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OXYGEN CONSUMPTION OF *TELLINA FABULA* GMELIN IN RELATION TO TEMPERATURE AND LOW OXYGEN TENSION – A *TELLINA FABULA* GMELIN OXIGÉNFOGYASZTÁSÁNAK FÜGGÉSE A HÖMÉRSEKLETTŐL ÉS OXIGÉNHIÁNYTŐL



ABSTRACT: The oxygen consumption of *Tellina fabula* from Dublin Bay and from Marseille were investigated in response to temperature and lowered oxygen tensions. The results indicate that respiratory stress became evident at rather lower temperatures than might have been expected by the LD₅₀ and that the stress seemed to be compounded under conditions of low oxygen. The response to low oxygen tensions indicated that *T. fabula* at lower temperatures was at best only capable of partial and rather slight oxyregulation, but a dramatic change to apparently complete regulation was often evident at the higher temperatures. The significance of these responses is discussed together with their effect on the ecology and distribution of *T. fabula*.

INTRODUCTION

Tellina fabula GMELIN is one of the commonest bivalves in the lower littoral and immediate sub-littoral (WILSON, 1976) and in Dublin Bay is found at low densities from around the low water mark to below the 15 m contour, reaching its maximum abundance at depths of 10 m or so (WALKER and REES, 1980; WILSON, 1982).

Its thermal tolerances have received considerable attention, particularly in comparison with the closely related and very similar *Tellina tenuis* DA COSTA, which is predominantly an animal of the mid to lower shore (ANSELL *et al.*, 1980; WILSON, 1978, 1981). The LD₅₀ for *Tellina fabula* would appear to be around 25°C for northern populations and 29°C for Mediterranean populations, with a difference of up to 2°C between winter- and summer-acclimatized specimens.

The oxygen uptake of *T. fabula* has been used to determine its LD₅₀ by WILSON (1981), although the rates measured were rather elevated, particularly at temperatures of 20°C and above. More detailed studies on oxygen uptake in the closely related *T. tenuis* (McMAHON and WILSON, 1981) have shown reverse acclimation in that the uptake rates of winter conditioned specimens were lower, at a given temperature, than those of summer conditioned specimens. The significance of this has been widely discussed (e. g. CALOW, 1975) and the implied reduction in energy demand is thought to allow conservation of stored energy reserves over the winter when food resources may be scarce.

McMAHON and WILSON (1981) also made observations on the oxyregulatory capability of *T. tenuis*, showing that it was a moderate to good regulator, and most bivalves display at best only moderate independence of uptake as environmental oxygen tension falls (BAYNE, 1967, 1971; McMAHON and WILSON, 1981; WILSON and DAVIS, in press). Two important influences on the degree of independence are temperature, which NEWELL *et al.* (1978) found to significantly alter the response to hypoxia of the gastropod *Crepidula fornicata* and body size (BAYNE, 1971, 1973; TAYLOR and BRAND, 1975b), although WILSON (1983) found that size was not a significant factor in a model of bivalve oxyregulation.

The effect of these two factors on oxyregulatory capability was therefore considered especially since *T. fabula* inhabits a slightly less well-oxygenated habitat than *T. tenuis* (WILSON, 1976) and related back to the effects of size and temperature on oxygen uptake rates. Discussion on the influence of various factors on the distribution of *T. fabula* especially in regard to its relationship with *T. tenuis* (ANSELL *et al.*, 1980; WILSON, 1977, 1978, 1979, 1981), have emphasised the importance of temperature and sediment character.

These experiments set out to continue the investigation and to extend the area of study into the effect on *T. fabula* of lowered oxygen tension.

MATERIALS AND METHODS

Two groups of experiments were performed, the first with specimens from Dublin Bay, Ireland, and the second with specimens from Marseille, France. The Dublin Bay specimens were dug from the low water mark, while the Marseille specimens were collected by SCUBA diving at depths of 5m to 8m. The Dublin Bay experiments were subdivided into winter-conditioned (W-C), that is collected in the months January to February with water temperatures of 9.0°C and summer conditioned (S-C), collected in July to August with water temperatures ranging from 15.0°C to 17.0°C. Only summer-conditioned Marseille specimens were used, and the water temperatures at time of collection ranged from 20°C to 23°C.

