

Effects of Water Temperature Changes on the Oxygen Consumption Rhythm in the Japanese eel, *Anguilla japonica*

Jong Wook Kim, Tae Won Lee¹⁾, IL Noh²⁾, Wan Soo Kim*

Marine Ecosystem & Conservation Research Division,

Korea Ocean Research & Development Institute, Seoul 425-600, Korea

¹⁾Department of Oceanography, Chungnam National University, Taejeon 305-764, Korea

²⁾Division of Marine Environment & Bioscience, Korea Maritime University, Busan 606-791, Korea

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Abstract

We investigated the effects of temperature changes on the oxygen consumption rhythm in Japanese eels, *Anguilla japonica*, using an automatic intermittent flow respirometer (AIFR). The endogenous rhythm of the oxygen consumption rate (OCR) in the eels ($n = 18$; 44-74 cm, 145-690 g), freshly collected by bag net from estuaries, was nearly synchronous with the tidal pattern of the estuarine collection site. The magnitude of mean OCR (mOCR) of eels showed variable range of 82.2 - 116.5 ml O₂ kg⁻¹ ww h⁻¹ under constant conditions. In case of increasing temperature from 25 to 38 °C, the OCR of eels exhibited a gradually increasing trend with a rhythmic pattern until 36 °C. Above 36 °C, the rhythms of the OCR dampened and the OCR decreased rapidly at around 36 - 37 °C. The OCR of the eels exhibited the maximum value at 38 °C, and then it sharply decreased. The results suggested that the critical thermal maximum (CTM) regarding the endogenous rhythms of the eels was at around 36 - 37 °C when water temperature increased at 0.5 °C/14 h following the acclimation at 25 °C. In case of decreasing temperature (0.5 °C/14 h) from 25 to 0 °C, the OCR of the eels displayed a abrupt decrease up to 23 °C, and between at 23 and 20 °C, there was an agitation which showed a slight increase in the OCR with a duration of 1-2 days. Below 9 °C, the OCR rhythm of the eels showed a constant state regardless of temperature decreasing. These results suggest that the Japanese eel has an upper incipient lethal temperature at 36 °C, with a lower thermal limit at 9 °C. The biochemical aspects of the eels influenced by water temperature need to be further studied.

Key Words : Japanese eel, *Anguilla japonica*, Oxygen consumption, Temperature, Critical thermal maximum, Rhythm

1. Introduction

As the eels migrate upstream or downstream, they remain in the estuary for a while in order to acclimate to environmental changes such as water temperature, salinity and tide. These environmental conditions exert a strong influence on fish behavior in the brackish water. The interaction of various

environmental factors makes the situation extremely complex (Tongioli et al., 1986). However, previous observations in the wild led us to believe that temperature may play a significant role in modulating and guiding the migration of glass eels (Gandolfi et al., 1984), elver (White and Knights, 1997) and silver eels (Okamura et al., 2002). In temperate species, including the Atlantic (*Anguilla anguilla* and *A. rostrata*) and New Zealand (*A. australis* and *A. dieffenbachii*) eels, decreasing water temperature is the onset of migration because the downstream run is mainly observed in autumn to winter when

*Corresponding author : Wan Soo Kim, Marine Ecosystem & Conservation Research Division, Korea Ocean Research & Development Institute, Seoul 425-600, Korea
Phone: +82-31-400-6204
E-mail: waskim@kordi.re.kr

water temperature decreases (Burnet, 1969; Cairns, 1941; Haro, 1991; Hivindstein, 1985; Pursiainen and Tulonen, 1986; Todd, 1981; Vøllestad et al., 1986; Westin and Nyman, 1979). These findings show the evidence of close relationship between water temperature and eels' migratory behavior.

The rhythmic patterns in fish behaviour and metabolic processes have been reported in relation to the tides (Gibson, 1992; Northcott et al., 1991a) and diel light conditions (Burrows et al., 1994; Kadri et al., 1997a, 1997b; Thetmeyer, 1997). The physiological rhythms of eels in the estuary also may exhibit endogenous circadian or circatidal patterns entrained to the diurnal and tidal cycle. The relationship between the endogenous rhythm and the environmental factors should be defined to understand physiological and behavioral aspects of this species. However, few data are available on the correlation between water temperature changes and metabolic activity rhythms in adult eels (Kim et al., 2002a).

