INTRODUCTION

The ability to maintain a relatively normal uptake of oxygen under conditions of low oxygen availability is important for organisms that may encounter low dissolved oxygen (hypoxia) frequently in their environment. In experimental conditions of declining dissolved oxygen (DO) concentration, mussel species vary in their ability to maintain oxygen consumption (OC) as the DO declines (Bayne, 1971a). Oxygen regulators can often be characterized by a critical dissolved oxygen (Pc) (Petersen and Petersen, 1990), above which the resting metabolic oxygen flux is relatively independent of oxygen availability. Below the Pc, regulation of oxygen flux fails (Bayne & Livingstone, 1977) and anaerobic metabolism, which is inefficient with respect to energy production may be activated in the tissues (Grieshaber et. al., 1988). The ability to regulate oxygen consumption (also called metabolic regulation) in water of reduced oxygen tension has been widely investigated for marine species of mussels from a range of different habitats (Brand & Roberts,1973; Taylor & Brand, 1975; Shumway & Koehn, 1982). Most of these studies concluded that the capability for metabolic regulation varies among species, and also varies with the environmental conditions, size, and physiological state of the animals.

The relationship between the capacity for metabolic regulation and respective habitats has been studied in some freshwater mussel species. Burky (1983) found that profundal sphaeriids, *Sphaerium simile* and *Pisidium casertanum*, are periodically exposed to hypoxia and are relatively oxygen independent (i.e., they have a low Pc). Lewis

(1984) also found that *Elliptio complanata* and *Anodonta grandis* (= *Pyganodon grandis*), inhabiting mud and sand in a small eutrophic Canadian lake, were exceptionally good oxygen regulators. In contrast, *C. fluminea* inhabiting only well-oxygenated habitats is a poor regulator (McMahon, 1983). McMahon (1991) suggested that species living in aquatic habitats periodically subjected to prolonged hypoxia are better able to regulate OC under declining dissolved oxygen conditions. However, the data are limited and no broad investigation of the Unionidae has been done, especially for species from riverine habitats.

The purpose of this study was to determine the ability of several unionid species from different habitats to regulate OC under declining DO. The resulting data can then be used in establishing DO water quality criteria for these species. As this study involved freshwater mussels often of limited availability, and included a state-listed species (*Elliptio lanceolata*), most experiments were non-invasive and the mussels were released to their collection sites after the experimentation.

MATERIALS AND METHODS

Mussels:

Adult specimens of 9 species of freshwater mussels were collected from various field locations. *Pyganodon grandis* (137.46 ± 11.48 g; ± SEM g, n=8 for the 24.5 °C measurements; 105.22 ± 9.06 g; ± SEM g, n=20 for the 16.5°C measurements) were

collected from Claytor Lake, Virginia. *Elliptio complanata* (38.37 ± 3.83 g; ± SEM g, n=17 for the 24.5 °C measurements; 64.92 ± 6.47 g; ± SEM g, n=12 for the 16.5 °C measurements), *Elliptio fisheriana* (14.09 ± 1.21 g; ± SEM g, n=10), and *Elliptio lanceolata* (10.09 ± 0.76 g; ± SEM g, n=20) were collected from pools of the Nottoway River, or sandy substratum and clay bank of the Rappahannock River, Virginia, respectively. *Villosa iris* (12.45 ± 0.93g; ± SEM g, n=20 for the 24.5°C measurements; 14.55 ± 1.10g; ± SEM g, n=16 for the 16.5°C measurement) and *Villosa constricta* (10.00 ± 3.92g; ± SEM g, n=19) were taken from riffles in the North Holston Fork River and Nottoway river, Virginia respectively. *Amblema plicata* (192.44 ± 8.23 g; ± SEM g, n=15), *Quadrula pustulosa* (156.7 ± 2.40 g; ± SEM g, n=22) and *Pleurobema cordatum* (210.04 ± 8.16 g; ± SEM g, n=16) were collected by diving in Kentucky Lake, lower Tennessee River, Tennessee. All of the mussels were acclimated in 30L aquaria with sand substratum and a flow-through, temperature-controlled (± 1 °C) system for one week before experiments were begun. A photoperiod of 12 light: 12 dark was used. The animals were fed a commercial algae diet (SUN Chlorella "A" granules by YSK international Corp., Japan) each morning at a concentration of approximately 60,000 cells/30L tank. Those animals to be used for measuring the OC rate were not fed in the morning, but were transferred to the respirometer chamber for acclimation.