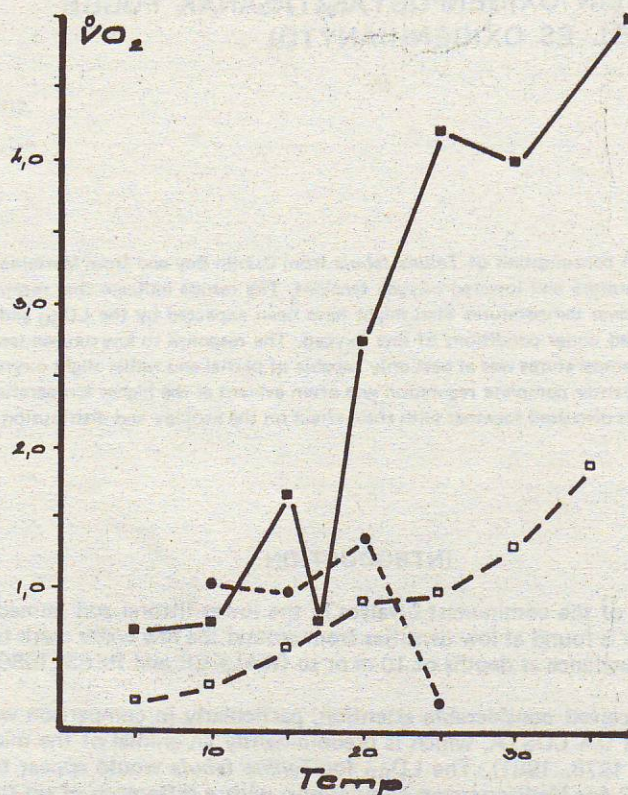


FIG. 1. *T. fabula*. Weight-specific oxygen uptake rates ($\dot{V}O_2$, $\mu\text{l O}_2 \text{ mg}^{-1} \text{ h}^{-1}$) of a 5 mg flesh dry weight standard animal with temperature (Temp, °C). (See also Table 1). Dublin Bay W-C (□), S-C (■) and Marseille (●) groups.

The experimental regime for both the temperature and low oxygen experiments was modified from that used by BURKY (1977) and is described more fully elsewhere (McMAHON and WILSON, 1981; WILSON and McMAHON, 1981; WILSON and DAVIS, in press). Briefly, it consisted of placing the animal or animals in a chamber which was water-jacketed to ensure that temperature was held constant, into which a polarographic oxygen electrode was introduced, and the chamber sealed.

For the temperature experiments which were performed mainly with Dublin Bay specimens, the oxygen consumption of the specimen(s) was monitored over the first 10% decrease from full air saturation in chamber oxygen concentration or for at least 30 minutes if less than 10% of the available oxygen had been removed over that period. Oxygen uptake rate determinations were then repeated, mostly in 5°C increments until the animal(s) showed marked signs of stress, such as the valves gaping and lack of response to tactile stimuli.

The respiratory response to hypoxia utilised much the same procedure as described above with the difference that the oxygen consumption rate was continuously monitored from near full air saturation ($pO_2 \approx 160$ Torr) down to either the oxygen concentration at which respiration ceased or zero air saturation. The weight specific oxygen uptake rate ($\mu\text{l O}_2 \text{ mg}^{-1} \text{ h}^{-1}$) was then calculated at intervals down the oxygen saturation curve, and standardised by expressing each as a fraction of the uptake rate at full air saturation. The resulting fraction values were then fitted to the quadratic equation $y = b_0 + b_1x + b_2x^2$ where y = standardised weight specific oxygen uptake rate and x = partial pressure of oxygen, expressed as Torr. The quadratic coefficient b_2 , usually expressed as $b_2 \times 10^3$, becomes an increasingly larger negative value as the degree of oxyregulation or oxygen independence, increases (MANGUM and VAN WINKLE, 1973).

