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FACTORS AFFECTING OXYGEN CONSUMPTION IN THE COOT CLAM *MULINIA LATERALIS* (SAY)

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ABSTRACT

The effects of intrinsic (body size, gill surface area and activity patterns) and extrinsic (temperature, salinity and oxygen concentration and food) factors on oxygen consumption were measured in the mactrid clam *Mulinia lateralis*. Both acclimated and acute rates of $\dot{V}O_2$ were measured under 9 salinity-temperature combinations and a model is presented which indicates that: 1) body size is the over-riding factor determining $\dot{V}O_2$, 2) acclimation temperature alone has no significant effect on either fed or starved animals 3) the interaction of acclimation temperature and salinity and exposure salinity is the strongest factor influencing $\dot{V}O_2$ after body size, 4) exposure conditions are more likely to determine energy levels of expenditure than acclimation conditions. Small individuals have a greater gill surface area per body weight than larger individuals. The degree of oxygen independence is dependent on both body size and on acclimation temperature and shows a slight increase after exposure to anoxic conditions.

Patterns of shell valve activity were altered and $\dot{V}O_2$ increased in response to algae, charcoal and algal extract.

There was no evidence of a complete temperature acclimation even after 3 weeks.

The scope for activity indicates that starved animals at high temperatures are at a greater energetic disadvantage than individuals at lower temperatures. Equations are presented for clearance/pumping rate, convection requirements and utilization efficiencies and indicate that metabolism increases faster in relation to body size than does pumping rate resulting in decreased net energy gain as the animals increase in size.

Survival of *M. lateralis* populations appears to be a combination of behavioural and physiological adaptations which allow successful exploitation of favourable conditions while at the same time leaving the animals vulnerable to long term stress conditions.

INTRODUCTION

The mud-dwelling bivalve, *Mulinia lateralis* is of considerable ecological significance (Calabrese 1970, Levinton 1970, Holland *et al.* 1977) and has been proposed as a useful species for genetic studies of shellfish (Calabrese 1969a). Rather surprisingly, however, relatively little is known of its general biology and physiology in relation to complex arrays of environmental and endogenous variances which impinge on the individual in the natural environment. One

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physiological parameter known to vary considerably both between and within molluscan populations is respiration rate and an understanding of physiological adaptation requires a knowledge of the limits of respiratory function (Bayne 1976). In bivalve molluscs, respiratory function may be affected by factors intrinsic to the particular species under study (e.g. body size, gill area, activity patterns) as well as by changes in virtually any environmental variable (e.g. temperature, salinity, oxygen concentration, food) (Bayne 1976, Vahl 1972, 1978, Shumway 1982, Shumway & Koehn 1982). Monitoring the effects of any one of these variables on a physiological function (i.e. oxygen uptake) does not provide a true picture of the species' response in the natural environment. While the alternative multi-factor approach has received considerable discussion in the literature (Kinne 1964, 1971, Alderdice 1972, Newell 1979), there remain few studies in which the combined effects of several environmental variables on physiological parameters have been investigated in molluscs (Widdows 1978a, b, Shumway 1981, Shumway & Marsden 1982, Shumway & Koehn 1982).

Although the question of distinguishing between the phenotypic and the genotypic basis for physiological variation has been recognized for many years (Prosser 1957, Bullock 1958) and genetic differences between bivalve populations have recently received considerable attention (Koehn 1981, Koehn *et al.* 1981), there is still little detailed evidence that observed genetic differences between bivalve populations are related to physiological variation.

It is the aim of the present study to present a detailed series of data on the filtration rate and associated energy expenditure, and to relate the physiological energetics of this highly opportunistic species (see also Shumway *et al.* 1983) to work on other bivalves as a baseline for use in subsequent physiological genetic studies of *M. lateralis*.

Much of this work would not have been possible without the continuous supply of animals and advice from Anne Ducharme and the technical assistance of T. Scott. L. Deaton provided assistance with field work and helpful discussions. D. Hickman assisted in measuring gill surface area, J. Davenport loaned the stress gauges and G. Dam provided technical advice. T. J. Hilbish provided helpful suggestions on feeding experiments. F. J. Rohlf, S. Ferson, D. Innes, D. Sampson and M. Hunter all provided statistical advice and computer services. This work has benefited greatly from discussions with the following people: L. Deaton, G. Lopez, J. Levinton, R. Malouf and R. Serrato and especially R. C. Newell. I thank them all for their time and interest. This work was funded by USPHS Grant #GM21133 to R. K. Koehn who provided laboratory facilities.

MATERIALS AND METHODS

Specimens of the coot clam *Mulinia lateralis* (Say) were collected from Port Jefferson Harbor, New York or supplied from the University of Delaware, Lewes, Delaware. They were maintained in the laboratory at various tempera-

tures and salinities and fed a mixture of *Thalassiosira maculata, Monochrysis lutheri* (Droop) and Tahitian *Isochrysis galbana* Parke daily. Other animals were maintained at various temperatures with no food for periods of up to 3 weeks.

To determine haemolymph osmolality, 8 μl blood samples were taken from clams previously acclimated to various seawater concentrations for 5 days. Samples were collected via capillary pipettes and measured immediately in a Wescor Vapor Pressure Osmometer.

Gill area was measured microscopically by 'floating' a demibranch on graph paper and determining total surface area directly in mm^2. Gill thickness, determined by measuring fixed sections, was found to be very small relative to the total surface area (range 0.025-0.1 mm) and was ignored in subsequent measurements for total surface area. Total surface area of the gills was determined by multiplying the surface area measured above by eight (four demibranchs, two sides each) and expressed as a function of tissue dry weight.

Oxygen consumption of individual clams was measured using either a Radiometer oxygen electrode in a closed system as described previously (Taylor & Brand 1975a, b, Shumway 1981, Shumway & Koehn 1982) or a Gilson differential respirometer. Unless it was the specific aim of the experiment to monitor response to declining oxygen tensions, the external PO_2 was not allowed to drop below approximately 80 % saturation. Tissue dry weights were determined by oven drying for 24 h at 60 °C. In all experiments, as wide a size range of clams as possible was utilized. All oxygen uptake data is expressed for a size range of individuals rather than for any one size.

In experiments to determine the effects of salinity on oxygen uptake, seawater collected from Blue Point Oysters Inc. (salinity approximately 28 ‰) was diluted with distilled water to give the appropriate salinity. Both fed and starved individuals were acclimated to a total of nine temperature/salinity combinations (see text). It was not possible to acclimate animals to the following conditions: 20 °C/7‰ (starved), 30 °C/14 ‰ (starved) and 30 °C/7 ‰ (fed and starved) either by direct transfer or by stepwise acclimation.

To determine the short-term or acute response to salinity/temperature combinations, the clams were transferred directly from the acclimation conditions to conditions of the experimental medium. Oxygen consumption was measured after 1 h in the experimental medium to ensure that the clams were open and pumping. It was found that the clams did not show any adverse effects of handling and opened up within minutes under most experimental conditions.

The effects of declining oxygen tension on oxygen uptake were determined by placing the clams in chambers and allowing them to deplete completely the existing oxygen supply. In some experiments the animals were then left under these anoxic conditions for 12 h after which the seawater was replaced with fresh, oxygenated seawater and the response to declining oxygen tension re-

measured. These data are presented in the form of quadratic equations:

$$R = B_0 + B_1 PO_2 + B_2 (PO_2)^2$$

where: R is the weight specific oxygen consumption; PO_2 is the partial pressure of oxygen; B_0 is the minimum rate of oxygen uptake found at very low PO_2; B_1 is the linear effect of PO_2 on R and B_2 is the deviation from linearity of the effect of PO_2 on R. The equation uses standardized data and according to Mangum & van Winkle (1973) the quadratic coefficient B_2 may be used as an index of a species' ability to regulate its oxygen consumption in declining oxygen tensions. The more negative the value of B_2, the more oxygen independent the animal.

Shell valve activity was measured via stress gauges attached to one shell valve with dental cement. Individual clams (approximately 10 mg dry wt.) were cemented by one valve to small pieces of slate and placed in glass bowls of aerated seawater. This facilitated viewing during the experiments. The changes in gauge resistances were displayed on a chart recorder (Djangmah *et al.* 1979) set at the 1 mV range. Activity was measured in the presence of various external stimuli over 24 h periods. Experiments were carried out in a constant temperature chamber at 20 °C.