Oxygen consumption:

Oxygen consumption was measured by placing single mussels in respirometer chambers equipped with an oxygen probe (YSI 5750) in the lid, a screen above the floor,

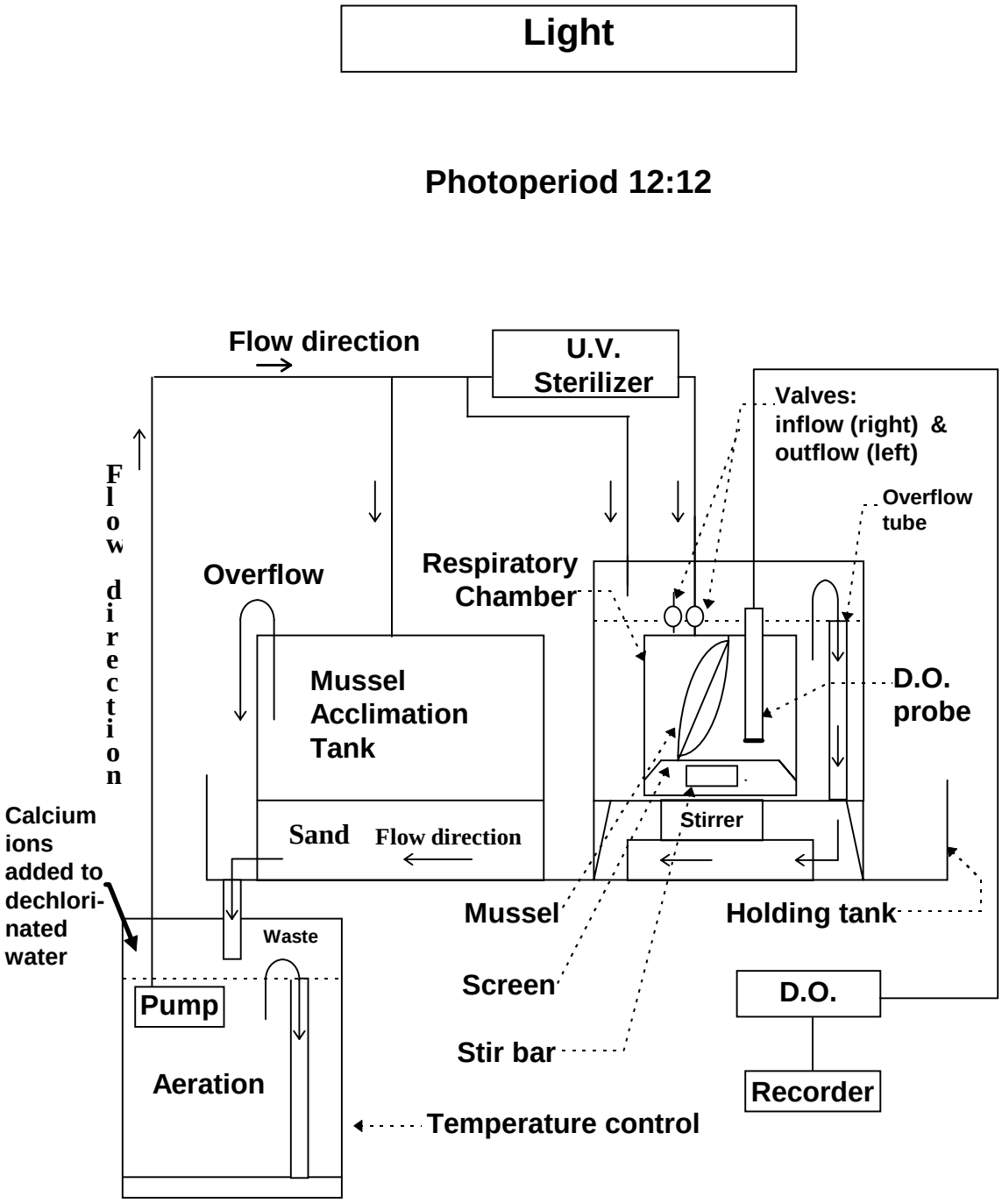

Fig. 1 Schematic design of the oxygen consumption apparatus for freshwater mussels.

and a magnetic stirring bar on the floor (Fig. 1).Water temperature was maintained at 24.5 °C. *Villosa iris*, *E. complanata*, and *P. grandis* were also monitored at a lower temperature (16.5 °C) from November to January. Animals were acclimated in the chamber for 3 hr before measurements began in the morning. In order to reduce microbial OC, the chamber was disinfected with boiling water between each experiment, and UV sterilized water continuously flowed through the chamber before the measurements began. An experimental run started with shutting off the flow, and then as the mussel consumed the oxygen in the chamber, the DO was recorded on a strip chart recorder. Different-sized chambers were used according to the size of the mussels, so that the duration of time to deplete the oxygen was more than 6 hr but less than 10 hr (except for the low temperature experiments) as the background OC tended to increase after 12 hr. The OC rate was expressed as mg O_2 kg^{-1} gross weight hr^{-1}. The background oxygen consumed by the probe and chamber also was measured and was usually ignored as it equaled less than 3% of the overall DO consumed by the mussels. After the mussels were exposed to declining DO, they were allowed to recover in the laboratory aquarium for at least one month to assess survival after this stress.