The present study was conducted to examine the effects of water temperature changes on the metabolic activity in terms of oxygen consumption of the Japanese eels *Anguilla japonica* when exposed to different temperature regimes. We measured the oxygen consumption rate (OCR) rhythms of the eels at a constant temperature regime similar to those at the collection site. And then, we also analyzed the changes in the OCR rhythms of those eels exposed to gradually increasing and decreasing water temperature.

2. Materials and methods

Japanese eels, *A. japonica*, were collected in the Keum River (25 psu, 25°C), mid-western coast of Korea using the bag net on August - October, 2003 and 2004. The eels collected were transported immediately to the laboratory then kept continuously immersed in a holding tank (25 psu, 25°C) of 100 L

under the laboratory conditions (12 h light [L]: 12 h dark [D]). Fish were not fed during the holding time, because we needed to exclude any effect on oxygen consumption due to feeding and digestion. Measurements of the OCR were conducted in 18 experiments for 18 individuals under constant darkness (Table 1). After each trial, total body lengths and wet weights of the eels were measured.

Experiments were carried out for three different experimental regimes based on temperature. In experiment I, eels were exposed to a constant temperature of 25°C in order to observe the endogenous rhythm for four replicate experiments at time periods of 303 - 394 h. In experiment II, eels were exposed to an increasing temperature regime (25 → 38°C) in order to observe the response of the OCR with increasing water temperature. The OCRs were measured in six replicate experiments at time periods of 276 - 392 h. In experiment III, eels were exposed to a decreasing temperature regime (25 → 0°C) in order to observe the response of the OCR with decreasing water temperature. The OCRs were measured in eight replicate experiments at time periods of 494 to 781 h, using an automatic intermittent-flow-respirometer (AIFR : one system with two chambers).

The OCRs of a pair of individuals were monitored simultaneously by placing one eel in each Plexiglas incubator chamber in a semi-circulatory system. Bacteria were filtered out from the water used in the experiments by sterile membrane filters (with two Sartorius Capsule Filters, input-pore diameter 0.2 µm and output-pore diameter 0.07 µm). We measured the background oxygen consumption of bacteria by running blanks (i.e., samples without eels) throughout the experimental period. Oxygen levels in the 10-L experimental chamber were maintained between 85% and 95% of saturation to minimize any physiologic stress on the eels due to hypoxia. When the oxygen level dropped below the

predetermined limit (85%), the magnetic drive gear pump and 3-way actuator valve (TX 350-1 DA-1/2, Ilyoung, Seoul, Korea) automatically flushed the chamber with oxygen-saturated seawater from a 20-L storage tank until the selected oxygen level was reached. No measurements were taken during this flushing. After each experiment, the chamber was rinsed with oxygen-saturated water and the probe voltage was examined to ascertain whether it had deviated from the pre-experiment gauge voltage. The magnetic drive gear pump (MS-Z, Ismatec Sa, Switzerland) produced horizontal water flow rates of 517.5 ml min⁻¹. After calibrating the oxygen probe (15 µ PO₂, Eschweiler, Germany), data collection began and it was controlled throughout the experiment automatically by a computer. Measurements were taken in a BOD incubator (VS1203P5N Vison Co., Seoul, Korea) under constant darkness. The digital controlling unit recorded the oxygen level through a picoammeter every second. Mean OCR values (mOCR; averaged oxygen consumption rate over the duration of the experiment) for the test eels were calculated and displayed graphically at 90-second intervals. All data, including local and experimental time (seconds), temperature (°C), air pressure (hPa), oxygen consumption (ml O₂ h⁻¹), and

oxygen levels (%), were stored directly on a hard disk for future analysis. More detailed descriptions of AIFR, including the location of the probe and a schematic of the apparatus, are provided in Kim et al. (1996, 2002b).

The rhythmicity of OCRs was determined using a maximum entropy spectral analysis (MESA) of raw data transformed into 10-min lag intervals. The time series were analyzed for periodicity using MESA spectra following the procedures and algorithms described by Dowse and Ringo (1989). The OCR was analyzed using the weighted smooth curve procedure at 2% individual error. Locally weighted least squares error method (KaleidaGraphy custom program for Macintosh, Synergy Software, Essex Junction, VT, USA) was used to plot a best-fit smooth curve through the center of the data. The values of 2% and 5% individual error obtained from the repeated tests yielded the best-fit curve. Statistical values were computed for each batch from the data points measured (Table 1). Maximum entropy spectral analysis (MESA) was used to estimate the dominant periodicity peaks in the oxygen consumption time series. The values presented in this study are mean±SD.