Filtration (clearance) rates were monitored by means of a Coulter Counter Model B. Initial experiments indicated that there was no significant difference between the clearance rate measured in flow-through and static systems, thus subsequent measurements were made on animals in closed systems. Individual clams were placed in 50 ml beakers with suspensions of *T. pseudonana* (Hustedt) at a concentration of 10 000 cells · ml^{-1}. Clearance rate was calculated as follows (Coughlan 1969; see also Newell 1979):

$$m = \frac{M}{t} \cdot \log_e \frac{\text{conc}_0}{\text{conc}_t}$$

where m is the filtration rate of a single animal; t is the time interval, M is the volume of the suspension, conc_0 is the initial concentration at time zero and conc_t is the concentration after time t.

In a series of experiments to determine the duration of elevated rates of oxygen uptake after feeding, several food sources were used (*T. pseudonana*, *Platymonas suecica* Kylin, *M. lutheri*, and *I. galbana* Parke). Where inert material was needed, activated charcoal was used (also at 10 000 · ml^{-1}). Non-particulate food extract was prepared as described by Thompson & Bayne (1972). Marked clams (all approximately 10 mg dry tissue weight) previously starved for at least two weeks, were placed in individual chambers with each of the various food sources and oxygen consumption was measured periodically for a subsequent period of 3 weeks.

Modelling methods

Experiments with *Mulinia lateralis* yielded data for both long term acclimation and short term exposure to a number of environmental conditions leading to complex interactions between salinity, temperature, body weight and condition (fed or starved) of the animal.

Previous authors have used the stepwise regression method for modelling such data (Lough 1975, see also: Newell 1979, Buxton *et al.* 1981). The stepwise procedure involves the progressive addition of variables to the model after which all variables in the model are examined and any variable that does not produce an F-statistic significant at the entry level is deleted. Only after this check is made and necessary deletions made can another variable be added to this model. The stepwise process ends when no variable has an F-statistic significant at the entry level or when the variable to be added to the model is one just deleted from it.

Data from the present experiments were modelled using the maximum R^2 improvement technique (Goodnight 1979). Rather than settle on a single model, this method looks for the 'best' one-variable model, the 'best' two-variable models and so forth. The main difference between the stepwise technique and the maximum R^2 improvement method is that all switches are evaluated before any switch is made in the method. In the stepwise method, the 'worst' variable may be removed without consideration of what adding the 'best' remaining variable might accomplish.

The general model employed was:

$$Y = a + b_1T_1 + b_2T_2 + b_3S_1 .+ . b_4S_2 \ldots\ldots$$

Data were entered for both fed and starved individuals; the overall regression for fed animals included 887 data points and that for starved individuals 556 data points.

RESULTS AND DISCUSSION

The effects of body size on $\dot{V}O_2$

Both the acclimated and acute rates of oxygen consumption were measured in air saturated seawater at various temperature/salinity combinations using both fed and starved individuals (see Figs 1, 2, 3). The rate of oxygen uptake ($\dot{V}O_2$; $\mu l\ O_2 \cdot h^{-1}$) is related to body size (W; mg) by the equation $\dot{V}O_2 = aW^b$ and this relationship varies considerably between experimental conditions. Values for the weight exponent, b, ranged from 0.338-0.882 but there was no correlation between acclimation or exposure conditions and b values (see Table 1).

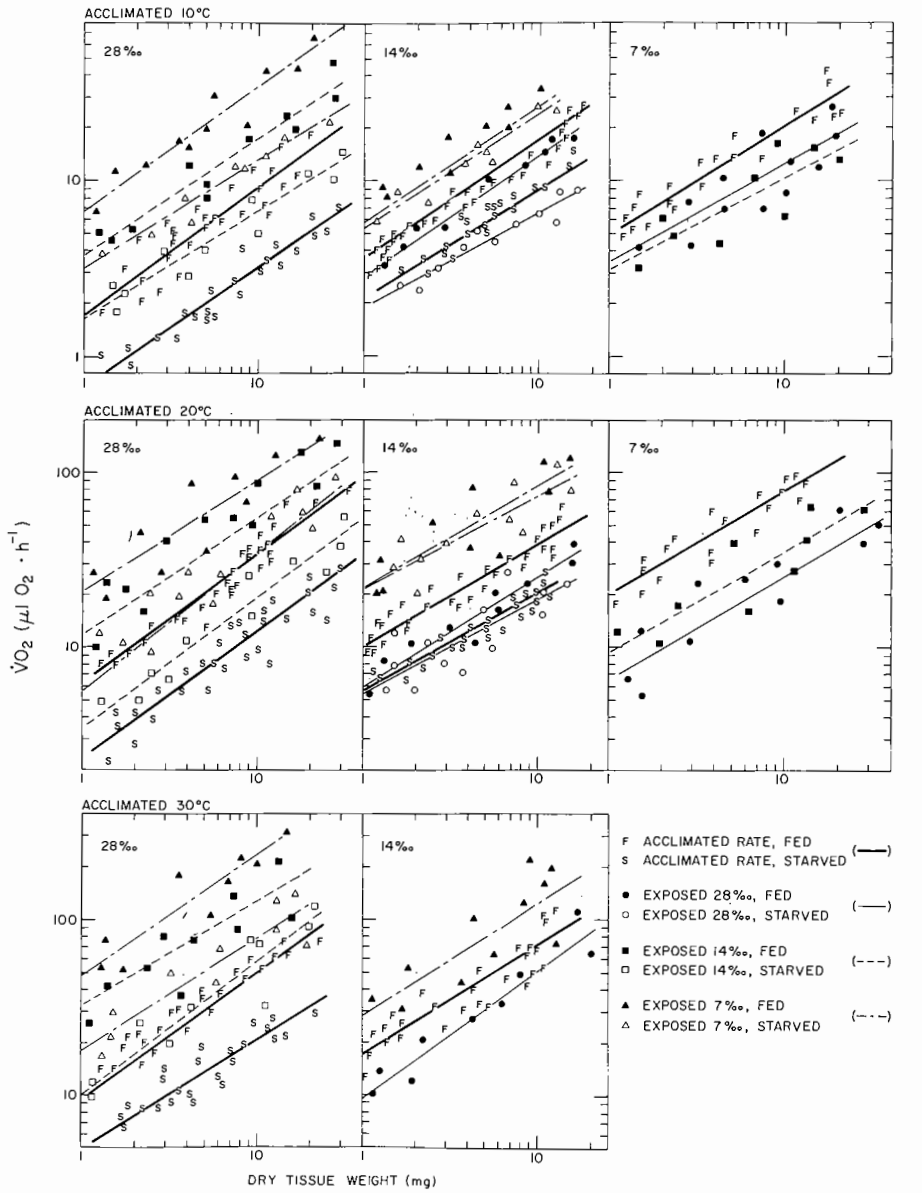

FIG. 1. The acute response to salinity change in *Mulinia lateralis* acclimated to different temperatures and salinities. Regression data are given in Table 1.

There have been any number of studies concerning the relationship between $\dot{V}O_2$ and body size (for reviews see Zeuthen 1947, 1953, vonBertalanffy 1957, Hemmingsen 1950, 1960) and many studies concerning this relationship in bivalve molluscs (see Bayne 1976, Newell 1979). The weight exponent, *b*, is

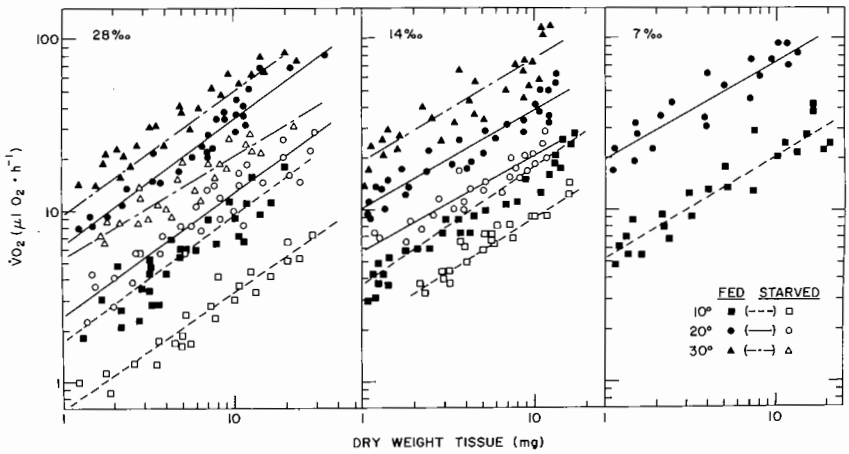

FIG. 2. Oxygen consumption rates after a 3 week acclimation period to various temperature/salinity combinations for both fed and starved *Mulinia lateralis*.

known to be affected by activity, temperature, salinity and ration level (Newell 1979, Zeuthen 1953, Krüger 1960, Newell & Roy 1973, Widdows 1978a,b). The weight exponent values in the present study were affected by temperature and salinity although not in any systematic fashion. Fed, acclimated animals had consistently higher b values than their starved counterparts; however, this trend was not evident upon exposure to abrupt changes in temperatures and salinities, and still no generalization can be made regarding the wide range in b values. While it is not uncommon to encounter a wide range of b values such as those reported here, it does point out the need to establish the exponent under the particular conditions being investigated rather than to assume the theoretical value of 0.67 or 0.73 (Zeuthen op. cit., Hemmingsen op. cit.) when correcting $\dot{V}O_2$ data for body size.