RESULTS

A. Villosa iris and Villosa constricta

The OC rate of *V. iris* (Fig. 2A) at 24.5 °C declined gradually as the DO declined,

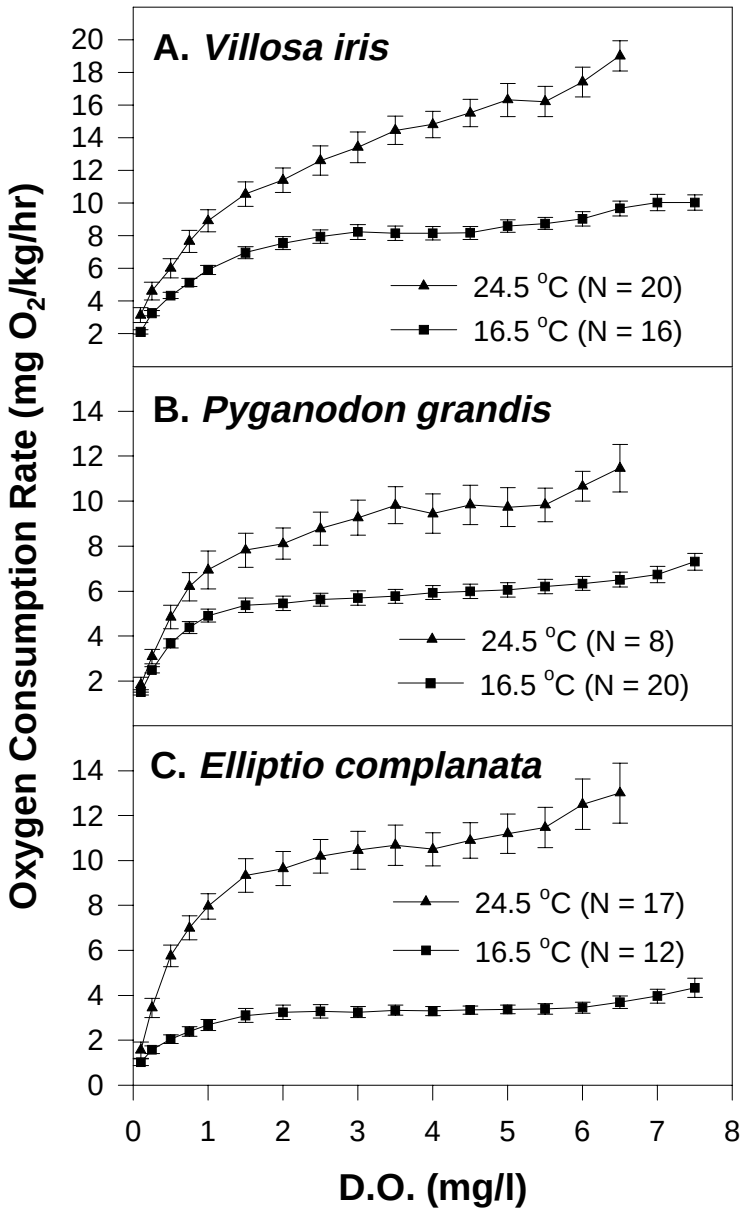

Fig. 2 The oxygen consumption rate of *V. iris*, *E. complanata*, and *P. grandis* under declining dissolved oxygen at 24.5 °C and 16.5 °C. Points are means ± 1 SEM.

which showed that they tend to be oxygen conformers. However, the ability to regulate the rate of OC of *V. iris* was much improved at 16.5 °C. The OC of *V. constricta* at 24.5 °C (Fig. 3A), on the other hand, behaved more like a regulator when DO ≥ 4 mg/l. In this species, the gross body weight of the males (12.07 ±1.38 g; ± SEM g, n=10) was significantly larger than that of brooding females (7.69 ±0.42 g; ± SEM g, n=9)(p=0.01), and males (Fig. 3B) seem to be better regulators than brooding females (Fig. 3C). The females also had significantly higher OC rates (21.3 ±1.64 mgO_2/kg/hr; ± SEM mgO_2/kg/hr, n=9) than males (16.9 ±1.10 mgO_2/kg/hr; ± SEM mgO_2/kg/hr, n=10) at DO = 5.5 mg/l (P=0.038) under normoxic conditions.

