Marine Biology Letters, 3 (1982) 1–23
Elsevier Biomedical Press

Review

OXYGEN CONSUMPTION IN OYSTERS: AN OVERVIEW

SANDRA E. SHUMWAY

Department of Ecology and Evolution, State University of New York, Stony Brook, NY, 11794, U.S.A.

(Received and accepted 1 October 1981)

INTRODUCTION

Oysters are a commercially important species worldwide and they inhabit a wide range of habitats. Their environment is characterized by wide variations in physico-chemical conditions and, as has been found in other species of bivalve molluscs (mussels, Bayne, 1976; scallops, Vahl 1972, 1978) a change in virtually any environmental variable affects the respiratory function of oysters. To understand the physiological adaptation of a species it is necessary to know the limits of respiratory function since many features of aerobic metabolism can be studied indirectly by measurement of the rate of oxygen consumption by intact animals (Bayne et al., 1976). This paper reviews current knowledge of respiration in oysters, dealing particularly with the mechanism of uptake and the endogenous and exogenous factors known to affect the rate of oxygen consumption.

GAS EXCHANGE/CIRCULATION

There has been some conjecture regarding the primary site of gas exchange in oysters. The circulatory system of oysters, like other bivalves, is comprised of a heart, arteries, veins and open sinuses. There is no respiratory pigment and the open sinuses make it virtually impossible for the heart to generate sufficient pressure to maintain effective circulation of blood through the entire circulatory system. Oysters, however, are unique in that they also possess two accessory hearts on the cloacal chamber wall as well as pulsating vessels in the mantle. These accessory hearts, first described by Hopkins (1934a) function primarily in the movement of blood in the mantle and facilitate gaseous exchange. Hopkins (1934b, 1936) and Pederson (1947) believed the mantle to be the primary respiratory site while the gills

0165-859X/82/0000–0000/$ 02.75

pump food and oxygen bearing water. Galtsoff (1964) on the other hand stated (pp. 121 and 200) that exchange of gases takes place primarily in the gills and that the mantle has a role of lesser importance in respiration. He later stated (pp. 259 and 260) that the location of the accessory hearts confirms the idea that the mantle and cloacal wall play significant roles in oyster respiration.

Two recent studies on the role of hemolymph in bivalve respiration have indicated that internal convection of body fluids due to heart activity plays no measurable role in oxygen uptake. Booth and Mangum (1979) ligated the anterior aorta in *Modiolus demissus* and found that oxygen uptake decreased by only 10–15% and concluded that blood plays a limited role in supplying oxygen to tissues. Famme (1981), using artificially perfused mussels, concluded that perfusion of tissues due to heart activity has an insignificant respiratory function in *Mytilus edulis*.

While these two studies have shown that hemolymph convection due to the pumping of the heart may not be significant in respiration they have not clearly shown that the hemolymph circulation per se plays no role. For animals such as bivalve molluscs with an 'open' circulatory system, any fluid circulating between the ventilated surfaces and deeper seated tissues would seem to be important in respiration. This circulation of fluid need not necessarily be initiated by heart activity. Any muscular activity which results in a pressure difference will enhance circulation in the blood sinuses. In the case of oysters, with large surface areas of mantle and gill tissue, coupled with the possession of accessory hearts, it seems likely that the hemolymph may indeed play a role in oxygen supply to the tissues.

SPECIES/GENERIC DIFFERENCES

The available information on oxygen consumption in oysters at full oxygen tension is summarized in Table I. Comparison of previously reported results is difficult, mostly due to the wide range of experimental conditions. Galtsoff (1964) gave a critical review of several studies on oxygen uptake in oysters and, while it is not the intention of this paper to discredit previous studies, it should be pointed out that many of the previous studies were carried out under rather precarious conditions (see Table I). In many cases it is difficult or impossible to ascertain the exact temperature and salinity of acclimation and/or measurement. In addition, animal condition at the time of measurement is often not noted clearly. Many authors specified that they had starved their animals for 24 h prior to experiments, others starved them for 'several days', still others used oysters directly from the field. Certainly no author specified a long enough starvation period to indicate a measurement of 'basal' or 'standard' rate. With the exception of Newell et al. (1977) who specified 'routine rate', these previous investigations were measuring some unspecified aspect of the active/routine rate of oxygen uptake, again making comparisons difficult. One further hindrance to comparing results between experiments is the presentation of data in forms ranging from 'ml oxygen consumed per

ml of shell cavity' to more conventional units. Wherever possible, the data in Table I have been converted to a standard form, ml oxygen consumed $\cdot h^{-1} \cdot g$ dry weight^{-1}, so that comparisons may be made between and within species.

The reported rates of oxygen consumption all fall within a fairly narrow range with two noticable exceptions in the very low values reported by Sparck (1936) and Hammen (1979). Sparck's oysters were narcotized and it is possible that the oysters used by Hammen were responding to a sudden temperature shock (see Table I, Notes) by closing the shell valves and thus decreasing their rate of oxygen consumption.

The genus *Ostrea* is mainly an inhabitant of fully saline water and cold climates, whereas *Crassostrea* tends to be a warmer water group typically found in brackish and estuarine environments. Although other physiological functions such as ciliary activity of the gills, heart rate and spawning have been shown to differ between oyster genera (Menzel, 1955), no clear picture emerges regarding any differences in oxygen consumption rates between *Ostrea* spp. and *Crassostrea* spp.