Gill surface area

The total gill surface area available for gas exchange (GA; mm^2) is related to dry body weight (W; mg) as the equation:

$$GA = 64.64\,W^{0.644} \quad (n = 20;\ r^2 = 0.884)$$

The gill in *M. lateralis*, as in other filter feeding bivalve molluscs, serves a dual function in feeding and in gas exchange. It has been stated previously that the ratio of respiratory surface to body weight is fairly constant between molluscan species, ranging from 8.66-9.3 $cm^2 \cdot g\,wet\ weight^{-1}$ (see Ghiretti 1966). Yonge (1947) gives estimates of 13.5 $cm^2 \cdot g\,wet\ tissue^{-1}$ for *M. edulis* and *Cardium echinatum* and Booth & Mangum (1978) reported a similar value of 13.9 for

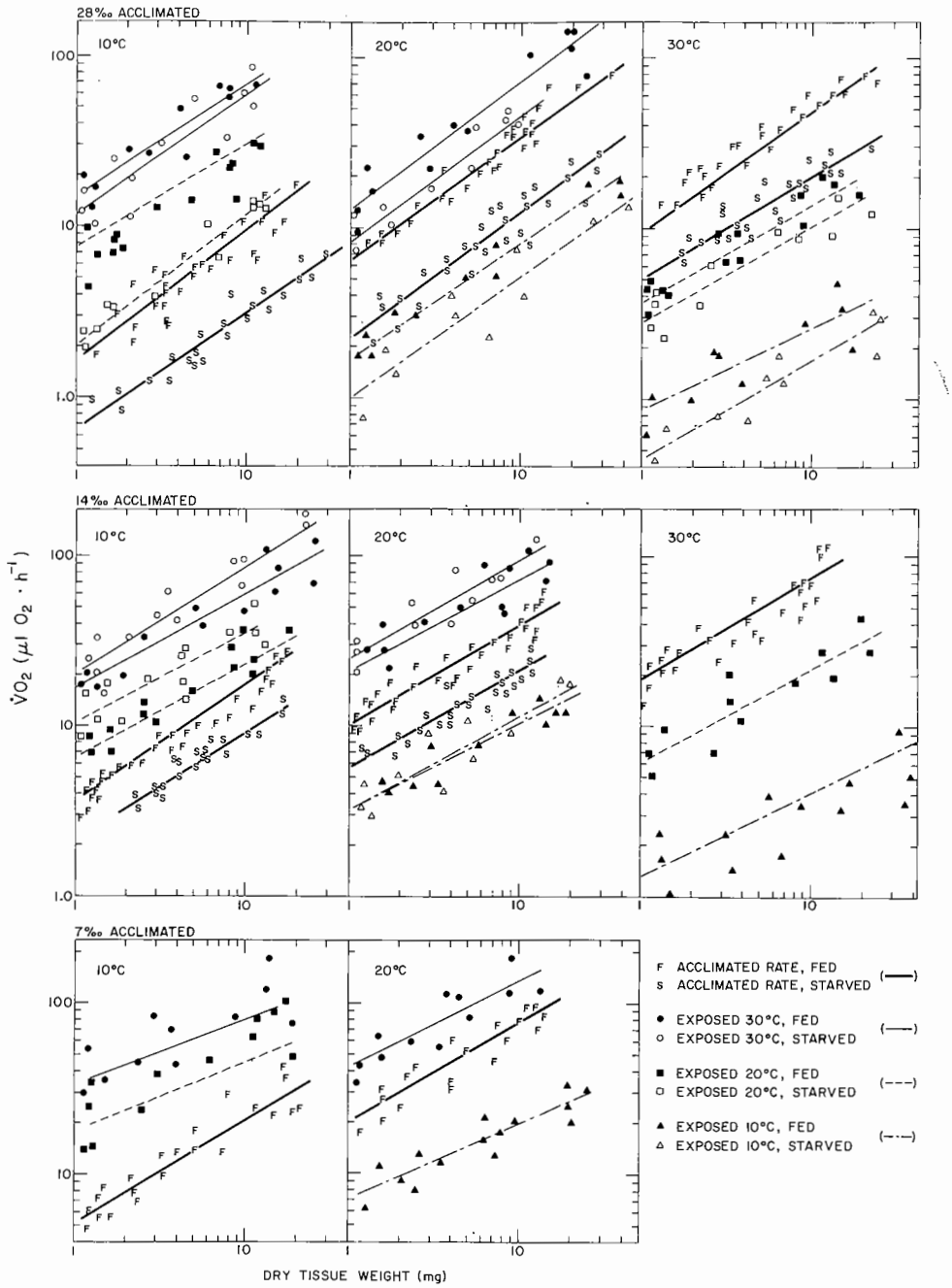

FIG. 3. The acute response to temperature change in *Mulinia lateralis* acclimated at different temperatures and salinities. Regression data are given in Table 1.

TABLE 1. Regression equations relating ($\dot{V}O_2$; $\mu l \cdot h^{-1}$) to dry body weight (W; mg) in *Mulinia lateralis* under different experimental conditions. Equation in form $\dot{V}O_2 = aW^b$. n = number of determinations; r^2 = correlation coefficient.

Acclimation conditions	Experimental conditions: 10°C/28‰				10°C/14‰				10°C/7‰			
	a	*b*	n	r^2	*a*	*b*	n	r^2	*a*	*b*	n	r^2
10°/28‰/F*	1.687	0.730	31	0.801	3.731	0.668	11	0.935	6.862	0.697	11	0.916
10°/28‰/S	0.6944	0.665	23	0.925	1.671	0.600	11	0.922	3.188	0.619	9	0.949
10°/14‰/F	2.911	0.686	9	0.978	3.332	0.671	21	0.939	5.372	0.635	9	0.924
10°/14‰/S	1.908	0.537	11	0.922	2.144	0.654	20	0.895	5.411	0.636	9	0.920
10°/ 7‰/F	3.365	0.569	12	0.669	3.093	0.536	9	0.681	8.120	0.617	21	0.884
20°/28‰/F	1.74	0.670	11	0.964	7.029	0.566	10	0.460	7.238	0.685	11	0.813
20°/28‰/S	1.00	0.723	10	0.878	3.447	0.768	10	0.886	13.071	0.695	11	0.892
20°/14‰/F	6.805	0.544	9	0.693	3.37	0.475	11	0.846	19.341	0.627	10	0.808
20°/14‰/S	6.760	0.422	11	0.741	3.24	0.555	11	0.797	14.130	0.882	10	0.741
20°/ 7‰/F	5.763	0.711	10	0.888	12.195	0.688	11	0.953	7.01	0.445	14	0.837
30°/28‰/F	0.850	0.489	10	0.728	14.127	0.820	10	0.953	11.547	0.581	11	0.444
30°/28‰/S	0.451	0.578	10	0.865	5.696	0.730	9	0.953	6.112	0.674	10	0.898
30°/14‰/F	6.373	0.644	10	0.770	1.31	0.490	13	0.432	17.316	0.684	9	0.880
	20°C/28‰				20°C/14‰				20°C/7‰			
	a	*b*	n	r^2	*a*	*b*	n	r^2	*a*	*b*	n	r^2
10°/28‰/F	7.48	0.620	15	0.259	4.028	0.655	9	0.744	9.438	0.539	10	0.761
10°/28‰/S	2.06	0.757	12	0.960	2.469	0.632	10	0.493	4.413	0.647	11	0.860
10°/14‰/F	4.12	0.614	10	0.863	6.50	0.599	14	0.893	7.906	0.558	8	0.747
10°/14‰/S	3.80	0.626	11	0.882	10.56	0.525	14	0.760	5.700	0.470	13	0.662
10°/ 7‰/F	4.06	0.517	8	0.916	6.165	0.515	10	0.810	18.64	0.384	14	0.277
20°/28‰/F	6.408	0.729	30	0.902	12.133	0.658	12	0.500	20.891	0.639	10	0.789
20°/28‰/S	2.460	0.691	30	0.865	3.574	0.729	11	0.933	5.875	0.773	13	0.624
20°/14‰/F	6.058	0.622	10	0.918	10.025	0.575	30	0.869	22.430	0.579	10	0.729
20°/14‰/S	5.771	0.512	13	0.650	5.654	0.553	27	0.846	22.459	0.515	11	0.699
20°/ 7‰/F	6.728	0.612	11	0.814	9.643	0.556	9	0.767	19.805	0.588	18	0.842
30°/28‰/F	3.786	0.574	14	0.880	16.517	0.721	10	0.910	33.435	0.684	9	0.911
30°/29‰/S	2.967	0.514	11	0.882	10.359	0.671	11	0.859	33.535	0.655	11	0.799
30°/14‰/F	8.317	0.730	11	0.922	6.28	0.533	12	0.796	22.824	0.664	11	0.951
	30°C/28‰				30°C/14‰				30°C/7‰			
	a	*b*	n	r^2	*a*	*b*	n	r^2	*a*	*b*	n	r^2
10°/28‰/F	14.81	0.663	11	0.870	10.223	0.478	9	0.709	10.327	0.700	9	0.690
10°/28‰/S	11.50	0.714	12	0.799	6.987	0.652	9	0.815	6.763	0.654	10	0.838
10°/14‰/F	6.961	0.688	9	0.790	16.69	0.553	13	0.887	14.236	0.789	11	0.771
10°/14‰/S	7.541	0.597	10	0.740	19.18	0.683	13	0.895	8.954	0.661	10	0.854
10°/ 7‰/F	18.666	0.448	10	0.634	15.809	0.604	10	0.667	35.92	0.421	11	0.630
20°/28‰/F	12.73	0.742	13	0.916	40.563	0.611	12	0.694	50.482	0.534	11	0.710
20°/28‰/S	8.109	0.755	10	0.914	14.598	0.716	10	0.921	30.145	0.527	10	0.885
20°/14‰/F	11.737	0.705	11	0.852	23.71	0.490	13	0.745	58.59	0.484	11	0.700
20°/14‰/S	13.32	0.491	13	0.257	25.38	0.559	12	0.833	63.966	0.338	12	0.468
20°/ 7‰/F	32.434	0.611	11	0.891	21.661	0.608	11	0.823	40.35	0.526	12	0.781
30°/28‰/F	9.698	0.632	25	0.932	31.928	0.599	9	0.817	48.765	0.672	9	0.850
30°/28‰/S	5.078	0.594	25	0.869	10.338	0.748	10	0.887	18.624	0.626	10	0.850
30°/14‰/F	9.842	0.725	9	0.922	19.920	0.613	27	0.828	28.400	0.657	11	0.676