B. Elliptio complanata, Elliptio fisheriana and Elliptio lanceolata

The OC curves of three *Elliptio species* at 24.5 °C (Fig. 4) exhibit regulation when DO ≥ 1~2 mg/l, indicating that they are able to regulate better than *V. iris* and *V. constricta*. *E. complanata* at 16.5 °C (Fig. 2C) also behaved like a regulator.

C. Pyganodon grandis

The OC curve of *P. grandis* at 24.5 °C (Fig. 2B) is similar to that of *E. complanata* (Fig. 2C). They both respond like regulators when DO ≥ 1.5 mg/l. The overall rate of metabolism of *P. grandis* is reduced at 16.5 °C, and the ability to maintain OC in low DO was improved.

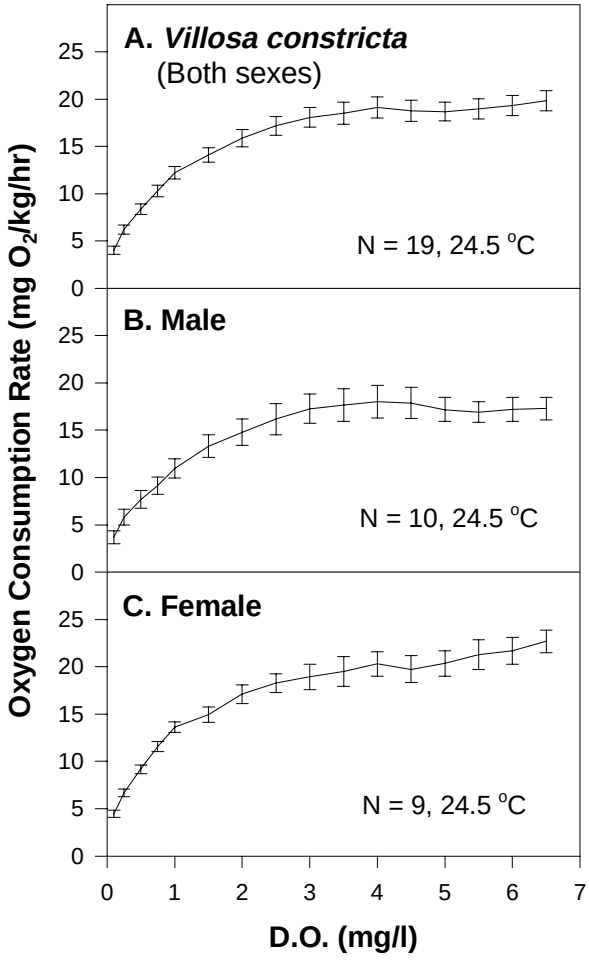

Fig. 3 The oxygen consumption rate of *Villosa constricta* under declining dissolved oxygen at 24.5 °C. The females have significantly higher oxygen consumption rates (21.3 ±1.64 mgO_2/kg/hr; ± SEM mgO_2/kg/hr, n=9) than males (16.9 ±1.10 mgO_2/kg/hr; ± SEM mgO_2/kg/hr, n=10) under normoxic conditions (i.e. at DO = 5.5 mg/l)(P=0.038). Points are means ± 1 SEM.