BODY SIZE

Several authors (for reviews see Zeuthen, 1947, 1953; Von Bertlanffy, 1957; Hemmingsen, 1960) have discussed the relationship between animal body size and the rate of oxygen consumption. The relationship is usually expressed in the form of an allometric equation: $Y = aX^b$, where Y is oxygen consumption, X is body weight and a and b are the slope and intercept of the log Y vs. log X regression, respectively. Published b values for oysters are given in Table I. In the case of Mitchell (1914) regression lines were calculated from his original data. Reported values for the weight exponent in oysters range from 0.370 to 0.734 for *C. virginica* and from 0.658 to 1.090 in *O. edulis*. The biological significance of the b value is still not clear. The value of b is known to be affected by temperature, season and food level (Kruger, 1960; Newell and Roy, 1973; Widdows, 1978) or as Hemmingsen (1960) put it 'quite unknown reasons'. Kruger (1960) suggested that a minimum of a 50-fold size range of animals is needed to accurately estimate the value of b. The wide range of b values reported for oysters is undoubtedly due to the measurement of respiration over too small a size range of animals.

ACTIVITY

One of the primary endogenous factors affecting oxygen uptake in oysters is shell valve movement and any factor which affects the degree to which the shell valves are, or remain open will affect water flow and necessarily affect oxygen consumption rates. Galtsoff (1964) described 5 discrete types of shell movement (A–E) in *Crassostrea virginica*. Type A, characteristic of 'normal' movements of an undisturbed oyster in which a steady current of water is maintained; Types B, C,

TABLE I

A summary of the available data on oxygen consumption in oysters.

Species	Weight range	Salinity (‰)	Temperature (°C)	*n*	*a*	*b*
Ostrea virginica (= *Crassostrea*)	42–262 g whole wt		19.5–20	9	0.763	0.438
			26–26.5	9	1.126	0.576
C. virginica	1.019–2.080 g dry tissue	30–31	24.5	41		
C. virginica	~3 in. animals (shell cavity 36 ml)					
C. virginica	100 g (total) (100 mm long, 70 mm wide)		25	6		
C. virginica	1.68–3.19 g dry wt	31.2–31.3	24–25	10		
C. virginica	0.1–100 g whole wt	35	10	37	0.171	0.734
			20	41	0.371	0.710
			30	45	0.423	0.603
C. virginica	mean wt. 18.6 g wet tissue	11.4	24	5		
C. virginica	0.02–0.9 g dry wt	28	10	175	0.094	0.601
			20	75	0.128	0.480
			30	76	0.271	0.449
		14	10	80	0.132	0.398
			20	83	0.292	0.482

Oxygen uptake (original units)	Method	Reference	Notes
decimilligrams $O_2 \cdot h^{-1} \cdot 100\ g^{-1}$	Winkler	Mitchell, 1914	Regression values calculated from Table II using equation 1 from Dame (1972) to calculate dry tissue wt. $r^2 = 0.945$; 0.958.
6.45–15.04 ml · h⁻¹ · 10 g⁻¹ 0.45–1.05 ml · h⁻¹ · g⁻¹ [a]	Winkler	Galstoff and Whipple, 1931	Animals kept on float in harbor at Woods Hole for 2 wk prior to use. Left in air overnight to assure opening.
~ 40 mg · h⁻¹ · animal⁻¹	Krogh syringe; Winkler	Collier, 1959	Used volume of shell cavity as standard of reference; uncontrolled temperature and salinity.
0.303 ± 0.083 ml · h⁻¹ · g wet wt⁻¹ 1.515 ml · h⁻¹ · g⁻¹ [a]		Hammen et al., 1962	Data supplied by P. Galstoff; no other details available.
3.97–7.29 mg · h⁻¹ 2.29–2.77 mg · h⁻¹ · g⁻¹ 1.60–1.90 ml · h⁻¹ · g⁻¹ [a]	Winkler	Galstoff, 1964	Data for $\dot{V}_{O_2}$/dry wt from Table 26.
μl · h⁻¹ · g⁻¹	Gilson (0.1–13 g total wt). Winkler (10–100 g wt)	Dame, 1972	Lines not significantly different for three temperatures. Fed animals starved 24 h prior to use.
1.83 μmol · h⁻¹ · g wet wt⁻¹ 0.206 ml · h⁻¹ · g⁻¹ [a]	Standard manometric methods	Hammen, 1979	Animals measured 1 day after capture; collected from and kept in SW at 10 °C. Reading represents an abrupt response to temp. shock, and probably explained low value (animal closed).
ml · h⁻¹	Oxygen electrode	Shumway and Koehn, 1982	Basal metabolic rates

[a]Converted values.

TABLE I (continued)

A summary of the available data on oxygen consumption in oysters.

Species	Weight range	Salinity (‰)	Temperature (°C)	*n*	*a*	*b*
			30	80	1.016	0.460
		7	10	63	0.173	0.375
			20	68	0.398	0.370
			30	73	0.759	0.410
C. gigas	4877–5145 cal. g^{-1}		5	3		
			10	3		
			15	3		
			20	3		
			25	3		
Ostrea edulis		sea water	~ 17	~ 10		
Gryphaea angulata			12	~ 10		
			25	~ 10		
O. edulus	~ 40–70 g whole wt	salt ponds	5 10 15 20 25			
O. edulis	adult (3–4 yr old)	32	~ 1 – 30	~ 200		
O. edulis	38–58 shell length	29.8	10–25	5/acclimation temperature		
			5–25 pooled	24	4.55	0.658
O. edulis	0.1 – ~ 3 g ash free dry wt	sea water	5 10 25	19 14 21	0.076 0.200 0.553	0.899 0.753 1.090
O. circumpicta Pils	286 g whole wt 38 g wet wt	sea water	22	1		

