $\pm$ SD in g)	Mantle length (mean $\pm$ SD in mm)	Oxygen consumption rate (mean $\pm$ SD in ml O ₂ /g/h)				
		Water temperature (°C)				
		10	15	20	25	30
0.05 $\pm$ 0.01	6.0 $\pm$ 0.6	0.35 $\pm$ 0.06	0.39 $\pm$ 0.05	0.56 $\pm$ 0.13	1.18 $\pm$ 0.15	1.39 $\pm$ 0.15
0.19 $\pm$ 0.02	9.9 $\pm$ 0.7	0.28 $\pm$ 0.04	0.33 $\pm$ 0.05	0.63 $\pm$ 0.10	1.07 $\pm$ 0.06	1.28 $\pm$ 0.15
0.48 $\pm$ 0.05	15.2 $\pm$ 1.0	0.34 $\pm$ 0.03	0.40 $\pm$ 0.05	0.63 $\pm$ 0.06	0.88 $\pm$ 0.15	1.30 $\pm$ 0.09
1.53 $\pm$ 0.08	23.4 $\pm$ 1.7	0.32 $\pm$ 0.02	0.40 $\pm$ 0.04	0.53 $\pm$ 0.04	0.75 $\pm$ 0.07	0.96 $\pm$ 0.08
3.60 $\pm$ 0.31	31.7 $\pm$ 1.6	0.33 $\pm$ 0.02	0.43 $\pm$ 0.04	0.51 $\pm$ 0.05	0.63 $\pm$ 0.10	0.86 $\pm$ 0.10

Table 3. Q_{10} in oxygen consumption rate of oval squid *Seioteuthis lessoniana* measured at 5 different water temperatures

Wet body weight (g) (mean $\pm$ SD)	Q_{10} values				
	10	Water temperature ($^{\circ}$ C)			30
		15	20	25	
0.05 $\pm$ 0.01	1.28	1.99	4.47	1.39	
0.19 $\pm$ 0.02	1.38	3.61	2.85	1.44	
0.48 $\pm$ 0.05	1.42	2.48	1.92	2.20	
1.53 $\pm$ 0.08	1.54	1.82	1.96	1.64	
3.61 $\pm$ 0.31	1.73	1.41	1.53	1.88	

Discussion

The effect of temperature on reaction rates in animals is approximately quantified by Q_{10} , which is the factor by which the reaction velocity increases for a rise of 10°C .¹²⁾ In most poikilotherms the metabolism rises or falls according to body temperature by about two and a half times per 10°C in the physiological range.¹³⁾ In some temperature-conforming animals the oxygen consumption gives Q_{10} between 1 and 2 over a limited range.¹²⁾ The resting or routine metabolism of squids increases continuously with increase of temperature. Q_{10} was calculated for several species of squids and octopuses, namely, 1.5 for *Loligo pealei* between 15 and 20°C ,¹⁴⁾ 2.7 for *L. opalescens* between 10 and 15°C ,¹⁵⁾ 5.6 for *Illex illecebrosus* between 8.3 and 18.2°C ,²⁾ 2.18 for *Octopus briareus* between 20 and 30°C ,¹⁶⁾ 2.14 for *O. cyanea* around 25°C ¹⁷⁾ and 2.1 for *O. vulgaris* between 11 and 21°C .¹⁸⁾ In the present study of 5 different mean body weight classes from 0.05 to 3.60 g, Q_{10} for *S. lessoniana* varied from 1.28 to 4.47 between two adjoining incubation temperatures with a 5°C interval from 10 to 30°C . Although the larger squid over about 0.5 g in body weight showed relatively constant Q_{10} between 1.42 and 2.48, Q_{10} of squids in early life stages of less than about 0.2 g in body weight widely varied from 1.28 to 4.47. This indicates that *S. lessoniana* is sensitive to environmental temperature in its early stages of life.

The rate of oxygen consumption (R) of *S. lessoniana* is almost directly proportional to the body weight of the squid (W) and can be expressed as $R = aW^b$. It is known that the exponent b for animals whose metabolic rate is directly proportional to body surface area is about 2/3. However, b for animals whose metabolic rate is proportional to body weight is 1.0.¹⁹⁾ In general, b for fishes is considered to be about 0.8 at 20°C .²⁰⁾ For cephalopods, b was reported to be 0.72–0.833 for *Octopus*,^{21,22)} 0.771–1.12 for *Sepia*,²³⁾ 0.473–1.275 for *Loligo*^{14,22)} and 0.87–1.252 for *Illex*.²⁾ The b for *S. lessoniana* in the present study ranged from 0.85 to 1.02, showing relatively high values but it was still within the range of the values of *Loligo* species previously reported. This indicates that the metabolism of this squid is almost proportional to body weight.

For *S. lessoniana*, two equations between the oxygen consumption rate (R) and body weight of a squid (W) with an inflection point at about 0.5 g in body weight were reported at 25°C , which were obtained by the same method as the present study. They were expressed as $R = 0.966W^{0.944}$ ($r = 0.991$) and $R = 0.807W^{0.813}$ ($r = 0.974$) for squid body weights ranging from 0.033 to 0.5 g and

from 0.5 to 7.16 g, respectively.⁸⁾ In the present study, there was no evidence of the presence of the inflection point at about 0.5 g in wet body weight found in the previous study.⁸⁾ Although no inflection point in the relationship between the oxygen consumption rate and body weight could be detected, it is probable that the effect of temperature may work in different way with body weight range.

During the juvenile period of about 10–25 mm in mantle length (at about 0.15–1.5 g in body weight), oval squids change abruptly in morphology and feeding behavior.^{4,9)} Indices of arm and tentacle lengths reach nearly those of adult squids. Their fins become elongated remarkably with growth within this period,⁴⁾ enabling attacks on food organisms. The diurnal pattern of feeding changes in this growth period from daytime feeding to all day feeding, with relatively higher activities in the dim light period,⁹⁾ which may reflect the activity of attacking of the squid. The daily food consumption rate also changes with growth up to a peak of 60–70% of body weight at about 0.5–1.0 g in body weight.⁷⁾ These changes in morphology and behavior with growth during the juvenile period from 0.15–1.5 g in body weight should be accompanied with a certain change in the basal metabolism of this squid. As a result, it is considered that R at these early stages of life tends to increase more rapidly with growth than at later stages.⁸⁾ Further, the present study suggests that the activity of squid in such early stages is strongly influenced by changes of water temperature.

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