

Effects of Oxygen Tension on Pumping, Filtration and Oxygen Uptake in the Ascidian *Phallusia mammillata*

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ABSTRACT: The effects of declining oxygen tension on pumping, filtration and oxygen uptake were studied simultaneously in *Phallusia mammillata* (Cuvier, 1815). Identical effects were observed on rates of pumping and filtration; these remain constant until the oxygen tension (pO_2) falls to a mean level of 119 mm Hg (concentration = $3.85 \text{ ml O}_2 \text{ l}^{-1}$) and then decrease. Below a pO_2 of 98 mm Hg ($3.18 \text{ ml O}_2 \text{ l}^{-1}$) the rates decrease more rapidly and become more variable. No particular rhythms emerged. Below a pO_2 of 119 mm Hg, rapid and rhythmic variations in the diameter of the cloacal siphon produce a pseudorhythm. Filtering efficiency stays constant, with values of 77 to 79%; the mechanism of mucus formation is not affected down to a pO_2 of 98 mm Hg. Below a mean pO_2 of 119 mg Hg – the critical tension – oxygen uptake decreases; *P. mammillata* fails to regulate oxygen consumption, and becomes a 'conformer'.

INTRODUCTION

As has been documented in Volume I of 'Marine Ecology', dissolved gases are of paramount importance for marine organisms (Fogg, 1972; Gunkel, 1972; Kalle, 1972; Wilber, 1972). Oxygen tension may affect the activity of filter-feeders. In lamellibranch molluscs, the reaction to declining oxygen tension is a complex phenomenon related to environmental variation – e. g. temperature, food ration, etc. (Bayne, 1971a, b; MacLusky and Stirling, 1975; Taylor and Brand, 1975). Few experimental data exist in the literature on the activity of ascidians, and none on the influence of oxygen tension on pumping and filtration rates. With an experimental apparatus previously described (Fiala-Médioni, 1973, 1978a, b), which measures pumping

and filtration rates simultaneously, it has been possible to study the activity of *Phallusia mammillata* under conditions of declining oxygen tension.

MATERIAL AND METHODS

Phallusia mammillata (Cuvier, 1815) was selected because it performs well under experimental conditions. Four different individuals were used for the 4 experiments of 27 to 31 h each. They were collected by SCUBA-diving in the harbour of Banyuls-sur-Mer (western Mediterranean coast of France) where this species is abundant on various hard substrata. The characteristics of the individuals used are summarized in Table 1.

Table 1. *Phallusia mammillata*. Characteristics of individuals collected in Banyuls-sur-Mer harbour. Bs: buccal siphon; Cs: cloacal siphon. –, +, ++: genital products absent, present, abundant, respectively

Experiment No. and collection depths	Length/width (cm)	Dry weight (g)			Siphon of diameter BS/CS (mm)	Sexual activity
		Test	Organs	Total		
1 3 m	12.0/5.5	1.807	0.848	2.655	10.0/7.0	++
2 4 m	11.0/5.5	1.642	0.976	2.618	15.0/9.0	–
3 5 m	11.5/4.0	1.377	0.620	1.997	12.0/6.5	+
4 2 m	10.5/5.0	1.632	0.780	2.412	9.5/7.0	+

Two methods were used simultaneously: a direct method using a hot film probe and an indirect method previously described (Fiala-Médioni, 1973, 1978a). Water velocities were calculated according to the linearized Collis and Williams law, as detailed in an earlier paper (Fiala-Médioni, 1978b). For the only probe used, the root mean square (Rms) error obtained by computer with the calibration data was 1.71 %.

The temperature of the experimental medium was maintained constant ($15\text{ }^{\circ}\text{C} \pm 1\text{ }^{\circ}\text{C}$) as well as the concentration (20.10^6 cells per liter $\pm 5\%$) of the algae (*Monochrysis lutheri*); pH and salinity were controlled at the beginning, during, and at the end of each experiment (Table 2). Oxygen tension was monitored according to a polarographic method, using an oxygen electrode connected to a 'Radiometer' analyser; every hour, readings were taken of partial pressure in the experimental medium. The $p\text{O}_2$ values were corrected with values obtained in a blank experiment (same conditions, without test individual).

RESULTS

Water-current Velocities

The average water velocities varied between less than 3 and 7.2 cm sec^{-1} , the maximum being 23.2 cm sec^{-1} (Table 3). Water velocities tended to decrease with time but, because the diameter of the cloacal siphon decreased simultaneously, water-velocity decrease was not as obvious as it would have been had the cloacal siphon remained fully open.