Oxygen uptake (original units)	Method	Reference	Notes
0.002 ml · h^{-1} · g wet wt^{-1} 0.008 0.012 0.022 0.026 0.01–0.130 ml · h^{-1} · g^{-1} [a]	Krogh Syringe; Winkler	Bernard, 1974	
~ 30 ml · kg^{-1} · h^{-1} 0.03 ml · h^{-1} · g^{-1} [a] ~ 10 ml · kg^{-1} · h^{-1} ~ 38 ml · kg^{-1} · h^{-1}	Winkler	Spärck, 1936	Pre-exposed to experimental conditions 24–48 h; Narcotized animals with ethyl-urethane; 10 animals measured per container.
2 cc · 100 g total wt^{-1} · 24 h^{-1} 5 cc 10 cc 20 cc 30 cc	Winkler	Pederson, 1947	Animals wrapped in gauze; containers turned to mix H_2O; animals kept in filtered sea water a few days prior to use.
28–173 µl · h^{-1} · g wet wt^{-1} 0.14–0.865 ml · h^{-1} · g^{-1} [a]	Winkler	Gaarder and Eliassen, 1955	Starved 'several' days; animals wedged open with glass rod; 'animals made familiar with conditions of oxygen or temperature days before experiment'.
~ 26–195 µl · 285 mg^{-1} · h^{-1} ~ 0.091–0.684 ml · h^{-1} · g^{-1} [a]	Oxygen electrode	Newell et al., 1977	Measured routine rate $\dot{V}_{O_2}$
	Winkler	Rodhouse, 1978	Original equation in the form $Q = aw^{\circ b}$, where w = AFDW, and a-resp. in cal. · h^{-1} b values not significantly different. Animals acclimated for 6 days, starved 24 h prior to use.
0.186 vol. % · 24^{-1} 0.122 ml · h^{-1} · g^{-1} [a]	Van Slyke	Nozawa 1929	

and D, representing shell valve activity in response to increased temperature, irritating substances and poisons, respectively, and Type E, associated with spawning activity in female oysters. Galtsoff (op. cit.) pointed out that the fact that shell valves are open does not necessarily mean that the animal is ventilating its gills, although he found that in the majority of his observations the opening of the shell valves coincided with the maintenance of a steady cloacal current. He further stated, based on a substantial amount of data, that *C. virginica*, when left undisturbed, were open from 17 to 24 h per day. These findings are in agreement with Loosanoff and Nomejko (1946) who found that subtidal oysters remained open on average approximately 94% of the time with no evidence of tidal influence. More recently, Higgins (1980), in a detailed study of the effects of food availability on valve movements in juvenile *C. virginica,* has shown that oysters fed continuously remained open 94.3% of the time while unfed animals were only open 35.1% of the time. Further, under steady state conditions, temperature per se has no direct influence on the duration of shell valve opening, although a rapid change in temperature may have more pronounced effects on shell opening (Galtsoff, 1964).

Brown and his co-workers (Brown, 1954; Brown et al., 1956) reported that *C. virginica* possesses a persistent lunar cycle of activity. They stated that, while appearing to possess no overt rhythm of opening of the shell valves, oysters possess 'statistical rhythms of opening'. These findings were subsequently refuted by Enright (1965) who reanalyzed the original data and found no such rhythms.

The effects of shell valve activity on oxygen consumption rates have been noted by several authors. Mitchell (1914) found that the main cause of variability in his respiration studies on *C. virginica* was the degree to which the shell valves were open. Nozawa (1929) reported that opening and closing of the oyster (*O. circumpicta*) is irregular at normoxia but gave no data on the actual effects this has on oxygen uptake rates. Collier (1959) found that *C. virginica* showed three distinct phases of gape, each one characterized by a magnitude of pumping rate leading to variable rates of oxygen uptake. These phases of gape do not seem to correspond to the different types of activity noted by Galtsoff and are presumably all part of the activity included by Galtsoff under Type A activity in 'normal' animals. A decrease in oxygen consumption with partial closing of the shell valves was also shown by Galtsoff (1964) and attributed to a decrease in rate of water transport.

A further complication is the effect of environmental variables on the pumping rate itself. Loosanoff (1950) has shown that pumping rate is temperature dependent, increasing steadily from 8 to 16 °C and remaining relatively constant between 16 and 28 °C. A further increase in temperature resulted in an increased pumping rate. In addition, ciliary activity also plays a major role in the movement of water over the gill surfaces and consequently, any factor affecting the rate of ciliary movement will also affect the respiration rate. Several environmental factors have been shown to affect ciliary activity in oysters and these will be discussed in a later section.

Based on the few available studies on shell valve movement in oysters, one can

expect that in fed oysters under 'normal', undisturbed conditions the shell valves will be open the majority of the time and pumping will be continuous. Any study involving oyster respiration, however, should take shell valve activity, pumping rate and/or ciliary activity into account as potential variable components.

Shell valve activity, pumping rate and ciliary activity can physically restrict the amount of oxygen made available to the oysters. In addition, these activities, along with other physiological processes (e.g. feeding, digestion, excretion) are energetically costly and the level of activity will also affect rates of oxygen comsumption. It is possible, by measuring both active and standard rates of oxygen consumption, to calculate the amount of energy available for activity and other physiological processes. The difference between the active and standard rates of oxygen consumption is known as the scope for activity (see Fry, 1947) and provides an index not only of the energy available for activity (both mechanical and physiological) but of the possible saving of energy reserves which could be achieved through reduced activity.