* F = fed; S = starved.

Modiolus demissus. Only Vahl (1973b) took into account the change in ratio between the gill surface area and body size with growth. He found gill area (A) in *Mytilus edulis* to vary with dry body weight (W) according to the equation $A = 34.34\,W^{0.65}$ cm^2. The equation reported here yields values for gill surface area comparable with previously published values. The point to be noted, however, is that as in *M. edulis*, small animals with high metabolic rates have higher gill : tissue ratios than larger animals with lower metabolic rates, e.g. in going from 1 mg dry tissue weight to 10 mg, the gill area decreases from 64.64 mm$^2 \cdot$ mg^{-1} to 12.90 mm$^2 \cdot$ mg^{-1}. Clearly, there is more gill tissue available on a weight specific basis for gas exchange in small animals than in larger individuals.

The effects of declining PO_2 on $\dot{V}O_2$

The degree of oxygen independence in *M. lateralis* exposed to declining oxygen tension is dependent on both body size and on acclimation temperature (Fig. 4, Table 2). These data represent starved individuals (1 week) as it was found in preliminary experiments that the response to declining PO_2 in fed animals was highly variable. Large animals were more oxygen independent than small animals

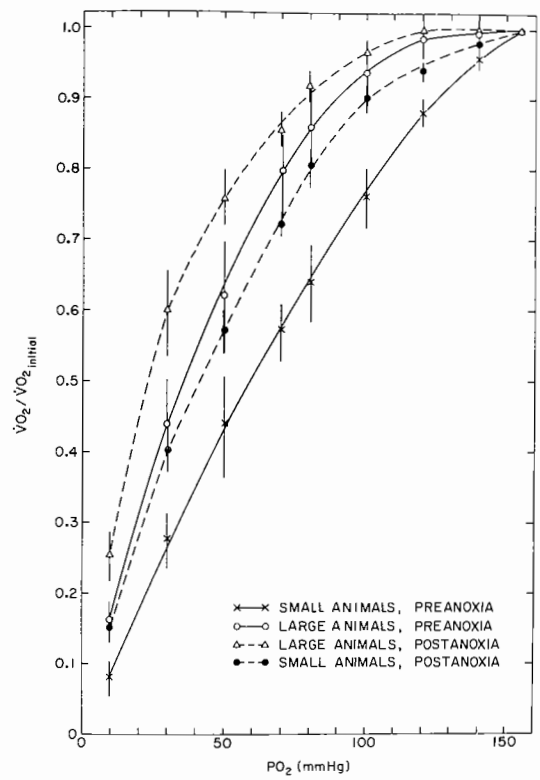

FIG. 4. Oxygen uptake in declining oxygen tensions in *Mulinia lateralis*. Data for large animals (>10 mm shell length) and small animals (<5 mm shell length) before and after 12 h exposure to anoxic sea water. Each point is the mean of 10 determinations. Error bars represent 95 % confidence limits (see Table 2).

TABLE 2. Values of B_2 ($\times 10^3$) in the expression $\dot{V}O_2 = B_0 + B_1PO_2 + B_2(PO_2)^2$ before and after exposure to 12 hours anoxia. Large animals greater than 10 mm total shell length; small animals less than 5 mm shell length. (r^2 = coefficient of determination; n = 10 for each set of conditions)

Acclimation conditions	Pre-anoxia	r^2	Post-anoxia	r^2
10 °C (large)	−0.1834	0.9336	−0.2010	0.9107
(small)	−0.0735	0.9452	−0.1003	0.9434
20 °C (large)	−0.1200	0.9862	−0.1247	0.9784
(small)	−0.0435	0.9939	−0.0961	0.9883
30 °C (large)	−0.0017	0.9546	−0.0015	0.9351
(small)	−0.0026	0.9004	−0.0019	0.9621

at all experimental temperatures prior to anoxic exposure. In addition, the degree of oxygen independence decreased with increased temperature in both large and small individuals. After exposure to 12 h anoxia, the degree of oxygen independence is greater in both size classes at 10 and 20 °C; at 30 °C, large specimens showed no difference between pre- and post-anoxic B_2 values and oxygen independence decreased in small animals after anoxic exposure. It should also be noted that the clams continued to extract oxygen from the external medium until zero PO_2 was reached.

Many authors have studied the response of marine invertebrates to declining oxygen tension (see Newell 1979, Herreid 1980 for reviews) and animals are typically characterized as either oxygen conformers (i.e. $\dot{V}O_2$ varies in direct proportion with PO_2) or oxygen regulators (i.e. $\dot{V}O_2$ is more or less independent of PO_2). The degree of regulation varies with any number of external factors (see Shumway 1982) and only recently has an effort been made to provide a precise means of comparing species' or individuals' oxyregulatory capabilities. Mangum & van Winkle (1973) proposed the use of a quadratic equation to relate $\dot{V}O_2$ to oxygen tension and further proposed that the quadratic 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. Few data of this type are available for bivalve molluscs (Taylor & Brand 1975a,b, Bayne 1971, 1973, Famme 1980, Shumway & Koehn 1982) and the mechanisms underlying such control are still not clearly understood. McMahon & Russel-Hunter (1974, 1977) have shown that it is the microhabitat and physiological ecology of individual species which dictate its response to declining oxygen tensions, and it is generally accepted that it is advantageous for the animal in question to be able to maintain aerobic respiration at normal rates for as long as possible when faced with continuously changing environments.

The degree of oxygen independence in *M. lateralis* is dependent on both body size and on acclimation temperature, and after exposure to anoxic conditions the degree of oxygen independence is greater in both small and large individuals at 10 and 20 °C. At higher temperature (30 °C) large individuals showed no such increase in independence and small individuals actually showed a decrease. An increased degree of oxygen independence after exposure to anoxic conditions has been reported for several species of gastropods (McMahon & Russell-Hunter 1978, Shumway 1981) and has been attributed to a short-term compensatory response that allows maintenance of relatively high aerobic metabolic rates rather than a switch to less efficient anaerobic pathways during occasional low oxygen concentrations. *M. lateralis* has been shown to maintain high levels of feeding, shell valve and locomotory activities under anoxia (Shumway *et al.* 1983). Further, it was shown in the same study that metabolic heat dissipation under anoxia is the same as under normoxic conditions. Thus, while *M. lateralis* shows trends toward increased oxygen independence these shifts are slight and are probably only of minimal significance in the species' adaptation to low oxygen environments.