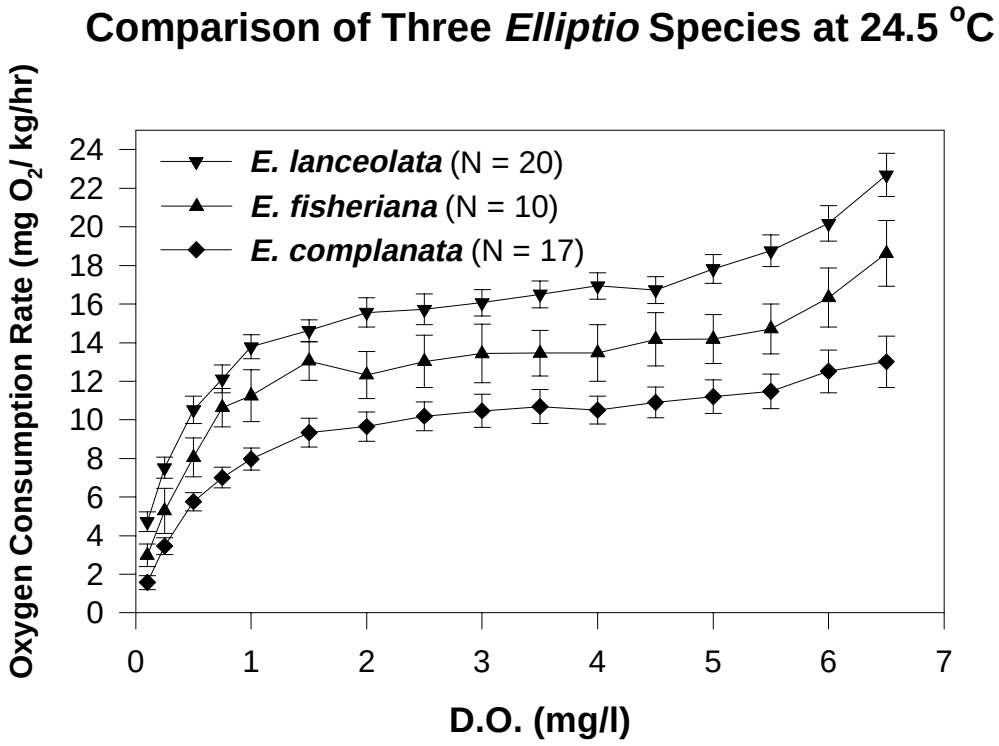

Fig. 4 The oxygen consumption rate of three *Elliptio* species under declining dissolved oxygen at 24.5 °C. Points are means ± 1 SEM.

D. Amblema plicata, Quadrula pustulosa and Pleurobema cordatum

The OC of *A. plicata* and *Q. pustulosa* under low DO at 24.5 °C (Fig. 5 A & B) is similar to that of *P. grandis*, in that they respond like regulators when DO ≥ 2.5 mg/l. *P. cordatum* (Fig. 5C), however, exhibited less ability to regulate OC than the other two species.

During one month recovery from the hypoxia stress, mussels were fed a per day. No mortalities occurred in *P. grandis, E. complanata, E. fisheriana, E. lanceolata, A. plicata* and *Q. pustulosa*. Two specimens of *V. constricta* and two of *P. cordatum* died. However, 50% of the *V. iris* died in the one month recovery period. At 16.5 °C, the tolerance of *V. iris* was much improved; no mortality occurred for several months after the experiment.

DISCUSSION

Oxygen consumption of bivalves is often calculated on the basis of the dry flesh weight. However, dry flesh weight requires sacrificing the specimen which I wanted to avoid in this study. It has also been found that the dry flesh mass can fluctuate by a factor of 2-3 over short time periods as gonad material is rapidly accumulated and then released (van Erkom Schurink and Griffiths, 1991), while the gross body or length is more stable. In a pilot study, a linear relationship between gross body weight and wet weight and dry weight was observed (r^2 = 90.3 and 88.6, respectively, n=22) for *E. complanata*; hence, the specific OC calculated by gross body weight reflects the relative values of that calculated