The approximate scope for activity for both oysters in general and specifically for *C. virginica* are shown in Fig. 1. These lines were derived by calculating the mean $\dot{V}_{O_2}$ (active) at specific temperatures for all species of oysters where data is available (from Fig. 2) to provide an estimate of the active $\dot{V}_{O_2}$ for oysters in general (◇—◇; Fig. 1). Using the basal metabolic rates for *C. virginica* reported by Shumway and Koehn (1982) (□—□) and the active/routine rates for *C. virginica* reported by Dame (1972) (○—○) it is possible to calculate an approximate scope for activity for both oysters in general and specifically for *C. virginica*. This is an approximate calculation, especially for oysters as a group, but indicates that oysters have

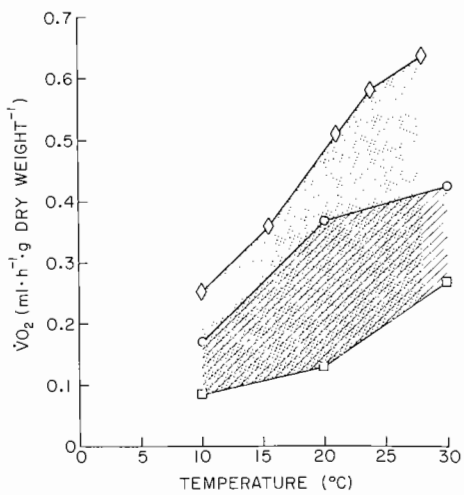

Fig. 1. The 'scope for activity' of oysters (stippled area) and *Crassostrea virginica* (slashed area). Data taken from Fig. 2; see text for explanation.

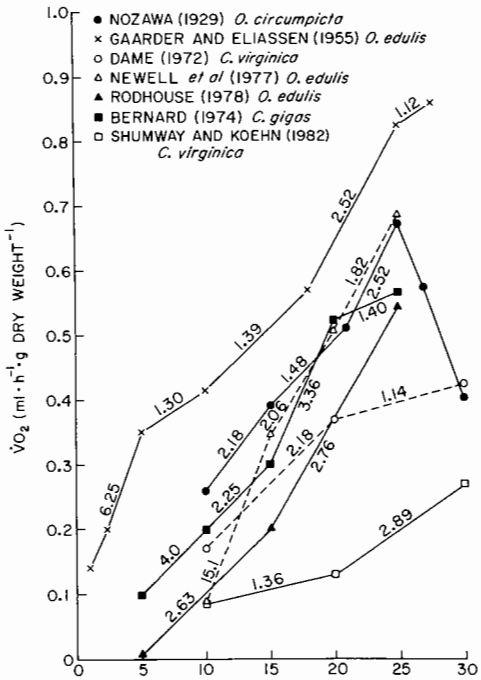

Fig. 2. A summary of the effect of temperature on the oxygen consumption rate of 4 species of oysters. Q_{10} values are indicated on the lines.

a considerable scope for activity over the normally experienced temperature range. It can also be seen that the energy saving at high temperatures is considerably higher than at low temperatures both for oysters as a group and for *C. virginica*, a feature likely to benefit intertidal organisms which are subject to elevated environmental temperatures during periods of limited food supply (Newell, 1979).

GENETIC COMPONENT

In addition to the well known endogenous factors affecting $\dot{V}_{O_2}$ already discussed, Koehn and Shumway (1982) have demonstrated a genetic component of respiration in *C. virginica*. They have shown that more heterozygous individuals have a lower basal metabolic rate than homozygous individuals. They have also demonstrated that the difference between homozygous and heterozygous individuals is amplified when the animals are faced with altered environmental conditions, the more heterozygous individuals being more physiologically homeostatic.

SALINITY

There is surprisingly little information available for the effects of temperature and/or salinity on oxygen consumption in whole oysters, though there is considerable data for individual tissues. While isolated tissues do not always exhibit the same metabolic response to environmental changes as intact animals (see King, 1965), it seems likely that some relationship should exist between the metabolic response of bivalve gills and intact animals since the gill is one of the primary sites of oxygen uptake.

Van Winkle (1968) found that oxygen consumption by *C. virginica* gills in the salinity range of 4–30 ‰ was relatively constant, with the exception of 'summer' animals which showed an increased $\dot{V}_{O_2}$ at 26 °C and 15–20 ‰. No explanation for this elevated rate was offered. The rate of oxygen uptake by oyster gills increased in dilute sea water, but that of adductor muscle declined and the mantle $\dot{V}_{O_2}$ was unaffected (Percy et al., 1971). In contrast, an increased rate of oxygen uptake of both oyster gills and mantle tissue in dilute (10 ‰) sea water was observed by Bass (1977), but no changes occurred in adductor muscle.

Only Galtsoff (1964) and Shumway and Koehn (1982) have reported the effects of salinity on oxygen uptake in whole oysters. Galtsoff found no significant change in respiration (active rate) of *C. virginica* after 3 days in dilute sea water; however, only a narrow salinity range (24.1–31.5 ‰) was studied. Although he reported that there was no significant difference, inspection of his data (Fig. 194, p. 211) indicates that for the oyster shown there is an elevated rate of oxygen uptake in dilute media. No information is given regarding the other 9 specimens examined. More recently, Shumway and Koehn (1982) have shown that the basal rate of oxygen consumption of *C. virginica* increased with decreasing salinity at 10 and 20 °C, results similar to those reported for isolated gill tissue (Percey et al., 1971; Bass, 1977). The maximum rate reported by Shumway and Koehn was seen at 30 °C and 14 ‰, corresponding to the rate reported for 'summer' oyster gills by Van Winkle (1968).