TABLE 3. Multiple regression equations relating log $\dot{V}O_2$ (R) to exposure temperature (T_2), salinity (S_2) and dry weight (W) in fed and starved *Mulinia lateralis*.

Acclimation conditions	Regression equation	r^2
Fed		
28 ‰ 10 °C	$R = 0.4806 + 0.0271T_2 - 0.0098S_2 + 0.5370 \log W$	0.6815
20 °C	$R = 0.6278 + 0.0408T_2 - 0.0233S_2 + 0.6693 \log W$	0.8681
30 °C	$R = 0.6882 + 0.0476T_2 - 0.0388S_2 + 0.6357 \log W$	0.9103
14 ‰ 10 °C	$R = 0.5177 + 0.0258T_2 - 0.0137S_2 + 0.6359 \log W$	0.8971
20 °C	$R = 0.8718 + 0.0280T_2 - 0.0209S_2 + 0.5467 \log W$	0.6911
30 °C	$R = 0.5927 + 0.0305T_2 - 0.0128S_2 + 0.5768 \log W$	0.4891
7 ‰ 10 °C	$R = 0.5028 + 0.0342T_2 - 0.0146S_2 + 0.5179 \log W$	0.7605
20 °C	$R = 0.7543 + 0.0269T_2 - 0.0085S_2 + 0.5427 \log W$	0.5796
Starved		
28 ‰ 10 °C	$R = -0.0787 + 0.0393T_2 - 0.0110S_2 + 0.6155 \log W$	0.7960
20 °C	$R = 0.7314 + 0.0286T_2 - 0.0304S_2 + 0.6404 \log W$	0.7905
30 °C	$R = 1.3312 + 0.0221T_2 - 0.0497S_2 + 0.5777 \log W$	0.7513
14 ‰ 10 °C	$R = 0.3105 + 0.0338T_2 - 0.0124S_2 + 0.5640 \log W$	0.7317
20 °C	$R = 0.8555 + 0.0274T_2 - 0.0225S_2 + 0.5217 \log W$	0.5953

Combined effects of temperature and salinity on $\dot{V}O_2$

Figs 1, 2 and 3, and Table 3 show quite clearly for fed, acclimated animals that:

a. at any given temperature, the rate of oxygen consumption increased with increased temperature and decreased with decreased temperatures
b. at any given acclimation temperature, oxygen consumption increased with a decreased salinity
c. at any given acclimation salinity, oxygen consumption increased with decreased salinity.

Starved animals showed the same response as fed animals; however, the variation was more pronounced in starved than in fed individuals.

Q_{10} values, calculated over a size range of individuals at all experimental conditions, were generally higher between 10-20 °C than between 20-30 °C at full salinity (28 ‰) but between 10-20 °C was essentially the same in both fed and starved individuals (Fig. 5, Table 4). Further, there was no evidence for complete temperature acclimation under any experimental conditions. Oxygen consumption rates increased with increased temperature and remained elevated, even in starved individuals after 3 weeks of acclimation.

The acute responses were not as clearly defined. The acutely measured rate of oxygen consumption was clearly dependent on temperature regardless of the acclimation conditions, but further interpretations are impossible without the use of multiple regression equations. Table 5 gives multiple regression equations

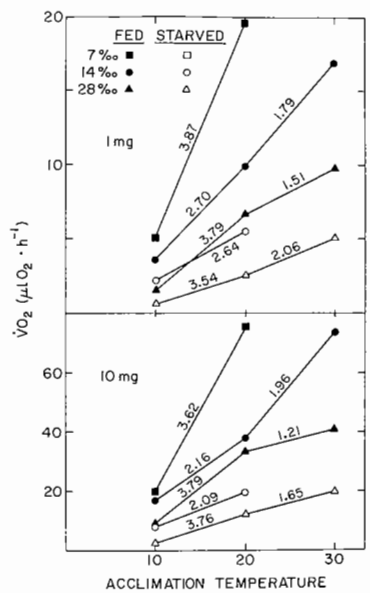

FIG. 5. The effect of acclimation to different temperatures and salinities on $\dot{V}O_2$, data for a 1 mg and 10 mg individual; values calculated from equations in Table 1. Q_{10} values are given on the lines.

TABLE 4. Q_{10} values for oxygen consumption rates in *Mulinia lateralis* acclimated to 10, 20 and 30 °C at three salinities. Values for fed and starved animals. (W = dry tissue weight in mg.)

Acclimation salinity	Q_{10}, fed	Q_{10}, starved
28 ‰	$Q_{10}(10\text{-}20) = 3.798\ W^{-0.0010}$	$Q_{10}(10\text{-}20) = 3.543\ W^{0.0258}$
	$Q_{10}(20\text{-}30) = 1.513\ W^{-0.0971}$	$Q_{10}(20\text{-}30) = 2.064\ W^{-0.0962}$
	$Q_{10}(10\text{-}30) = 5.748\ W^{-0.0490}$	$Q_{10}(10\text{-}30) = 7.313\ W^{-0.0352}$
14 ‰	$Q_{10}(10\text{-}20) = 2.702\ W^{-0.0961}$	$Q_{10}(10\text{-}20) = 2.640\ W^{-0.1012}$
	$Q_{10}(20\text{-}30) = 1.788\ W^{0.0380}$	
	$Q_{10}(10\text{-}30) = 4.830\ W^{-0.0291}$	
7 ‰	$Q_{10}(10\text{-}20) = 3.868\ W^{-0.0287}$	

relating log $\dot{V}O_2$ to acclimation (T_1S_1) and exposure (T_2S_2) temperatures and salinities and body weight (W).

From the model, it becomes clear that dry tissue weight is the over-riding factor determining $\dot{V}O_2$. Several other points emerge which would otherwise probably be overlooked. The effect of acclimation salinity is insignificant in starved animals and is of very little significance in fed animals. In addition, acclimation temperature alone has no significant effect on either fed or starved

TABLE 5. Multiple regression equations relating log $\dot{V}O_2$ of fed and starved *M. lateralis* as a function of log dry weight (W), acclimation (T_1, S_1) and exposure (T_2, S_2) temperature and salinities. Terms are listed in order of decreasing significance.

Fed $n = 887$, $r^2 = 0.7391$		Starved $n = 556$, $r^2 = 0.7908$	
Term	Coefficient	Term	Coefficient
a	$+0.3231$	a	-0.2005
log W	$+0.5204$	log W	$+0.6075$
$T_1S_1S_2$	-1.15×10^{-4}	$T_1S_1S_2$	-7.60×10^{-5}
T_2	$+5.88 \times 10^{-2}$	$S_1T_2S_2$	$+5.39 \times 10^{-5}$
$S_1T_2S_2$	$+7.39 \times 10^{-5}$	T_2	$+5.51 \times 10^{-2}$
T_1S_2	$+1.59 \times 10^{-3}$	S_2	-1.76×10^{-2}
S_1T_2	-1.93×10^{-3}	S_1T_2	-1.27×10^{-3}
$T_1S_1T_2$	$+6.20 \times 10^{-5}$	T_1T_2	-1.89×10^{-3}
T_2S_2	-1.14×10^{-3}	$T_1S_1T_2$	$+3.99 \times 10^{-5}$
T_1T_2	-8.84×10^{-4}		
S_2	-1.39×10^{-2}		
T_1S_1	$+6.64 \times 10^{-4}$		
log WS_1S_2	$+2.38 \times 10^{-4}$		
S_1	$+1.02 \times 10^{-2}$		

animals; however, the $T_1S_1S_2$ interaction term is the strongest factor influencing the rate of oxygen consumption after tissue weight.

M. lateralis has been well studied with respect to its salinity and temperature tolerances from eggs through adults both in the field and in the laboratory. Kennedy *et al.* (1974) demonstrated that temperature sensitivity decreased in the following order: 2-3 hour cleavage stage, trochophore larvae, straight hinge veliger. Calabrese (1969b, 1970) and Calabrese & Rhodes (1974) showed that although the larvae grew in temperature/salinity combinations ranging from 20-30‰ and 20-30°C, optimal conditions for embryos were 22.5-30‰ and 15-25°C while optimal conditions for larvae ranged from 20-27‰ and 7.5-27°C. Optimal culture conditions for raising the clams from egg to metamorphosis were given as 22.5-27.5‰ and 20-25°C. Lough (1975) further analysed data from Calabrese (1969b) using response surface techniques and showed that veliger larvae exhibited a much greater tolerance to low temperature and a wider range of salinity tolerance than early embryos and further showed that maximum growth required higher temperatures and salinities than maximum survival.