Pumping Rates

Pumping rates varied between 3224 and 5766 ml h^{-1} (Fig. 1); expressed as dry weight of organs, these rates were: 5097 to 6391 $\text{ml h}^{-1}\text{g}^{-1}$ (Table 3). In all experiments, pumping rates decreased after 12 to 15 h. Three phases emerged: (1) from a normal level of oxygen

tension down to $p\text{O}_2$ mean values of 119 mm Hg (concentration of $3.85\text{ ml O}_2\text{ l}^{-1}$), pumping rates displayed a mean value of 6012 $\text{ml h}^{-1}\text{g}^{-1}$ and a small coefficient of variation ($< 15\%$); (2) down to a $p\text{O}_2$ mean value of 98 mm Hg (concentration of $3.18\text{ ml O}_2\text{ l}^{-1}$), mean pumping rates decreased to 5307 $\text{ml h}^{-1}\text{g}^{-1}$ and variability rose to between 15 and 30 %; (3) in the third phase the coefficients of variation exceeded 30 %; only a few values could be calculated; after 19 or 21 h the velocities of the water current decreased below 3 cm sec^{-1} ; this is the minimum value for calibration of the probe.

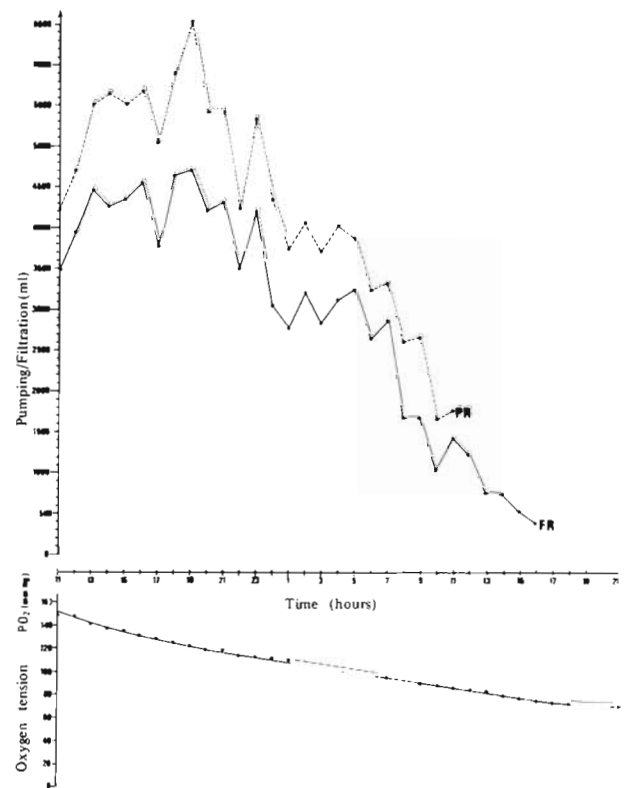


Fig. 1. *Phallusia mammillata*. Rates of pumping (PR) and filtration (FR) in relation to oxygen tension

Table 2. *Phallusia mammillata*. Experimental conditions. Min: minimum, Max: maximum temperature; S_0 : initial salinity; S_F : final salinity; O_{20} : initial oxygen concentration; O_{2F} : final oxygen concentration; pH_0 : initial pH; pH_F : final pH. Concentration of *Monochrysis lutheri* in the experimental medium was $20 \cdot 16^6$ cells l^{-1} ($\pm 5\%$)

Experiment No.	Temperature ($^{\circ}\text{C}$)			Salinity (‰)		Oxygen concentration ($\text{ml O}_2\text{ l}^{-1}$)		pH	
	Min.	Max.	Mean	S_0	S_F	O_{20}	O_{2F}	pH_0	pH_F
1	14.7	15.2	15.06	37.92	38.20	5.28	2.44	7.8	7.5
2	14.7	15.8	15.17	37.80	38.41	5.09	3.07	7.9	7.4
3	14.8	15.3	14.98	37.97	38.32	4.99	2.60	8.0	7.3
4	14.9	15.3	15.13	37.88	38.11	5.15	2.24	8.1	7.5

Table 3. *Phallusia mammillata*. Oxygen uptake, water velocity, pumping rate, filtration rate and filtering efficiency obtained in the 4 experiments during three phases. CV %: coefficient of variation; pumping and filtration are expressed as ml h⁻¹ and in ml h⁻¹ g⁻¹ dry weight of organs; avg: average values