The cause for an increase in $\dot{V}_{O_2}$ at reduced salinity remains unclear. It is apparently not attributable, at least in oysters, to stimulated ciliary activity, as Vernberg et al. (1963) have shown that normal ciliary activity continues down to 12 ‰; further dilution causes inhibition of activity. Schleiper (1929) has suggested that the response in dilute sea water is a result of increased metabolic costs required to maintain an osmotic gradient between the interior and exterior of the cells. The amount of work involved in ion transport is only about 1% of the total energy budget (Potts and Parry, 1964). Since *C. virginica* is an osmotic conformer, it is unlikely that the energy demand of maintaining osmotic balance can account for the observed increases in oxygen consumption. A change in external salinity, however, will most likely cause some change in the ionic strength of the cells. Studies with crustacean gills (Munday and Thomson, 1962; King, 1965) have indicated that the observed increase in $\dot{V}_{O_2}$ in dilute media may be a consequence of active transport,

or the effects of osmotic swelling of mitochondria. The increased rate of oxygen consumption in dilute media of *C. virginica* is probably due to a combination of a salt buffering capacity of the intracellular organic molecules and the salt sensitivity of the respiratory enzymes as has been shown for the mussel, *M. edulis* (Lange, 1968).

TEMPERATURE

While there have been a multitude of studies of the effects of temperature on metabolic rate in marine invertebrates (for reviews see Kinne, 1971; Newell, 1979) little attention has been paid to oysters. Like salinity responses, the metabolic response to temperature change also varies between tissues. Van Winkle (1968) found that oxygen consumption of gill tissue in *C. virginica* was greater at higher temperatures than at lower ones but found no general pattern of acclimation. In a series of season x experimental temperature interactions he reported cases of no adaptation, translation and rotation of the slope and position of the R–T curve (see Prosser, 1973 for discussion of acclimation patterns). Percy et al. (1971) measured oxygen uptake of gills, adductor muscle and mantle seasonally and reported reverse acclimation (Type 5 of Precht, 1958) in both gill and mantle tissue; however, adductor muscle showed no such acclimation. Bass (1977) also found acclimation responses to vary between individual oyster tissues. Again, gill tissue showed the greatest ability to compensate for temperature alterations while mantle tissue showed little compensatory ability and muscle none. While gill tissue exhibited a shift of the R–T curve to the left following cold acclimation and a shift to the right following warm acclimation, none of the tissues showed a rotational change of the R–T curves to indicate the use of alternate enzymatic pathways in response to temperature change.

The metabolic response of intact oysters to temperature is not as well documented, nor do the results agree with those obtained from isolated tissues. Previous studies have shown that $\dot{V}_{O_2}$ in oysters (*O. circumpicta, O. edulis* and *C. virginica*) increases steadily from approximately 1 to 25 °C with maximum $\dot{V}_{O_2}$ occurring at approximately 25 °C and that below 5 °C and above 25 °C oxygen consumption decreases rapidly (Mitchell, 1914; Nozawa, 1929; Gaarder and Eliassen, 1955) (see Fig. 2). Dame (1972), Newell et al. (1977) and Shumway and Koehn (1982) indicate that $\dot{V}_{O_2}$ increases with increasing temperature for 5–30 °C with no evidence of a suppressed rate at 30 °C. Inspection of Fig. 2 shows that between 5 and 25 °C the slopes of the R–T curves for active/routine oxygen uptake differ little between *Ostrea* spp. and are all significantly greater than the slope of the R–T curve for both the standard and active rates of *Crassostrea* spp. This is possibly a reflection of the fact that *Ostrea* tends to be a genus of colder waters whereas *Crassostrea* is more commonly found in warmer climates, the cold water species showing a greater response to warmer temperatures than the warm water species.

It appears that intact oysters show no evidence of acclimation of the rate of oxygen consumption at different temperatures. In general, if acclimation has occurred, cold acclimated animals have a higher $\dot{V}_{O_2}$, and a lower Q_{10} at lower temperatures than warm acclimated animals which show the opposite effect at the same temperature. Newell et al. (1977) found no evidence of rotation or level change of the R–T curve for routine oxygen consumption in *O. edulis* even after 70 days acclimation, conforming to Type 4 of Precht or Pattern I of Prosser (1967, 1973). Shumway and Koehn (1982) measured basal rates of oxygen consumption in *C. virginica* acclimated to various temperatures for 3 wk and found that, depending on the temperature–salinity combinations used, the oysters showed partial (Precht Type 3) or no acclimation (Precht Type 4).

A lack of capacity adaptation means animals will have difficulty maintaining vital functions at a constant rate (level) when faced with increasing temperatures and with no evidence of capacity adaptation or acclimation, energy expenditure must also increase with environmental temperature. Newell and co-workers reported compensatory changes in filtration rate with increasing temperature in *O. edulis* as opposed to a reduction of energy losses from metabolism, as might be expected, but it remains to be seen whether similar compensation takes place in *C. virginica*.

What causes the depressed rate of oxygen consumption with decreased temperature and vice versa? Mitchell (1914) attributed the decrease above 25 °C to shell-valve closure, whereas Gaarder and Eliassen (1955) attributed the decrease at both high and low temperature to ciliary paralysis. Galtsoff (1964) suggested that there should be a correlation between the effect of temperature on ciliary motion of gill epithelium and $\dot{V}_{O_2}$ of whole animals. Ciliary activity of oyster gill has been shown to be highly temperature dependent (*C. virginica* and *O. equestris*, Menzel, 1946; *C. virginica*, Galtsoff, 1928a, b; Vernberg et al., 1963), as has pumping and filtration rate (*C. virginica*, Loosanoff, 1958; *O. edulis*, Walne, 1972; Newell et al., 1977), the amount of activity decreasing with decreasing temperature.