Table 1. Summary of the experimental parameters used to measure the oxygen consumption rate (OCR) of adult Japanese eels, *Anguilla japonica*, under different temperature regimes at 25 psu

	Experiment I: constant temperature for adult eels	Experiment II: increasing temperature for adult eels	Experiment III: decreasing temperature for adult eels
Temperature (°C)	25	25 40	25 0
Oxygen saturation level (%)	85.5-94.8	85.3-96.8	85.1-95.7
Duration (h) of the experiments	303-394	276-392	494-781
Number of experiments (n)	4	6	8
Number of individuals (N)	4	6	8
Total Length (cm)	50.3±6.0	44.0±4.2	74.0±1.4
Weight (g)	200.0±28.3	145.0±7.1	690.0±14.1
Ranges of mean oxygen consumption (ml O ₂ kg ⁻¹ ww h ⁻¹)	82.2-116.5	21.2-417.3	6.9-42.7

Values are mean±SD

3. Results

3.1. Experiment I : Constant temperature similar to the collection site

The OCRs of the eels exhibited rhythmic patterns throughout the experiment under constant temperature ($25.0 \pm 0.1^\circ\text{C}$) and darkness (Fig. 1). The amplitudes of OCRs were highly variable, ranging from 13.5 to 170.3 $\text{ml O}_2 \text{ kg}^{-1} \text{ ww h}^{-1}$ and fitted to a weighted smooth curve of 2%. The mOCRs were $82.2 \pm 18.7 \text{ ml O}_2 \text{ kg}^{-1} \text{ ww h}^{-1}$. The OCR peaks did not exactly overlapped with the high tides. Instead, the OCR peaks lagged slightly behind the times of the high tides of the collection site (Fig. 1). Similar patterns of endogenous circadian and circatidal rhythmicity

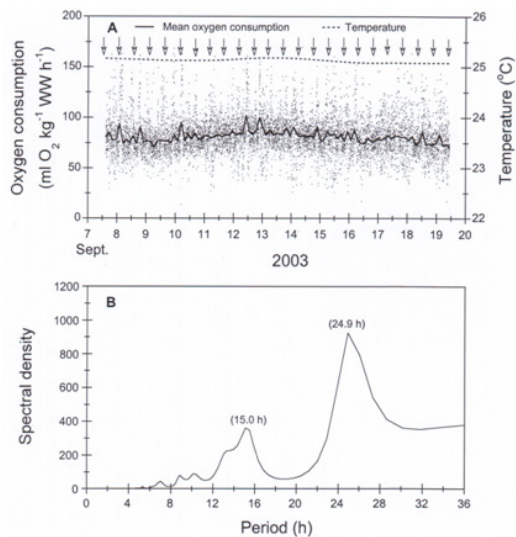


Fig. 1. The pattern of the oxygen consumption rate (OCR: $\text{ml O}_2 \text{ kg}^{-1} \text{ ww h}^{-1}$) by a Japanese eel, *Anguilla japonica*, over a 312 h period. The experiment was conducted in constant darkness at $25.0 \pm 0.1^\circ\text{C}$ and oxygen saturations of 85.5 to 94.8%. Arrows indicate the scheduled times of high tide at the location where the glass eels were collected. Maximum entropy spectral analysis (MESA) spectra of the data presented in Fig. 1. Period lengths (h) corresponding to the dominant peaks in the MESA plots are given in parentheses.

were observed in the other three replicates. The mean OCRs of the eels on four replicate experiments are shown in Table 1. Fig. 1B is a MESA plot of the data presented in Fig. 1A. During the 12 days (ca. 284 h) experiment, the OCR peaked at 24.9 h intervals, corresponding to the circadian rhythm. The instantaneous OCR also showed minor peaks at short intervals of 15.0 h.