Experi- ment No.	Hours of experi- ment	Temper- ature mean (°C)	Oxygen concen- tration (ml l ⁻¹)	Oxygen uptake μl h ⁻¹	Water velocity (cm sec ⁻¹)			Pumping rate			Filtration rate			Filtering efficiency		
					Min.	Max.	Avg.	CV %	ml h ⁻¹	ml h ⁻¹ g ⁻¹	ml h ⁻¹	ml h ⁻¹ g ⁻¹	ml h ⁻¹	ml h ⁻¹ g ⁻¹	Mean %	CV %
1	15	15.10	3.87	520	743	< 3	15.1	6.7	16.77	5145	6067	4012	4731	10.18	78	5.29
	24	15.05	3.10	425	607	< 3	10.2	5.4	20.85	4377	5162	3432	4047	19.72	79	4.53
	30	15.03	2.48	515	736	< 3	11.6	< 3	< 3	< 3	< 3	2914	3436	39.53		
2	12	15.20	4.08	420	600	< 3	4.5	6.1	21.08	5766	5908	4389	4496	7.92	76	3.48
	19	15.16	3.51	405	579	< 3	11.6	3.9	7.65	4975	5097	3790	3883	20.77	76	4.49
	27	15.15	3.07	275	393	< 3	17.3	< 3	< 3	< 3	< 3	2997	3071	39.46		
3	13	14.90	3.73	385	550	3.9	16.3	5.9	13.90	3522	5680	2853	4602	9.10	81	6.30
	21	14.95	3.03	340	486	< 3	11.2	5.4	19.75	3224	5200	2515	4056	20.18	78	5.70
	28	15.10	2.60	205	293	< 3	< 7.1	< 3	< 3	< 3	< 3	1972	3181	38.75		
4	13	15.05	3.72	550	786	4.2	20.7	7.2	15.20	4985	6391	3938	5049	8.36	79	4.72
	20	15.10	3.08	455	650	< 3	17.2	6.5	20.35	4500	5769	3420	4385	21.40	76	5.10
	30	15.25	2.35	365	522	< 3	15.1	< 3	< 3	< 3	< 3	1775	2276	33.50		
Means																
1st phase:			3.85	469	670		6.5	6.5	16.77	5145	6012	4012	4720	< 15	79	
2nd phase:			3.18	406	580		5.3	5.3	20.85	4377	5307	3432	4090	15 <= 30	77	
3rd phase:			2.63	340	486		< 3	< 3	< 3	< 3	< 3	2991	2991	> 30		

Pumping Rhythm

Pumping rates did not display any particular rhythm (Fig. 1); they decreased with oxygen tension after the first phase. In the second phase, the siphons were sometimes closed, while the diameter of the cloacal siphon became more variable. In probe recordings, a pseudo-rhythm was observed in relation to the rhythmic movements of the orifice of the cloacal siphon. These movements became more frequent in the third phase (below pO₂ = 98 mm Hg) (Fig. 2).

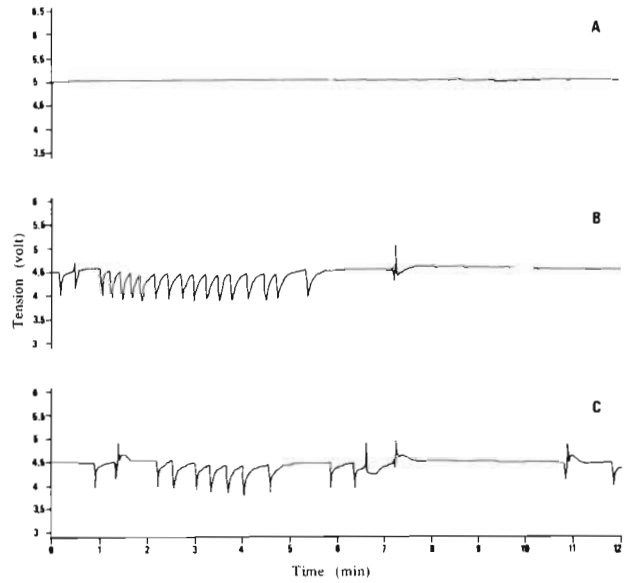


Fig. 2. *Phallusia mammillata*. Recordings of water-current velocity obtained with Probe A: down to mean oxygen tension of 119 mm Hg; B: pO₂ between 119 and 98 mm Hg; C: pO₂ values lower than 98 mm Hg. The pseudo-rhythm observed in B and C is related to fast and rhythmic changes in cloacal siphon diameter

Rate and Rhythm of Filtration

Filtration rates showed the same response as pumping rates: they were maintained at a mean value of 4720 ml h⁻¹g⁻¹ dry weight of organs (Table 3); with coefficients of variation lower than 15 %, down to a mean pO₂ of 119 mm Hg (concentration of 3.85 ml O₂l⁻¹). Below this pO₂ value down to pO₂ of 98 mm Hg (3.18 ml O₂l⁻¹) it decreased with declining oxygen tension, to a mean value of 4090 ml h⁻¹g⁻¹ and a coefficient of variation between 15 and 30 %. At still lower pO₂ levels, variability exceeded 30 % with a mean rate of 2991 ml h⁻¹g⁻¹.