Adult animals have not been as extensively studied in the laboratory and more attention has been paid to temperature than to salinity. Castagna & Chanley (1966) reported that, although *M. lateralis* survived from 2.5-30‰ in the laboratory, the clams are normally found in salinities ranging from above 8‰ and become uncommon above 25‰. Breuer (1957) reports this species in Alazan Bay, Texas in salinities ranging from 1.4-75.1‰ with a mean salinity of 50.7‰. Kennedy & Mihursky (1971) reported an upper temperature tolerance of 30-33.5°C depending on the temperature of acclimation. Thus it has been shown that tolerance to temperature and salinity varies with age, size, developmental state and temperature/salinity interactions.

Castagna & Chanley (1973) stated that small bivalves often succumbed to lethal salinities more rapidly than did larger individuals of the same species. The general model presented here indicates that salinity is not one of the prime factors determining distribution in *M. lateralis* and that both acclimation conditions and the interaction of several factors play a major role in determining the species' response and sensitivity to temperature and salinity alterations.

Oxygen consumptions has been shown here to increase rapidly and significantly with decreased salinity irrespective of size. The effects of salinity on $\dot{V}O_2$ in intact bivalve molluscs has been studied by many authors (Potts & Parry 1964, Bayne 1976, Shumway & Koehn 1982). However, the reasons for increased $\dot{V}O_2$ in lowered salinities have still not been clearly established. It has been suggested that these increases are due to osmotic work (Schlieper 1955), salt effects on respiratory enzymes (Lange 1968) and increased locomotor activity (see Kinne 1971). *Mulinia lateralis* has been shown here to be a strict osmotic conformer (Fig. 6) which would apparently rule out osmotic work and since no

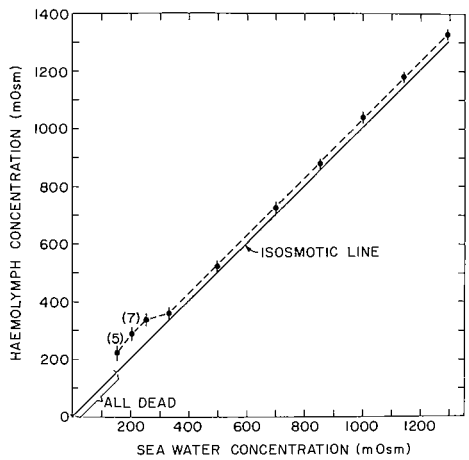

FIG. 6. Osmotic concentration of the haemolymph of *Mulinia lateralis* after 5 d exposure at each salinity. Each point is the mean of 10 determinations except where noted. Error bars represent 95 % confidence limits.

other possibilities were specifically tested, further speculation is unwarranted. It is apparent, however, that the amplitude of the salinity effect is partially influenced by the temperature of acclimation and exposure (see Tables 3, 5).

The effects of temperature on marine invertebrates have been widely studied (for reviews see Kinne 1970, Newell 1969, 1979, Newell & Branch 1980). Activity level in many species increases with increasing temperature and requires energy expenditure. No data is available here for activity changes with respect to temperature so it is not known how much of the observed increase in $\dot{V}O_2$ is attributed to physical activity but, based on laboratory observations, it is presumed to be small. Physiological rate functions, such as oxygen consumption, are affected by temperature changes and these are discussed below.

Kennedy & Mihursky (1972) studied the effects of temperature on respiration rate in *M. lateralis* and showed that the metabolic rate was depressed at high temperatures (30 °C) in cold-acclimated animals, that *M. lateralis* demonstrated acclimation pattern IIIA of Prosser (1958) and that Q_{10} values increased with increased body size. They also pointed out that of the species studied (*Mya arenaria, Macoma balthica* and *M. lateralis*), *M. lateralis* was the most variable in its responses and was least capable of compensating for temperature change. The results reported here do not support these findings in that 1) no complete acclimation is seen here, 2) the rate of oxygen consumption increased with increased temperature regardless of the acclimation conditions (see Fig. 2, Tables 1, 3) and 3) the effect of body size on Q_{10} in this study was minimal (Fig. 5, Table 4). These discrepancies are difficult to explain. However, it is possible that the high variability of *M. lateralis* in its responses reported by Kennedy & Mihursky masked the true responses. The results reported here are similar to those of Newell *et al.* (1977) for *Ostrea edulis* and Ansell & Sivadas (1973) for species where no complete temperature acclimation was seen after long periods

of acclimation. As the temperatures increased, the energetic/metabolic costs in *M. lateralis* also increased conforming to Pattern I of Prosser (1967, 1973) and Type 4 of Precht (1958, Precht *et al.* 1973). The slightly lower Q_{10} values at higher temperature ranges will result in some energy conservation. However, there are also disadvantages associated with the increases in $\dot{V}O_2$ at higher temperatures (see below).

Of considerable interest here is the difference between starved and fed individuals. It has been shown here that the fed and starved rates of oxygen consumption vary considerably (see Tables 1, 3, 5, Figs 1, 2, 3).

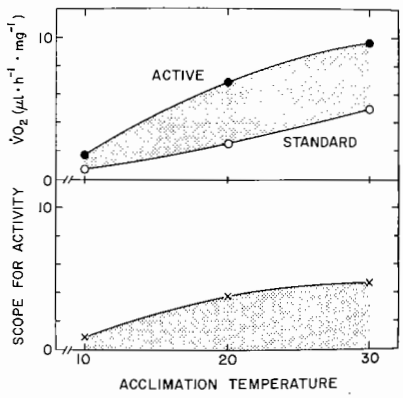

FIG. 7. The 'scope for activity' in *Mulinia lateralis* at different temperatures.

Fig. 7 shows the effect of temperature on the scope for activity, calculated as the difference between active and standard metabolism. It is shown that the scope for activity increases almost two-fold between 10 and 20 °C and remains constant between 20 and 30 °C. These values are taken from animals acclimated at the given temperature and 28 ‰. Temperature affects active/standard rates to essentially the same degree. There is a very low scope for activity at 10 °C which increases and is about equal at 20 and 30 °C. Table 5 shows the component terms of the model ranked in order of their importance to the overall regression, and it is shown that the interaction of acclimation and exposure temperatures and salinities is the most important extrinsic factor determining the rate of oxygen consumption in *M. lateralis*. It is also interesting to note that acclimation salinity or temperature alone do not significantly influence $\dot{V}O_2$, i.e. exposure conditions are more likely to determine levels of energy expenditure when exposed to altered environmental conditions. More important, the significance of the multi-variable approach over single factor analyses is clearly demonstrated. Newell (1979) has shown that the lowest energy expenditure by an animal is usually in the temperature/salinity regime to which the organism has been acclimated, and this is generally borne out in the present study (see Table 1). Acute transfer to increased or decreased temperature/salinity combinations resulted in increased oxygen uptake levels.

The scope for activity provides an index of both the energy available for activity (mechanical and physiological) and the possible saving of energy reserves which could be achieved through reduced activity (Newell 1979, Fry 1947). The scope for activity in *M. lateralis* is low at low temperatures and increases with increasing temperatures to a possible energetic saving of about 2.5 fold at 30 °C. Similar energetic savings associated with cessation of activity have been reported for a variety of other marine invertebrates (see Newell 1979 for review). The general indication is that being starved at high temperatures represents a greater stress than at lower temperatures (see Table 4, Fig. 5). Like *Donax vittatus* (Ansell & Sivadas 1973), *M. lateralis* shows an exaggerated increase in metabolic rate in response to temperature increases within the normally experienced range of temperatures. This increase or exploitation of the increased temperature also leads to an increased vulnerability when left under these stressful conditions for prolonged periods of time in that the animals may be forced to utilize valuable energy reserves.

The effects of temperature and salinity on respiration are further complicated by their interaction as seen from the model presented (Tables 3, 5).

Behavior

During the course of the experiments reported here, many observations were made on the behavior of *Mulinia*. The clams displayed a considerable amount of foot activity, small animals more so than large ones. This activity consisted of a 'probing' motion, apparently in an effort to burrow and a 'leaping' motion in which the clams would actually flip themselves over. The amount of movement was so great in small individuals that it precluded the use of sectioned petri-dishes for isolation of individuals as they actually 'jumped' out. It was not possible to quantify this activity and the foot acitvity did not appear to affect the recordings of shell valve movement. Further, re-establishment of normal activity (re-opening of shell valves, re-extension of siphons) following disturbances was almost immediate.