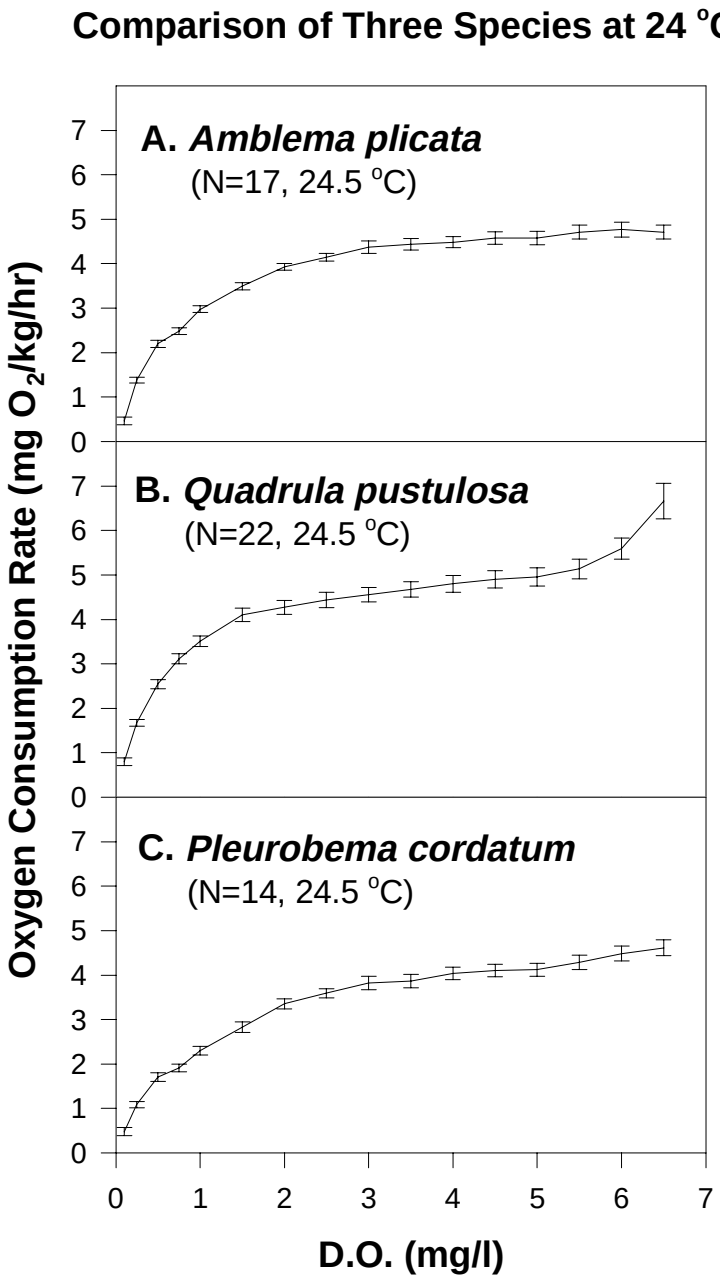

Fig.5 The oxygen consumption rate of *A. plicata*, *Q. pustulosa*, and *P. cordatum* under declining dissolved oxygen at 24.5 °C. Points are means ± 1 SEM.

by wet weight or dry weight. Furthermore, in this study we focused on the pattern of the OC rather than comparing the absolute values of specific OC among different species.

Ideally to compare the capacity to regulate OC in low DO, one could use Pc as an indicator. A good regulator would have a low Pc point. However, in many situations it is not possible to judge the Pc for a species, as the OC declines gradually instead of having a sharp turning point (e.g., Herreid, 1980). A number of different models have been used to describe the relationship between OC and DO (Mangum and Van Winkle, 1973; Bayne and Livingstone,1977). In lieu of being able to use Pc, the value K1/K2 taken from the hyperbolic model (Bayne, 1971a), $VO_2=PO_2/(K1+K2\times PO_2)$, has been used as an index of respiratory independence to oxygen content, where VO_2 is weight-specific OC rate and PO_2 is the oxygen partial pressure in water (DO may be substituted for PO_2). In this model, K1/K2 can be used as an index of respiratory independence of oxygen content (Fig. 6A). The lower the K1/K2 value, the greater the capacity to regulate OC, since VO_2 is more like a constant ($\cong$1/K2) under varying dissolved oxygen levels. Conversely, the higher the K1/K2 value, the smaller the capacity to regulate OC, since VO_2 is more dependent on DO ($\cong$ DO/K1). Hence, both the K1/K2 and Pc are useful for heuristic purposes; the smaller the value of each, the better the animal can regulate OC under hypoxia. The value of K2 can also be used as an index of OC in normoxic conditions. Since 1/K2 is the theoretical maximum rate of OC at high DO, a lower K2 means a higher rate of OC. The values of K1 and K2 are calculated from the regression of DO/ VO_2 and DO (Fig. 6B).