Galtsoff (1928a, b), however, found that below 5 °C no current was produced by *O.* (*Crassostrea*) *virginica* gills even though the cilia were beating and attributed the lack of current to impaired ciliary co-ordination on the gill surface. Menzel (1946) found no such lack of co-ordination but rather a gradual slowing a ciliary activity and eventually complete cessation. In intact animals, the decrease of ciliary activity will mean a decrease in pumping rate and a concommitant decrease in oxygen consumption due to a decrease in the amount of oxygenated sea water passing over the gills. While reduced ciliary activity on the gill surface and/or a reduced pumping rate certainly have a major effect on the amount of oxygen made available to the animal, they are not the cause of reduced $\dot{V}_{O_2}$ per se. Since the same response is elicited from individual tissues, depression of $\dot{V}_{O_2}$ of intact animals at low experimental temperatures cannot be solely attributed to ventilatory system breakdown at low temperature or to direct depressant action on metabolism by central nervous tissue. More likely, a modification of metabolism occurs at the

cellular level. The biochemical mechanisms for temperature acclimation at the cellular level have been extensively reviewed (see Somero and Hochachka, 1976) and will not be dealt with here.

DECLINING OXYGEN TENSION

Several authors have investigated the response of marine invertebrates to declining oxygen tension (see Newell, 1979; Herried, 1980 for reviews). Animals have been characterized as either oxygen conformers (i.e., $\dot{V}_{O_2}$ varies in direct proportion with P_{O_2}) or oxygen regulators (i.e., $\dot{V}_{O_2}$ is more or less independent of P_{O_2}). The point at which oxygen consumption ceases to be oxygen independent and becomes oxygen-dependent is known as the critical oxygen tension (P_c) and is not always easy to determine precisely. P_c is now known to vary between molluscan species or individuals with temperature and/or salinity (Bayne, 1971; Newell et al., 1977; Hawkins and Ultsch, 1979; Shumway, 1981; Shumway and Marsden, in press), body size (Bayne 1971, 1973; Taylor and Brand, 1975b; Shumway, 1981), ventilation rate (Bayne, 1971, 1973), likelihood of experiencing hypoxia (Bayne, 1973; Murdoch and Shumway, 1980) and 'degree of openness' (Famme, 1980). With the exception of Taylor and Brand (1975a, b), Bayne (1971, 1973) and Famme (1980), all of the above studies were carried out with gastropods. Data for bivalves are sparse.

A precise means of representing a species' or individual's oxyregulatory capabilities is essential if data are to be used for comparisons between and within species. Mangum and van Winkle (1973) proposed that oxygen consumption is related to declining oxygen tension as follows:

$$R = B_0 + B_1 P_{O_2} + B_2 (P_{O_2})^2,$$

where R is the weight specific oxygen consumption (ml $O_2 \cdot h^{-1} \cdot g$ dry wt^{-1}); P_{O_2} is the partial pressure of oxygen; B_0 is the minimum rate of oxygen uptake found at very low P_{O_2}; B_1 is the linear effect of P_{O_2} on R, and B_2 is the deviation from linearity of the effect of P_{O_2} on R. The equation uses standardized data, i.e. the initial value is expressed as 1.0 and subsequent values as fractions of 1.0. A strict oxyregulator (oxygen independent species) would then have $B_0 = 1$ and B_1 and B_2 would equal zero whereas a strict oxyconformer (oxygen dependent species) would have both B_0 and B_2 equal to 0 and $B_1 > 0$. Mangum and van Winkle (op. cit.) further suggested that the second order coefficient, B_2, could be used as an index of a species' ability to regulate its rate of oxygen uptake in declining oxygen tensions; the more negative the value of B_2, the more oxygen independent, i.e., the better the regulating capabilities of the animal.

Previous studies (Nozawa, 1929; Galtsoff and Whipple, 1931; Gaarder and Eliassen, 1955; Shumway and Koehn, 1982) indicate that oysters have remarkably

good capabilities for regulating $\dot{V}_{O_2}$ in declining oxygen tensions under otherwise normal conditions. It can be seen from Fig. 3 that P_c values differ significantly between species and it is interesting to note yet another generic difference in that *Crassostrea* shows better oxyregulatory ability than the two *Ostrea* species. P_c values for *O. circumpicta* and *O. edulis* are in the approximate regions of 50 and 85 mm Hg, respectively, whereas the P_c value for *C. virginica* is much lower at approximately 30 mm Hg. (Nozawa (1929) reported that $\dot{V}_{O_2}$ in *Ostrea circumpicta* was oxygen independent until the external P_{O_2} reached 0.1% of normal; however, plotting his original data yields the results presented in Fig. 3.) As discussed above, a more precise means of estimating P_c is by use of the quadratic coefficient. Table II gives the B_2 values for the data in Fig. 3 and points out clearly the differences between the species.

It has been shown that acclimation and exposure salinity and temperature modify the effects of external oxygen tension on $\dot{V}_{O_2}$ in *C. virginica* to varying degrees (see following section). The ecological significance of an animal's ability (or lack of it) to regulate oxygen uptake at reduced oxygen tension is not clear. It appears from studies on individual tissues, as well as intact animals, that no single explanation for the effect of environmental variables on $\dot{V}_{O_2}$ is possible in that temperature, salinity, and oxygen tension all interact simultaneously (Shumway and Koehn, 1982). McMahon and Russell-Hunter (1974, 1977) have shown that it is the microhabitat

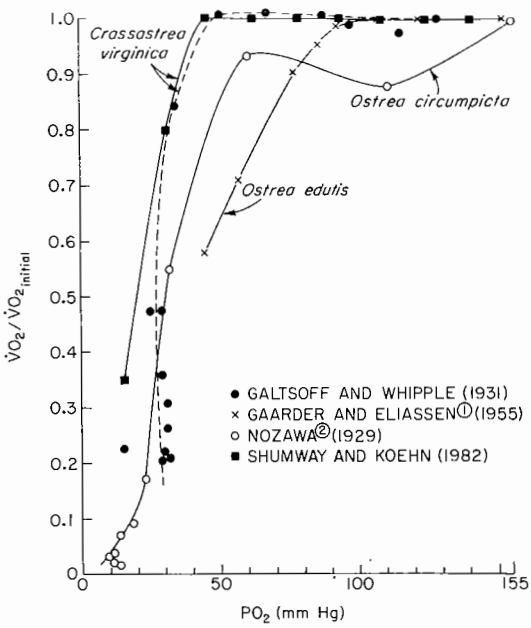

Fig. 3. The response of 3 species of oysters to declining oxygen tension. (1) Assuming oxygen saturation at 5.1 ml·l^{-1}; (2) assuming oxygen saturation at 5.5 ml·l^{-1}; (3) response at 20 °C, 28 ‰ salinity.