3.2. Experiment II : Exposure to increasing water temperature (25 → 38°C)

The OCRs of the eels were measured at time periods of 276 - 467 h with increasing water temperature ($\Delta t = 0.5^\circ\text{C}/14 \text{ h}$). The observed mOCRs were highly variable, ranging from 21.2 to 417.3 $\text{ml O}_2 \text{ kg}^{-1} \text{ ww h}^{-1}$. The mOCR of a test eel exhibited a gradual increase with a rhythmic pattern up to around 36°C (Fig. 2). Above 36°C , the rhythms

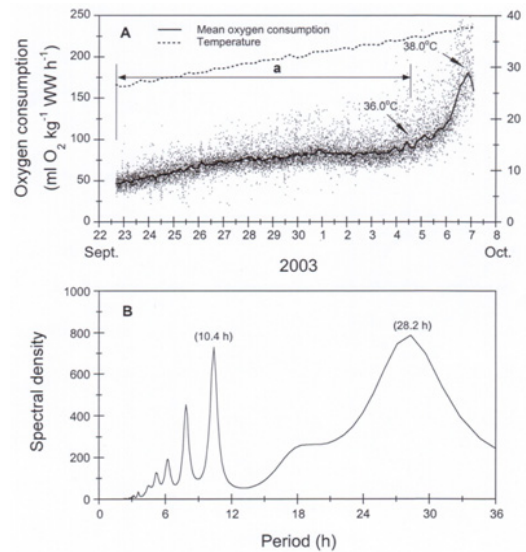


Fig. 2. The pattern of the oxygen consumption rate (OCR : $\text{ml O}_2 \text{ kg}^{-1} \text{ ww h}^{-1}$) by a Japanese eel, *Anguilla japonica*, which was subjected to a temperature increase from 25 to 38°C ($\Delta t = 0.5^\circ\text{C}/14 \text{ h}$), during 392 h period. Maximum entropy spectral analysis (MESA) spectra of the data presented in Fig.2A. Period lengths (h) corresponding to the dominant peaks in the MESA plots are given in parentheses.

of the OCR dampened and thereafter mOCR increased rapidly up to 38°C. The OCR of the eels exhibited a maximum value at 38°C and sharply decreased after that. Similar pattern of the OCR was observed in all the other five replicates. Fig. 2B is a MESA plot of the data presented in Fig. 2A. During the 312 h experiment, the OCR peaked at 28.2 h intervals, corresponding to the 14 h exposure cycles. The instantaneous OCR also showed minor peaks at short intervals of 10.4 h.

3.3. Experiment III : Exposure to decreasing water temperature (25 → 0°C)

The OCRs of the eels were measured at time periods of 494 - 781 h with decreasing water temperature ($\Delta t = 0.5^\circ\text{C}/14\text{ h}$). The observed mOCRs showed a range from 6.9 to 42.7 ml O₂ kg⁻¹ ww h⁻¹. The eight replicate experiments showed similar results and the

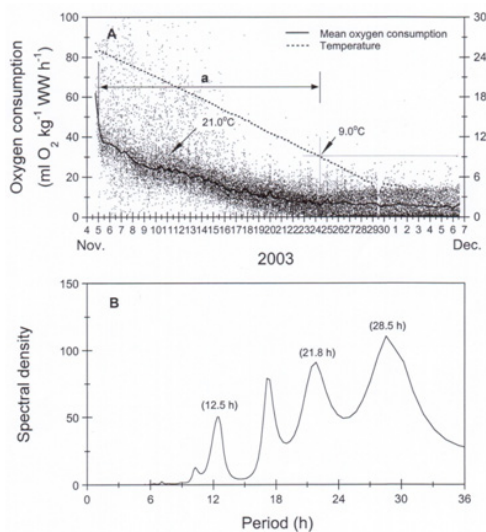


Fig. 3. The pattern of oxygen consumption rate (OCR: ml O₂ kg⁻¹ ww h⁻¹) by a Japanese eel, *Anguilla japonica*, which was subjected to a temperature decrease from 25 to 0°C ($\Delta t = 0.5^\circ\text{C}/14\text{ h}$), during 781 h period. Maximum entropy spectral analysis (MESA) spectra of the data presented in Fig.3A. Period lengths (h) corresponding to the dominant peaks in the MESA plots are given in parentheses.

magnitude of the OCR matched the decreased temperature in the experimental apparatus (Fig. 3A). The OCR of the eel displayed a abrupt decrease up to 23°C, and between 23 and 20°C, there was an agitation which showed a slight increase in the OCR with a duration of 1-2 days. Below 9°C, the OCR rhythm of the eel showed a constant state regardless of the temperature decreasing. Similar pattern of the OCR was observed in all the other seven replicates. Fig. 3B is a MESA plot of the data presented in Fig. 3A. The test eels showed a rhythmicity and OCR peaks corresponded to the temperature changes. During the 781 h experiment, the OCR peaked at 28.5 h intervals and showed minor peaks at short intervals of 12.5 h.