Large animals are commonly found deeper in the sediment whereas small individuals are confronted with disturbance of the surface sediments and face being buried. In light of the known increase in oxygen requirements of all size classes at increased temperatures (see Figs 2, 3; Table 4), it is of interest to note that Shumway *et al.* (1983) have shown small individuals of *M. lateralis* to be more tolerant of anoxic conditions than larger individuals at the same experimental temperature. The rapid re-establishment of normal activity following perturbation seen in *M. lateralis* has also been noted in *Donax incamatus* (Ansell & Trevallion 1969), another species commonly exposed to unstable sediments. In the presence of a diminished capacity for increased pumping rate coupled with an increased energy demand, an increased tolerance of anoxia and

rapid re-establishment of normal activity following disturbances may be of adaptive significance for a species such as *M. lateralis*, which is commonly exposed to such physically unstable environments.

Shell valve activity and pumping rate

Clearly, any factor which affects the activity level of the animal will in turn affect the rate of oxygen consumption, an increase in activity causing an increased oxygen demand. Two of the most obvious of such activities are shell valve activity and pumping rate. It has been demonstrated here that shell valve activity in *M. lateralis* can be altered considerably by the addition of external stimuli (see Fig. 8). It was found in general that shell valve activity in the absence of any external stimulus was minimal and highly variable and that the most consistent patterns of activity were elicited when particulate material (algal food and charcoal) was added to the external media.

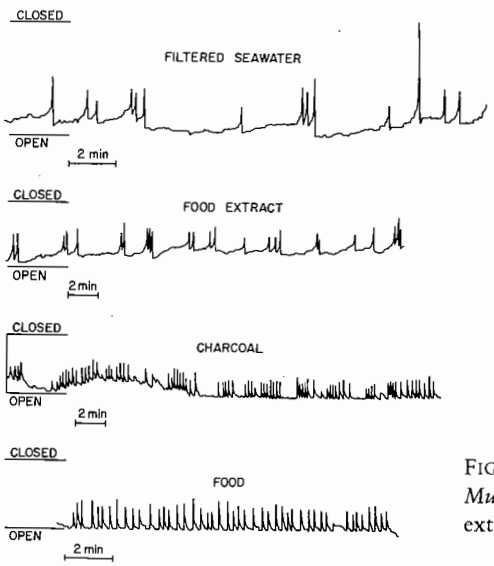

FIG. 8. Actual traces of shell valve activity in *Mulinia lateralis* in the presence and absence of external stimuli. See text for explanation.

Another factor which clearly has a marked effect on the rate of oxygen consumption is pumping rate. If a retention efficiency of 100 % is assumed, the filtration rate can be used as representative of the amount of water flowing through the mantle cavity. Filtration rate (C; ml · h^{-1}), measured as the clearance of a suspension of *T. pseudonana*, is dependent on body size (Table 6; Fig. 9). At 10 and 20 °C the clearance rate varies with the 0.3434 and 0.3365 power of body weight (d) respectively; at 30 °C the effect of body size becomes more

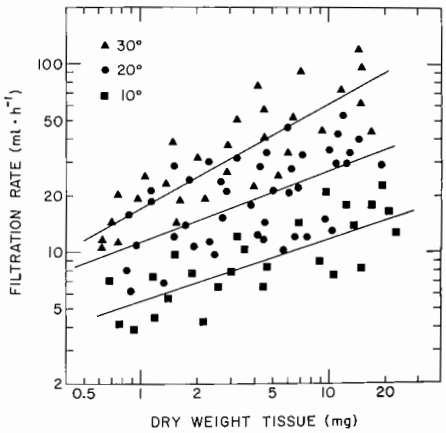

FIG. 9. Filtration rate in *Mulinia lateralis* in relation to body size at three different temperatures. Regression data are given in Table 6. Estimates are based on clearance of a suspension of the unicellular alga *Thalassiosira pseudonana* at a concentration of 10^5 cells · ml^{-1}.

TABLE 6. Regression data for clearance (= filtration) rate versus body size in *Mulinia lateralis*. Data were fitted to the equation $C(ml \cdot h^{-1}) = c\ W^d$ where W is dry tissue weight in mg. (n is number of determinations; r^2 is the correlation coefficient.)

Acclimation temperature	c	d	n	r^2
10 °C	5.511	0.343	26	0.763
20 °C	11.919	0.356	44	0.576
30 °C	17.238	0.556	30	0.847

TABLE 7. Q_{10} values for clearances rates in *Mulinia lateralis*. W = tissue dry weight in mg.

$Q_{10}(10\text{-}20) = 2.163\ W^{0.0131}$
$Q_{10}(20\text{-}30) = 1.446\ W^{0.200}$
$Q_{10}(10\text{-}30) = 1.768\ W^{0.107}$

pronounced where $d = 0.5565$. It can be seen (Fig. 9) that there is considerable variation amongst individuals at any given temperature. Q_{10} values for clearance rate decreased with increasing temperature (Table 7). These Q_{10} values indicate that small animals at high temperature (20-30 °C) cannot increase the pumping rate with increased temperature and the subsequent increase in $\dot{V}O_2$ requirement as well as larger individuals. There is thus likely to be an increasing discrepancy between the energy gained from ingestion of the filtered food and the energy expended in metabolism as the exposure temperature is increased. That this effect is more marked in small individuals than in large ones suggests that thermal 'stress' effects are size dependent in *M. lateralis*.

Like other physiological functions, filtration activity varies with body size (Newell 1979). Several authors have studied the effect of body size on filtration rates (for reviews see Winter 1978, Newell 1979) and the value for the weight exponent, generally lies between 0.66 and 0.92 (Newell 1979) although lower values have also been reported (Vahl 1973a, Srinivasan 1968, Thompson &

Bayne 1974). Jørgensen (1976) has postulated a value of about 0.76. It has been shown here that, as in other bivalves, filtration rate increased with increased body size, although the weight exponents were considerably lower than those previously reported (Fig. 9; Table 6). The clearance rate also increased with increased temperature and the increase relative to body size was greater at high temperature that at low ones. The Q_{10} values (Table 7) indicate that small animals at high temperatures cannot increase their pumping (filtration) with increased temperature to the same degree as larger animals.

Convection requirements and utilization efficiency

When the rate of oxygen consumption and the pumping rate are known, it is possible to calculate both the extraction coefficient and the convection requirements. Changes in pumping rates with body size will in turn have marked effects on both extraction efficiencies and convection requirements.

Table 8 summarises the equations relating oxygen uptake, clearance rate, convection requirements (the amount of water pumped/the amount of oxygen consumed) and extraction coefficients (amount of oxygen used/amount of oxygen available) to body size in *M. lateralis*. It is shown that at any given temperature, the extraction coefficient, the ratio of μl O_2 consumed: ml O_2 available, increases with body size and that the increase is more pronounced in smaller animals. The values for extraction efficiency ($E \times 100$) range from 4.61 (1 mg animal at 10 °C) to 23.29 (10 mg animal at 20 °C). The convection requirement is negatively correlated with body weight (negative exponent, $d - b$) indicating that metabolism increases faster in relation to body size than does pumping rate. The convection requirement decreases with increased temperature in small animals. Further, it decreases with increased body size at both 10 and 20 °C whereas the difference between sizes is minimal at 30 °C.

To calculate the utilization efficiency and convection requirements from the data reported here it was necessary to assume that the filtration rates as measured

TABLE 8. Equations relating oxygen uptake ($\dot{V}O_2$; μl $O_2 \cdot h^{-1}$), clearance rate (C_w; ml $H_2O \cdot h^{-1}$), convection requirement (CR; ml water pumped · μl O_2 available^{-1}) and the extraction coefficient (E; μl O_2 consumed · μl O_2 available^{-1}) to dry body weight (W; mg) where: $\dot{V}O_2 = aW^b$; $C_w = cW^d$; $CR = C_w/\dot{V}O_2$ ($[c/a]W^{[d-b]}$); $E = \dot{V}O_2/C_w x([a/cx]W^{[b-d]})$. x is the amount of oxygen available (μl dissolved O_2 · ml seawater^{-1}).

Acclimation temperature	$\dot{V}O_2$		C_w		CR		E	
	a	b	c	d	c/a	$(d\text{-}b)$	a/cx	$(b\text{-}d)$
10	1.687	0.730	5.511	0.343	3.267	−0.387	0.0461	0.387
20	6.408	0.729	11.919	0.356	1.860	−0.373	0.0986	0.373
30	9.698	0.632	17.238	0.556	1.777	−0.076	0.1245	0.076

TABLE 9. Per cent oxygen utilization in bivalve molluscs.