TABLE II

Values of B_0, B_1 and B_2 in the expression $\dot{V}_{O_2} = B_0 + B_1 P_{O_2} + B_2(P_{O_2})^2$ (r = correlation coefficient) for three species of oysters calculated from data in original publications. Data for *C. virginica* (Shumway and Koehn, 1982) for animals at 20 °C, 28 ‰.

Species	B_0	B_1	B_2 ($\times 10^3$)	r	Source
Ostrea circumpicta	−0.1638	0.0206	−0.0873	0.933	Nozawa (1929)
Ostrea edulis	−0.0472	0.0175	−0.0707	0.978	Gaarder and Eliassen (1955)
C. virginica	−0.3788	0.0317	−0.1684	0.760	Galtsoff and Whipple (1931)
C. virginica	+0.2500	0.0265	−0.2120	0.868	Shumway and Koehn (1982)

and physiological ecology of individual species which dictates its response to declining oxygen tensions and this appears to be the case for oysters as well.

It is clear, however, that it is advantageous for the oyster to be able to maintain aerobic respiration at normal rates for as long as possible when faced with continuously changing environments. Oysters may be subjected to long periods of aerial exposure resulting in short periods of feeding. Aerial respiration has not been reported in oysters, the lack of which probably results in uneconomical use of its stored food due to anaerobiosis. In addition, they will be subjected to considerable fluctuation in salinity, temperature and oxygen concentration. It is thus to the animal's benefit to be able to make maximum use of the available oxygen during submersion.

The mechanisms for $\dot{V}_{O_2}$ regulation in marine bivalves during declining P_{O_2} have been studied by Van Dam (1935, 1954), Bayne (1971), Brand and Roberts (1973) and Famme (1981) and include changes in ventilation of gill surfaces and changes in the frequency of the heart beat; however, these mechanisms are still not clearly understood. Bayne (1971) found that, in regulating individuals of *M. edulis*, cardiac output during hypoxia increased whereas in conforming individuals it did not, implying some relationship between circulation of body fluids and oxygen supply to tissues. Booth and Mangum (1979) concluded that blood plays a limited role in supplying oxygen to tissues in *M. demissus* and Famme (1981) concludes that hemolymph circulation has no measurable influence on the rate of $\dot{V}_{O_2}$ in declining P_{O_2} in *M. edulis*. No such data are available for oysters.

In order for an animal to maintain a constant rate of oxygen uptake in declining oxygen tension Newell (1979) has suggested that a change in irrigatory rate and/or extraction efficiency is necessary. In *Arctica islandica* (Taylor and Brand, 1975a, b) and *Mytilus edulis* (Bayne et al., 1976) a move towards oxygen dependence has been demonstrated to coincide with a reduction in irrigation. It was thought (Galtsoff and Whipple, 1931) that in oysters, the dependence of oxygen consumption in P_{O_2} might be due to inhibition of ciliary activity of the gill and a consequent decrease in the rate of water flow over the gills. They showed that there was no significant difference in the rate of water flow at 0.69 and 5.45 $ml \cdot l^{-1} \cdot O_2^{-1}$ ($n = 89$;

approximately 19–152 mm Hg), i.e. as the oxygen tension decreases, the amount of water flowing through the oyster remains approximately the same. Several other workers (Gray, 1924; Nomura, 1932, 1933; Aiello, 1960; Usuki, 1962a, b), however, have shown that ciliary movement in oyster gills is highly sensitive to the lowering of P_{O_2}.

Van Winkle and Mangum (1975) pointed out that the primary determinant of a species' response to declining P_{O_2} is the path of oxygen permeation to aerobic tissues. Oysters have no respiratory pigment and the primary source of oxygen is probably across the entire body surface, primarily the gill epithelium and the mantle. Under normal conditions, the amount of oxygen in sea water will be far in excess of that needed to maintain a concentration gradient across the body surface, the organism should be able to maintain a constant $\dot{V}_{O_2}$. At the point where the available oxygen is no longer sufficient to supply the gill cells, i.e., environmental P_{O_2} is less than or equal to the internal P_{O_2} and diffusion is no longer possible, the ciliary activity will decrease, causing the irrigation rate to decrease and a shift toward oxygen dependence will occur. One possible explanation for the generic differences in P_c/B_2 values seen above is a difference in surface areas available for oxygen uptake between the two groups. It is known that *Ostrea* have large gill ostia whereas *Crassostrea* have small ones (Menzel, 1955) although relative numbers of ostia are not available. If this size difference results in a difference in gill surface area available, i.e. smaller ostia will result in a greater surface area than large ostia, this would explain the ability of *Crassostrea* to maintain a constant $\dot{V}_{O_2}$ over a wider range of P_{O_2} values.

Any external factor which effects the activity of the gill tissue, the irrigation rate or the degree to which the shell-valves remain open might be expected to affect the rate of oxygen uptake under conditions of declining P_{O_2}. Often environmental factors are affecting each of these responses simultaneously, again pointing out the need for whole animal studies as opposed to studies involving individual tissues, since as pointed out previously, the responses of individual tissues do not always reflect the response of the intact animal.