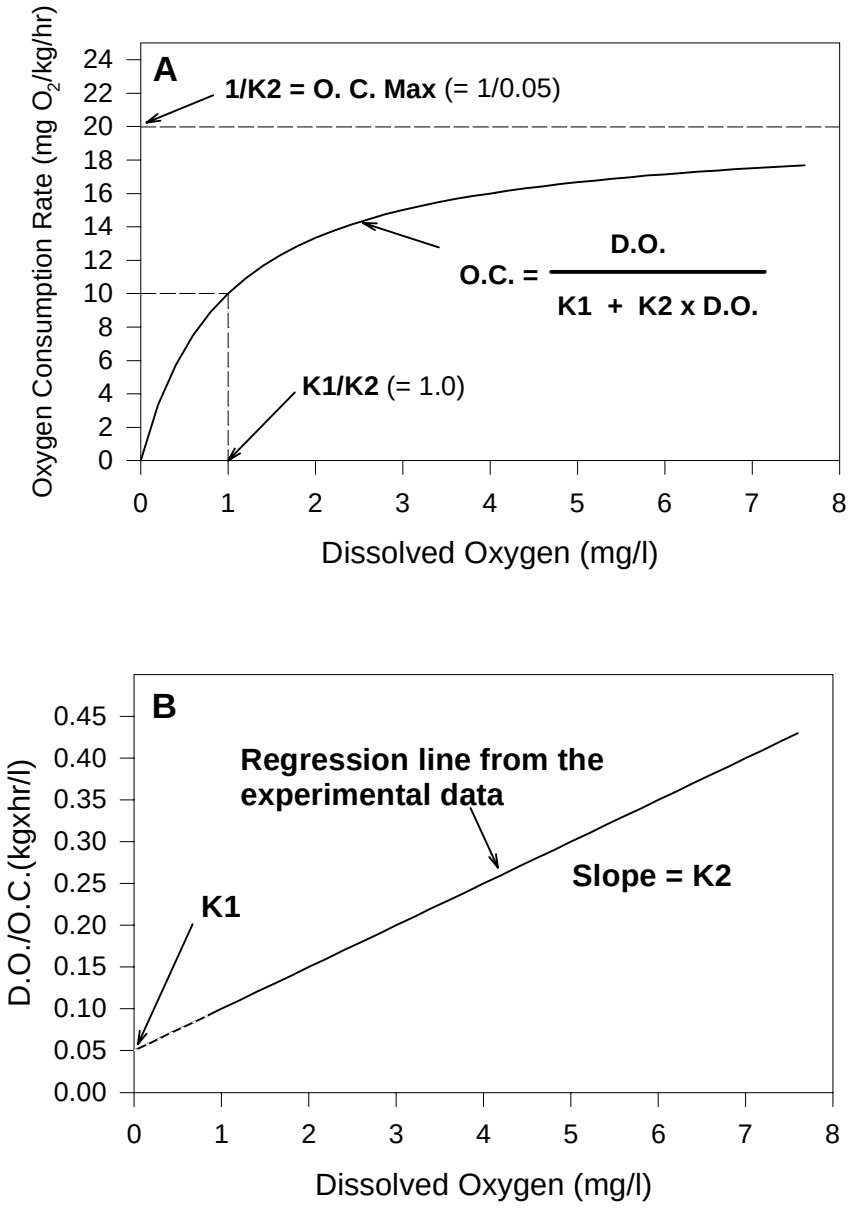

Fig. 6 The hyperbolic model for predicting oxygen consumption rate under declining dissolved oxygen (A) and the relationship between the dissolved oxygen and the quotient of dissolved oxygen and the weight-specific oxygen consumption (B).

From examination of the K1/K2 values of different species in this study, I found that the ability to regulate OC of adult mussels is seemingly correlated with their aquatic habitat type (Table 1). The *V. iris* and *V. constricta*, living in riffles, and *P. cordatum*, occurring in areas of moderate flow, have the poorest ability to regulate. *Pyganodon grandis, A. plicata, Q. pustulosa* and *E. complanata*, which live in lentic habitats and lotic areas where DO may be low during the summer, have a greater ability to regulate OC than *Villosa* species. The *E. fisheriana*, which lives in sand and is possibly exposed to hypoxia when burrowed deeply into the sand, has the greatest ability to regulate OC. Sheldon and Walker (1989) studied two Australian freshwater mussel species (Hyriidae) and found that the animals adapted to lotic environments showed little or no regulatory ability in low DO. My results agree with the suggestions of McMahon (1991) that species living in aquatic habitats periodically subjected to prolonged hypoxia have a greater ability to regulate OC under declining DO.

The effect of muscular activities on the Pc (and hence K1/K2) has been reported for crustaceans (Teal and Carey, 1967; Spoek, 1974; Taylor, 1976). In general, heightened activity raises the Pc. McMahon et al. (1974) noted that crayfish require many hours to settle down from handling, or they will behave as conformers. I observed a similar phenomenon. The mussels must be acclimated in the lab for two or more days and be adjusted to the chamber longer than 2 hr or they will behave as conformers. The acclimation period in the chamber cannot be too long (i.e., 12 hr), however, or the animal may close up and will not open until it is removed from the chamber.

TABLE 1- Summary of K1/K2 of different species and their habitats. K1 and K2 were obtained from the regression of the VO_2/D.O. to D.O., where K1 is the intercept and K2 is the slope. The VO_2 is the oxygen consumption per gross body weight. 12 observations (from D.O. 5.5 to 0.5 mg/l) were used for the regression of each species, r^2 (%) ranged from 98.8% to 99.9%.

Species	Temp. (°C)	Habitat	No. of Mussels	K2	K1/K2
A. plicata	24.5	mud, sand, or gravel of river[1]	19	0.186	0.771
E. complanata	24.5	pool or riffle of river[2]	17	0.080	0.568
	16.5		12	0.278	0.307
E. fisheriana	24.5	along bank of river[2]	10	0.065	0.407
E. lanceolata	24.5	sand bottom of river[2]	20	0.052	0.497
P. cordatum	24.5	medium to large rivers in sand or gravel with moderate flow[1]	14	0.194	1.152
P. grandis	24.5	profundal area of lake[2]	8	0.090	0.608
	16.5		20	0.153	0.377
Q. pustulosa	24.5	mud, sand, or gravel of medium to large river[1]	22	0.179	0.611
V. constricta	24.5	riffle area of river[2]	19	0.045	0.786
Male	24.5		10	0.049	0.760
Female	24.5		9	0.041	0.800
V. iris	24.5	riffle area of river[2]	20	0.050	1.310
	16.5		16	0.105	0.587

[1]Cummings & Mayer (1992).
[2]Neves (1995).