Species	Per cent O_2 utilized	Source
Cardium tuberculatum	6-10	Hazelhof (1939)
Modiolus demissus	7-8	Booth & Mangum (1978)
Mya arenaria	3-10	van Dam (1935)
Pecten irradians	2.5-6.8	van Dam (1954)
Pinna nobilis	3-8	Hazelhof (1939)
Solen siliqua	7-12	Hazelhof (1939)
Mulinia lateralis	4-12	Present study

approximated the true ventilation rate and, as pointed out by Bayne *et al.* (1976), this is true if filtration efficiency is high. Preliminary experiments indicated that this was the case with *M. lateralis* and the values reported here should, therefore, be a good approximation of the ventilation rate. In general, the efficiency of utilization in bivalve molluscs is low (Table 9) and increased oxygen demands are met, when possible, by increasing pumping rate, extraction efficiency or both. The values for utilization efficiency reported here are similar to previously reported values for other bivalves. Utilization efficiency in *M. lateralis* increased with increased body size at 10 and 20 °C. However, the effect of body size was greatly diminished at 30 °C.

It was found that the convection requirement for *M. lateralis* decreased with increased temperature in small animals and decreased with increased body size at both 10 and 20 °C. The effect of body size was again minimal at 30 °C, probably a result of high temperature stress. The negative exponent (see Table 8) for convection requirements is a consequence of the fact that metabolism increases faster in relation to body size than does pumping and indicates that the net energy gain becomes progressively less as the animals increase in size. Similar results have been reported for *C. edule* and *M. edulis* (Vahl 1973a, b). It has been postulated that this lowered energy gain might explain the slow growth rate observed in large individuals (Newell 1979).

Increased metabolic requirements at high temperature are thus met by a lowered convection requirement coupled with an increased extraction efficiency and small animals enjoy a greater advantage than larger individuals.

The effects of external stimuli on shell valve activity and $\dot{V}O_2$

Shell valve activity patterns were found to vary considerably depending on the stimulus present in the external medium (Fig. 8). Animals placed in filtered seawater showed sporadic and irregular patterns of shell-valve activity. When algal extract was added, the clams became slightly more active, but the pattern

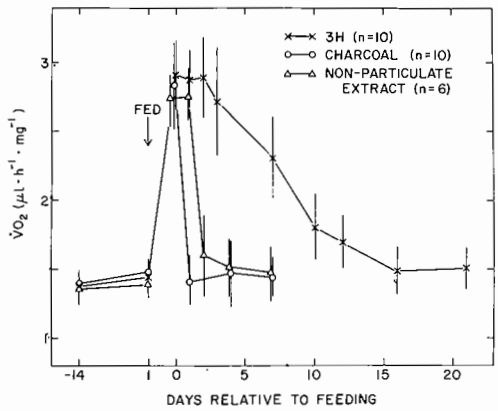

FIG. 10. Oxygen uptake in *Mulinia lateralis* in response to various stimuli following 14 days of starvation. Data from Table 10. Error bars represent standard deviations.

remained erratic. In the presence of inorganic particulate matter (charcoal) activity levels increased and became considerably more regular. The most regular and consistent activity patterns were seen in clams that were fed a culture of *T. pseudonana*.

The effects of these stimuli on $\dot{V}O_2$ are shown in Fig. 10 and Table 10. It is seen that respiration rate increased immediately after addition of a food stimulus, be it algae, charcoal or algal extract. The respiration rate increased from a basal

TABLE 10. The effects of various food sources on the pre-feeding $\dot{V}O_2$/post-feeding $\dot{V}O_2$ ratio in *Mulinia lateralis*. Values ± standard deviation; n = number of determinations.

Food	pre-feeding $\dot{V}O_2$ / post-feeding $\dot{V}O_2$	n
Thalassiosira pseudonana	1.87 ± 0.22	10
	no response	1
Platymonas suecica	1.57 ± 0.54	4
	no response	6
Monochrysis lutheri	1.75 ± 0.29	8
	no response	2
Isochrysis galbana	1.84 ± 0.40	10
	no response	1
Non-particulate extract (*T. pseudonana*)	1.96 ± 0.22	6
Activated charcoal	1.95 ± 0.29	7
	no response	2
Sediment extract	1.69 ± 0.33	3
	no response	3

or standard rate to an active rate almost immediately. It was not possible to distinguish a 'routine' rate of $\dot{V}O_2$ as described by Bayne *et al.* (1976).

Although the rate of $\dot{V}O_2$ increased initially in response to all three types of stimulus, the rate only remained elevated in the presence of algae (Fig. 10). When charcoal or algal extract were added to the medium, $\dot{V}O_2$ rose sharply to an active $\dot{V}O_2$ and returned to the standard rate usually within 2 days. The rate of oxygen uptake in animals fed on algae did not return to a basal rate for at least 14 days post-feeding.

Table 10 shows the effects of 7 individual stimuli on the pre-feeding/post-feeding $\dot{V}O_2$ ratio. It can be seen that addition of each of these stimuli caused an increase in $\dot{V}O_2$ relative to the starved or basal rate. In a total of 63 experiments, 17% of the animals showed no response to the stimulus; only algal extract elicited an increased rate in all experiments.

While the direct effect of these changes in shell valve activity on $\dot{V}O_2$ were not measured, the effects of the various stimuli on $\dot{V}O_2$ were and the results are summarised in Table 10. In all cases, addition of any external stimulus elicited an increased rate of oxygen consumption. However, removal of the stimulus did not always produce similar responses. Active $\dot{V}O_2$ in algal-fed clams remained elevated for at least 2 days after removal of the food. In all cases, the $\dot{V}O_2$ increased significantly upon introduction of an external stimulus. Removal of the non-particulate extract resulted in a decreased $\dot{V}O_2$ after about 2 days, whereas removal of the charcoal suspension resulted in an almost immediate decrease in $\dot{V}O_2$. Oxygen consumption in animals fed algal cells did not return to basal level for at least two weeks. Similar responses were reported for the mussel *M. edulis* (Thompson & Bayne 1972) in that non-particulate stimuli resulted in an immediate return to pre-feeding $\dot{V}O_2$ levels whereas removal of particulate food resulted in maintained active metabolism for at least a further hour. However, in the above study the mussels were fed continuously and, after an initial increase in $\dot{V}O_2$ over pre-feeding rates, a new 'routine' rate of metabolism, intermediate between the active and basal rates, was established. In the present study, *M. lateralis* were not continuously fed and a routine metabolic rate was not established. Increases in $\dot{V}O_2$ following addition of food have been observed for a number of animals (Saunders 1963, Wallace 1973, Crisp *et al.* 1978) and the initial phase of the increase is usually attributed to mechanical costs of increased activity, whereas the sustained increases in $\dot{V}O_2$ are attributed to the specific dynamic action of the food, or physiological cost of feeding (Bayne & Scullard 1977). An increase in shell valve activity, most probably coupled with an increased pumping rate, in the presence of particulate material (see Figs 8, 10) has been demonstrated her for *M. lateralis* and this increased activity requires energy. While it was not possible to calculate the actual metabolic cost of this activity, the energy expended during feeding must here also be divided between the actual cost of pumping and the specific dynamic action of the food.

SUMMARY

M. lateralis is a classic example of a highly transient, opportunistic species (Sanders 1956) with its high rate of fecundity and short generation time. Its high growth rate and high reproductive rate are typical of an exploitive strategy (Newell 1980) for maximizing energetic gain from the environment. It has been shown in the present study that *M. lateralis* can take advantage of favorable environmental conditions such as salinity, temperature and food availability as they occur, but the animals are not capable of metabolic regulation and are thus vulnerable to prolonged periods of environmental stress.

M. lateralis is also characterized by population crashes or catastrophic die-offs. The species is known to set in high densities only to disappear within 1-2 years (Levinton 1970). Santos & Simon (1980) reported *M. lateralis* to occur in densities of about $74000 \cdot m^{-2}$ prior to annual summer die-offs. The present study seem to confirm that these physical parameters are the major causes of the die-offs since the metabolic rate would be elevated at the higher temperatures when less oxygen is available. Further, previous studies (Shumway *et al.* 1983) have indicated that *M. lateralis* remains active under these anoxic conditions and this is yet a further drain on the energy reserves of the clams. Levinton (1970) believes that the *M. lateralis* populations are controlled primarily by physical factors and this assumption is supported by the findings of Santos & Simon (1980) who found low dissolved oxygen levels coupled with high temperatures to be the suspect causative agent in their population die-offs. Levinton & Bambach (1970) also showed that juvenile mortality in *M. lateralis* was at least partially attributed to clogging of the ctenidia. The present study indicates that fluctuations in abundance are attributable not only to harsh environmental changes but also to short term alterations of the environment leading to increased rates of oxygen consumption and metabolic burnout. This is especially true if the environment becomes resource limited during periods of increased metabolic rate when energy reserves may become depleted. Survival of these transient communities seems to be a combination of behavioural and physiological adaptations which allow successful exploitation of favourable conditions while at the same time leaving the animals vulnerable to long term stress conditions.

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