RESULTS

The oxygen uptake rates of a standard 5mg dry flesh weight *T. fabula* are shown in Fig. 1 and in Table 1 along with the relationship between size and oxygen uptake rates. Fig. 1 shows the rather high rates noted by WILSON (1981) for the S-C specimens only, along with a surprising fall in the uptake rate at 17°C. To what extent this may be attributed to the smaller number, or smaller size range used is unclear, and the calculated Q_{10} value (Table 1) has omitted this data.

The onset of heat stress of the S-C group again occurred between 25°C and 30°C, but that of the W-C group, and, surprisingly, of the Marseille group occurred between 20°C and 25°C (Fig. 1). At these temperatures too, the b (slope) values (Table 1) linking oxygen uptake rate to body size began to differ considerably from their expected norm around 0.7 (PROSSER, 1973). The mean Q_{10} values, for the W-C Dublin Bay 5-20°C, S-C Dublin Bay 5-25°C, and Marseille 10-20°C groups was 2.70, 2.80 and 1.42 respectively.

TABLE 1. *T. fabula*. Oxygen uptake with temperature and size. Group a — winter-conditioned Dublin Bay, b — summer conditioned Dublin Bay, c — summer conditioned Marseille, showing experimental temperature (Temp, °C), number of replicates (n) together with slope (m) and correlation coefficient (r) values of the equation $y = mx + c$ where $y = \log_{10}$ uptake ($\mu\text{l O}_2 \text{ animal}^{-1} \text{ h}^{-1}$) and $x = \log_{10}$ weight (mg), the uptake rate ($\mu\text{l O}_2 \text{ h}^{-1}$) of a 5.0 mg dry body weight standard animal (s.a.) and the respiration quotient (Q_{10}): *denotes significant at $P = 0.05$.

Group	Temp	n	m	r	s. a.	Q_{10}
a	5	17	0.505	0.62*	0.207	2.40
	10	17	0.547	0.63*	0.321	3.25
	15	17	0.517	0.57*	0.579	2.46
	20	15	0.706	0.65*	0.909	1.16
	25	15	0.765	0.48*	0.977	1.80
	30	15	0.457	0.29	1.312	2.10
	35	15	0.382	0.23	1.901	
b	5	20	-0.095	-0.06	0.696	1.15
	10	16	0.427	0.33	0.746	4.97
	15	11	0.508	0.37	1.663	2.73 ¹
	17	6	0.985	0.55	0.759	2.36
	20	11	0.572	0.74*	2.747	0.92
	25	11	0.407	0.54*	4.222	1.52
	30	11	0.241	0.17	4.050	
c	35	11	0.111	0.06	4.994	
	10	4	0.673	0.89*	1.038	0.88
	15	6	0.530	0.69	0.974	1.96
	20	4	0.507	0.86*	1.365	0.02
	25	5	0.143	0.19	0.214	

¹ Q_{10} between 15°C and 20°C.

The degree of oxygen independence, as measured by the $b_2 \times 10^3$ values is shown in Fig. 2, along with the effect of temperature. It can be seen that the degree of independence in both Dublin and Marseille specimens increased with temperature, and the increase was particularly dramatic in the Marseille experiments (Fig. 2, Table 2). One way analysis of variance indicated a highly significant difference between the groups ($F_{7,45} = 8.29, P < 0.001$).

The nature of the relationship between oxyregulation and temperature, weight and starting $\dot{V}O_2$ is shown in Table 3. As mentioned there was strong, though not significant in the case of the Dublin specimens, correlation between temperature and oxygen independence, and the same pattern, but a negative correlation, was seen with independence and the starting oxygen consumption. The Dublin specimens had a strong correlation between days maintained in the laboratory, which, as the animals were not fed in the holding tanks amounts to days of starvation; and oxygen independence. In the Marseille specimens weight was strongly correlated with oxyregulation. The introduction of the acclimatization temperature as a factor changed the relationship very little and the correlation between $b_2 \times 10^3$ and the temperature difference (i. e. experimental — acclimatization temperature) was only fractionally better at $r = 0.445$ than with experimental temperature alone.