OTHER FACTORS

Galtsoff (1964) reported a significant decrease in $\dot{V}_{O_2}$ of *C. virginica* 1 mth after spawning and a generally depressed level of $\dot{V}_{O_2}$ during the cold season (October–April). He also noted that pH had a pronounced effect on $\dot{V}_{O_2}$; a pH of 6.5 caused a 50% decrease in $\dot{V}_{O_2}$ and a pH of 5.5 caused a 90% decrease. Van Winkle (1968) reported no significant differences between respiration rates for gill tissue from summer and winter acclimated *C. virginica,* whereas Percy *et al.* (1971) reported marked seasonal differences in the respiration rate between gill, mantle and adductor muscle. They reported that both gill and mantle tissues had lower rates of respiration in the autumn than in the summer while adductor muscle showed the

opposite response. In all tissues, the major part of the metabolic shift occurred during late August/early September. They showed that the autumnal depression of respiration rate in mantle and gill tissues was not solely attributable to non-respiring glycogen stores as might be suspected and suggested that the differences resulted from a modification of metabolism occuring at the cellular level.

MULTIFACTOR EFFECTS

The few studies already mentioned in which effects of environmental variation on whole oyster respiration were investigated have all taken the traditional experimental approach of varying one factor while holding others constant. Galtsoff (1964) recognized that the combined action of several factors produces a far greater effect than that caused by any single factor and the importance of the multifactor approach has been reemphasized by Kinne (1964, 1971) and Alderdice (1972). Yet, there are few studies dealing with the combined effects of the most prominent environmental variables: temperature, salinity and oxygen tension (Bayne, 1971; Newell et al., 1978; Hawkins and Ultsch, 1979; Shumway, 1981; Shumway and Marsden, in press). All of these studies demonstrated that environmental factors acting in consort yield different responses when compared with the same factors acting independently.

Buxton et al. (1981) studied the combined effects of exposure and acclimation temperatures on filtration, oxygen consumption and scope for growth in the oyster *Ostrea edulis*. They generated a series of multiple regression equations which indicated that both assimilated ration and oxygen consumption were controlled by complex interactions between exposure and acclimation temperatures rather than by a simple dependence on either variable. Based on these equations they were able to calculate the conditions for optimal growth in *O. edulis* and found that in addition to holding the oysters at temperatures between 15 and 20°C, short-term increases in temperatures up to 25°C might additionally enhance growth – a fact which would not be readily apparent from more conventional experimental approaches.

In a recent study, Shumway and Koehn (1982) investigated the combined effects of temperature, salinity and oxygen tension on oxygen uptake in *C. virginica* and demonstrated that *C. virginica* has an 'elastic' or euryplastic (Alderdice, 1972) physiology in that they are able to withstand a broad range of environmental variation. This is demonstrated in Fig. 4 which shows the wide range of temperature–salinity–oxygen combinations over which the oysters can utilize the available oxygen. They used multiple regression equations to provide a concise means of describing these relationships and concluded the following.

(1) As the acclimation salinity decreases, the effect of exposure temperature becomes more pronounced.
(2) As the acclimation salinity decreases, the effect of exposure salinity decreases.
(3) As the acclimation temperature increases, the effect of exposure salinity decreases.

(4) As acclimation temperature increases, the effect of exposure temperature increases.
(5) There is little or no evidence for temperature acclimation in this species.
(6) The oyster shows a good ability to regulate its $\dot{V}_{O_2}$ when exposed to declining oxygen tensions at all temperature–salinity combinations tested although animals acclimated to low temperature/high salinity combinations are relatively better at $\dot{V}_{O_2}$ regulation. The degree of regulation decreases with increasing temperature and/or decreasing salinity.

CONCLUSIONS

A review of the available literature on oxygen consumption in oysters reveals that (1) respiration in oysters is a complex function affected by a number of endogenous and exogenous factors; (2) with respect to their respiratory physiology, oysters are

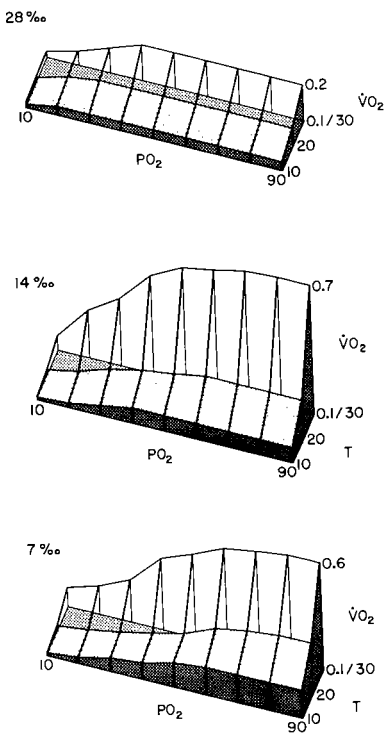

Fig. 4. A graphic representation of the combined effects of temperature, salinity and declining oxygen tension on the rate of oxygen consumption in *C. virginica*. From Shumway and Koehn (1982).

highly adapted to life in constantly fluctuating environments; and (3) there are differences between the genera *Crassostrea* and *Ostrea* (ranges of values for the weight exponent, *b*; responses to declining oxygen tension) which bear further investigation.

ACKNOWLEDGEMENTS

I wish to thank Drs. B.L. Bayne, R.C. Newell, R.I.E. Newell and R.K. Koehn for helpful discussions and encouragement. This research was supported by NSF grant DEB 7908862 and NIH GM 2113. This is a contribution from the Department of Ecology and Evolution, State University of New York, Stony Brook, N.Y. 11794.

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