Filtering Efficiency

Pumping and filtration rates gave quasi-parallel curves (Fig. 1), clearly revealing a constant filtering

efficiency. Values of 76 to 81 % (mean 79 %) were obtained in the first phase (until pO_2 at 119 mm Hg) and 76 to 79 % (mean 77 %) in the second phase (until $pO_2 = 98$ mm Hg); both sets of values had a small coefficient of variation (mean = 4.95 %). Formation of the mucus sheet was not affected by declining oxygen tension, at least not down to a pO_2 of 98 mm Hg. The decrease in filtration rate was thus related only to the decrease in pumping rates.

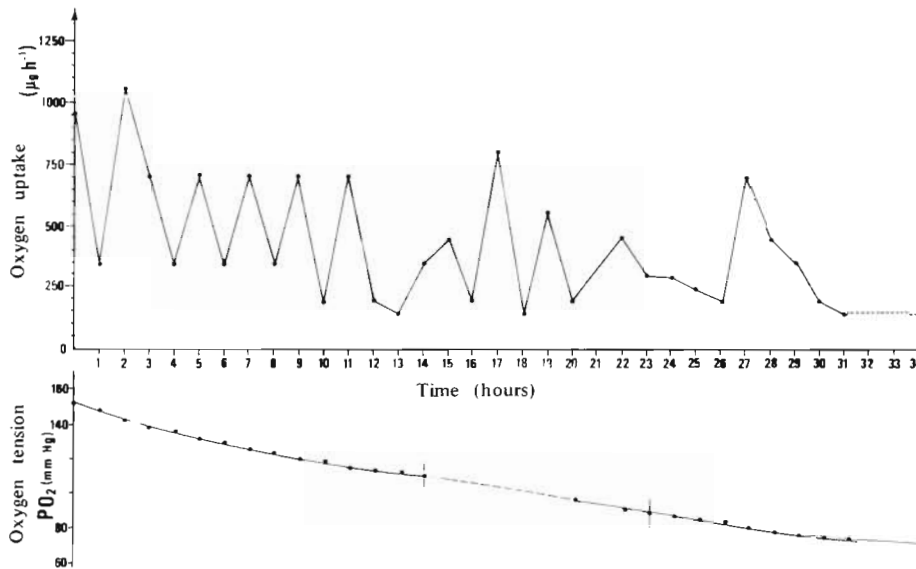


Fig. 3. *Phallusia mammillata*. Oxygen uptake expressed in micrograms per hour ($\mu\text{g h}^{-1}$) in relation to oxygen tension

Rate and Rhythm of Oxygen Uptake

Oxygen uptake remained constant down to pO_2 values of 70 mm Hg only in one ascidian. In the other individuals, this rate was independent of oxygen decrease only down to a pO_2 of 119 mm Hg (concentration of $3.85 \text{ ml O}_2 \text{ l}^{-1}$), with values of 550 to $786 \mu\text{g h}^{-1}$. Below 118 mm Hg the rate decreased, with a range of 486 to $650 \mu\text{g h}^{-1}$, and below 98 mm Hg the values varied from 293 to $736 \mu\text{g h}^{-1}$. When expressed in relation to the dry weight of the organs, the mean rates of oxygen uptake were 846 , 732 , and $603 \mu\text{g h}^{-1} \text{g}^{-1}$. The values of oxygen uptake were irregular, with alternatively high and low values (Fig. 3).

DISCUSSION

Phallusia mammillata displays constant and normal rates of pumping, filtration and oxygen uptake down to a mean pO_2 of 119 mm Hg. This value represents a critical tension for this species under the environmental conditions offered in our experiments. *P. mammillata* is able to regulate its activity ('regulator') down to

a mean pO_2 of 119 mm Hg (a value which varies for different individuals between 110 and 158 mm Hg); below this value it becomes a 'conformer'. This critical tension is close to that reported by Fisher (1976) at 15°C for *Styela plicata* (129 mm Hg).

In the first phase, oxygen uptake is not affected by decreasing oxygen tension, and varies between 385 and $550 \mu\text{l h}^{-1}$ (550 and $786 \mu\text{g h}^{-1}$) or 430 and $705 \mu\text{l h}^{-1} \text{g}^{-1}$ organ dry weight, with a mean of $592 \mu\text{l h}^{-1} \text{g}^{-1}$

(614 and $1007 \mu\text{g h}^{-1} \text{g}^{-1}$ with a mean of $846 \mu\text{g h}^{-1} \text{g}^{-1}$). For *Ciona intestinalis*, Jørgensen (1952) gave values of 600 to $900 \mu\text{l h}^{-1}$. Fisher's (1976) value at 15°C for *Styela plicata* was $300 \mu\text{l h}^{-1} \text{g}^{-1}$ organ dry weight.

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