4. Discussion

We found that the metabolic activity of silver phase eels, *A. japonica*, was affected by environmental changes and adapted to the changes of extrinsic circumstances. The eels collected in the estuary were isolated from any external stimuli, such as light, temperature, food, salinity and tide, which might affect the rhythmic activity of the test animals. Nevertheless, the eels displayed the strong periodic respiration rhythms of 24.0 - 24.9 h and the weak ones of 10.6 - 15 h in OCR under constant darkness and temperature condition (Experiment I). This result suggests that the eels exhibit corresponding responses with the rhythmicity of the environment they live such as the sun and the tide. The mature eels in the river start their downstream migration to the river mouth and spend some time in the estuary before their entering the sea (Okamura et al. 2002). The eels in the estuary, already accustomed to a circadian rhythm simultaneously adapts to a circatidal rhythm entrained by tide. The fact that this rhythmic activity persists in the absence of any obvious exogenous influences suggests that it is

under the control of a biological clock (Wipplhauser and McCleave, 1988).

In the Experiment II (of increasing water temperature), the eels' OCRs paralleled upward with gradual increasing temperature ($\Delta t = 0.5^\circ\text{C}/14\text{ h}$) up to 36°C . Thereafter, the respiration rhythms of the eels were dampened at around $36 - 37^\circ\text{C}$ and showed a peak value at 38°C . These results suggest that the increase of water temperature significantly affects the rhythmicity of eels' OCR. By corollary, it can be thought that 36°C is the "upper incipient lethal temperature" (UILT) and the range of $36 - 37^\circ\text{C}$ is the "critical thermal maximum" (CTM) for the metabolic activity of Japanese eels. When the eels were exposed to 38°C , however, the metabolic activity rhythm was not recovered. It is believed that the dampening pattern of the OCR was great enough to affect the rhythmicity of the eels. It appears, therefore, that eels' exposure between 36 and 37°C causes severe physiological damage to the activity rhythmic pattern. When fish are exposed to very low or high temperatures, their metabolic activity is reduced or increased as a result of the severe physiological stress (Kim et al., 2003). Under these circumstances, the fish are expected to reduce their locomotion activity (Mehner and Wieser, 1994), swimming speed (Brett, 1971), acid-base regulation and/or osmotic balance (Reynolds and Casterlin, 1980), and growth rates (Jobling, 1988; Morgan, 1992). The CTM may also be affected by body size (Barrionuevo and Fernandes, 1995), each individual (Menasveta, 1981) and physiological conditions (Woiwode and Adelman, 1992) of the test animals. Eels are essentially a warm-water species showing optimal growth at $23 - 26^\circ\text{C}$ and ceasing to grow at around $13 - 15^\circ\text{C}$ (Tesch, 2003). Many technical developments in eel culture have been focused on control of water temperature, because eel growth is limited to optimal water temperature of this species (Tesch, 2003). The experiments were conducted

with a 14 h exposure period, which is not a common divisor of 12 or 24 h in order to examine the eels' OCR rhythmicity. The eel's OCR showed strong peaks at 28.2 h intervals, corresponding to the experimental exposure conditions ($\Delta t = 0.5^\circ\text{C}/14\text{ h}$). This result suggests that water temperature change surely affects the OCR of the eels with clear rhythmicity. It is reported that when the glass eels were exposed to a cyclic increase or decrease in water temperature ($1^\circ\text{C}/14\text{ h}$), the OCR peaks displayed a clear rhythmicity at 14 h intervals (Kim et al., 2002a). Therefore, our observation of eels' thermal limits which may affect physiological state and the survival of the eels, can offer a meaningful information for appropriation of optimal temperature in the eel culture.