The ability to regulate OC was related to the physiological health of the mussels. In this study, *E. complanata* lost the ability to regulate OC after being kept in the lab aquarium for several months. Most of these mussels closed in the middle of the experiment before they could deplete the DO. The condition of these animals was poor, as indicated by increased water content in the body tissues and greater mortality.

Temperature is a key factor controlling tolerance of mussels to low oxygen, not only because DO declines as temperature increases, but because as poikilotherms, mussel metabolism is dependent on temperature. The amount of an increase in some physiological process over a 10 °C temperature rise is called the Q_{10}. At DO = 5.5 mg/l, where the OC of animals was stable, the Q_{10} of *V. iris*, *E. complanata*, and *P. grandis* was 2.26, 3.58 and 1.91, respectively. These are similar to the results of Polhill (1996), who reported an approximate Q_{10} of 2.6 for heart rate in *P. cataracta* and 1.9 for *U. imbecillis*. The high Q_{10} for *E. complanata* may be partly an artifact caused by the use of larger specimens in the study at 16.5 °C, than those tested at the higher temperature.

In the present study, *V. iris* had the poorest ability to regulate OC among the species tested. However, its ability to regulate increased when the temperature was lowered to 16.5 °C. At a low temperature, the 1/K2 (which can reflect the theoretical maximum of the OC) is reduced; hence, the improved ability to regulate OC (reduced K1/K2) at low DO could partly result from the reduced 1/K2.

Oxygen consumption of brooding female *V. constricta* was higher than that of males. These results are opposite to those found in *Pyganodon cataracta* (Tankersley et al. and Dimock, 1993). Tankersley (1992) proposed that brooding females have lower OC as a consequence of modifications of the hydrodynamics of water transport and circulation within the mantle cavity, reductions in the surface area of gill and mantle tissue available for oxygen exchange, and changes in feeding (filtration) rates resulting in nutritive stress and a decline in physiological condition. As all the females in our study were gravid with glochidia in their marsupial demibranchs, the respiratory mechanism of brooding *V. constricta* may be different from that of *P. cataracta*. In addition, the body size of male *V. constricta* was significantly larger than that of females, so the observed differences may be due to different body weight, as smaller animals have higher weight-specific OC.

Some studies have examined the mechanisms of respiratory regulation in mussels by investigating changes in oxygen consumption, oxygen utilization efficiency, mantle cavity ventilation, and heart activity during declining oxygen tension. Most of these investigations have concentrated on the marine mussel *Mytilus edulis* (Bayne, 1971b, Famme et al.,1981; Shick et al., 1986; Wang and Widdows, 1991) and other intertidal species (Mangum & Burnett, 1975; Booth & Mangum, 1978). Subtidal species such as *Arctica islandica* also have been investigated (Taylor & Brand, 1975). The results show that different species have various abilities to regulate OC by using different physiological mechanisms. For example, during hypoxia *A. islandica* achieved respiratory independence by increasing ventilation, while *Mytilus* increased the level of oxygen utilization when DO

was low. These different mechanisms are related to different patterns of pumping activity between subtidal and intertidal bivalves (Brand and Taylor, 1974). Other studies have examined the influence of reduced oxygen availability on freshwater bivalves (Burky, 1983; Burky et al., 1985; Hornbach, 1985; Hornbach, 1991; Massabuau et al., 1991). Different species have different strategies to regulate OC under declining oxygen content. For example, *Anodonta cygnea* maintains OC independent of ambient oxygen down to a low level by maintaining arterial blood PO_2 at low values, independent of oxygen partial pressure in the inspired water (Massabuau et al., 1991). In my study, I simultaneously measured the heart rate and OC in *P. grandis* (Appendix 1A and 1B) and found that these mussels increased heart rate to help maintain the OC before the DO reached a Pc.

If we assume that the Pc approximates the acute DO requirement of freshwater mussels, the DO at 24.5 °C for *A. plicata*, *Q. pustulosa*, and *E. complanata* should be kept higher than 2 to 3 mg/l to prevent latent mortality. For *P. cordatum*, DO should be above 3.5 to 4 mg/l, and for *V. iris*, DO should be higher than 6 mg/l to ensure that metabolic rate does not fall below standard metabolism. However, OC data do not provide a conservative DO criterion for holding freshwater mussels. When the heart rate and OC were simultaneously measured in *P. grandis* (Appendix 1A and 1B), specimens increased their heart rate before the DO reached the Pc. Therefore, if energy cost increased, the anaerobic metabolism may be activated at a DO above the Pc.

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