In Experiment III (of decreasing temperature), the OCR of the test eel paralleled downward with gradual decreasing temperature ($\Delta t = 0.5^\circ\text{C}/14\text{ h}$) to 23°C , and showed temporary agitation at around $20 - 23^\circ\text{C}$. Thereafter, OCR continuously decreased up to $9 - 10^\circ\text{C}$. Lam (1982) speculated that water temperature is one of the major environmental factors regulating annual reproductive cycles of teleosts. Yamamoto and Yamauchi (1974) first produced eel larvae from artificially induced mature male and female Japanese eels in aquarium with temperature setting at 23°C . Tanaka (1998) observed the developmental processes of eel larvae with temperature setting at $22 - 23^\circ\text{C}$, and in the rearing experiments of eel larvae, he conducted the feeding trials with filtered seawater, temperature set at $21 - 22^\circ\text{C}$. In summary, many investigators usually set temperature regime at $21-23^\circ\text{C}$ for the experiments relating to the culture of eels. This temperature regime may fall within the optimal temperature range of the eels. Our observation of the agitation of OCR at $20-23^\circ\text{C}$ might be related to the intrinsic metabolic activity of the eels which prefer this temperature regime for their optimal growth (Tesch, 2003)

Meanwhile, Mehner and Wieser (1994) conducted long term measurements of the diurnal pattern of oxygen consumption in fasting juvenile perch at 15 and 20°C. They observed a fluctuation of the average rate of daily oxygen consumption which can be linked to a change in the major fuel for energy metabolism, and also observed that the sequence in the use of metabolic fuels depends on environmental temperature. A similar switch of metabolic fuels to lipids has been observed in the European eel, *A. anguilla* L. (Larsson and Lewander, 1973) and in the cod, *Gadus morhua* L. (Kamra, 1966). In the present study, the temporary agitation at 20 - 23°C may be caused by the changes of physiological processes due to the switch of metabolic fuels for reproduction and/or food deprivation. Since this study simply investigated the correlation between OCR and water temperature, related biochemical studies are needed to elucidate the relationship between the respiratory adaptation on the rate of change in temperature and metabolic activity.

Below 9°C, the OCR rhythm of the mature eel showed a constant state regardless of temperature decreasing. This result relates to the behavior of the eels. The eels usually remain in the estuary for some time before seaward migration, and they undergo various morphological and physiological changes. Long-distance migration for spawning may make the eels choose a certain temperature regime to save their energy. As the annual migration pattern of silver eel suggests, there may be a certain lower thermal limit (Tesch, 2003). During its vertical migration, the eel is exposed to a wide range of water temperature (13 - 22°C), which indicates that eels must have great thermal tolerance during oceanic migration. The swimming depths preferred by the eels are temperature dependent (Tesch, 2003). Tesch et al. (1991) observed that silver eels in the Baltic Sea preferred to swim above the thermocline, rather than encounter the cooler water below it.

The present study suggests that the constant respiration rhythm of OCR below 9°C relates to the migratory behavior of eels. As this temperature regime is extremely low to survive in the natural environment, eels are likely to move in a little higher temperature range than 9°C. Thus, we can conclude that the lower thermal limit of the migrating eels would be 9°C.

In summary, exposed at constant temperature of 25°C, the endogenous rhythm of the OCR in the eel was nearly synchronous with the tidal pattern of the collection site. In case of the experiment of temperature increasing, the OCR pattern paralleled with the temperature increasing, exhibiting upper incipient lethal temperature (UILT) at 36°C, with a critical thermal maximum (CTM) at around 36 - 37°C. In the experiment of decreasing temperature the OCR rhythm abruptly decreased from 25 up to 23°C, and thereafter it has an agitation at 23-20 °C, which we speculate this might be caused by the changes of physiological processes due to the switch of metabolic fuels for reproduction and/or food deprivation. The fact that below 9 °C the OCR rhythm of the eel showed a constant state regardless of temperature decreasing, relates to the migratory behavior of the eels. For migrating eels, 9°C would be a lower thermal limit. In other words, the eels would prefer to remain in water column having a temperature over 9°C during oceanic migration in order for them to save energy.

In order to clarify their behavioral characteristics, the biochemical aspects of eels influenced by water temperature changes should be further studied.

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