TABLE 2. *T. fabula*. Mean (\bar{x}) and standard deviation (s. d.) of $b_2 \times 10^3$ values with temperature.

		Temperature				
		0-5	6-10	11-15	16-20	21-25
Dublin	\bar{x}	-0.030	-0.005	-0.038	-0.046	—
	s. d.	0.053	0.020	0.025	0.028	—
Marseille	\bar{x}	—	0.081	-0.001	-0.015	-0.247
	s. d.	—	0.074	0.067	0.023	0.194

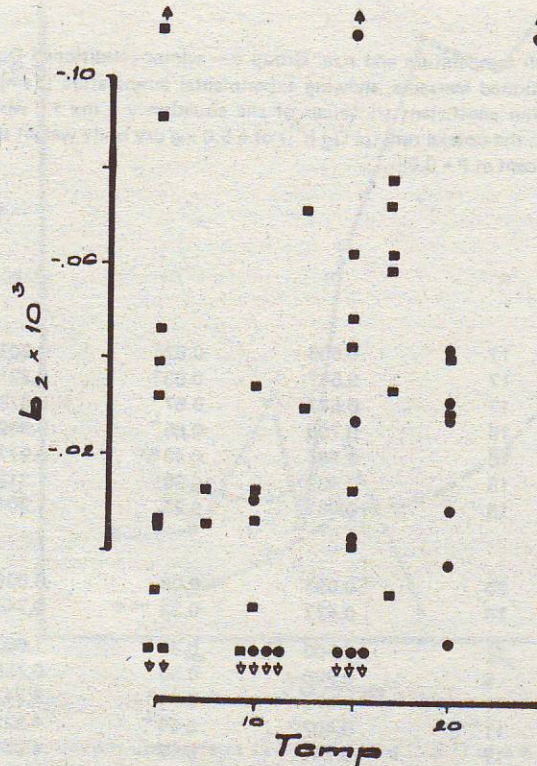


FIG. 2. *T. fabula*. $b_2 \times 10^3$ values temperature (Temp, °C). Dublin Bay (■) and Marseille (●) groups: arrows denote values out with those on axis.

In Fig. 3, the $b_2 \times 10^3$ values of individuals have been plotted against those obtained by the same individual in the previous run, to ascertain whether some animals were behaving consistently as oxyconformers or oxyregulators. The correlation was, however, low for both the Dublin and Marseille groups separately and together ($r = 0.22$, $P = 0.22$, $r = 0.31$, $P = 0.14$; and $r = 0.08$, $P = 0.34$ respectively) and it was concluded that individuals may vary from one experiment to another as to their degree of independence.

DISCUSSION AND CONCLUSIONS

Several factors have been shown to affect the degree of oxygen independence of bivalves including size (BAYNE, 1971, 1973; TAYLOR and BRAND, 1975b), starvation (BAYNE, *et al.*, 1976) and ventilatory activity (NEWELL *et al.*, 1978; TAYLOR and BRAND, 1975a).

The results presented here give limited support to the effect of size on oxyregulation, in that the degree of oxygen independence shown by Marseille specimens significantly increased with size as found by TAYLOR and BRAND (1975b) for *Arctica islandica*, while size did not seem to affect the response of the Dublin animals, nor was there significant correlation when both groups were considered together.

Starvation is thought to affect the degree of independence though the lowering of the ventilation rate (BAYNE *et al.*, 1976), which results in an apparent increase of the oxyregulatory capability. The results reported here, how-

ever, show firstly that, in the Dublin group, starvation increased the degree of independence, and over both groups starvation showed no correlation with oxygen independence, and secondly, that low initial oxygen uptake rates were correlated with higher $b_2 \times 10^3$ values. The latter would therefore appear to imply that a low initial respiration rate would allow a greater capacity for the animal to adapt to lowering oxygen tensions by either increasing ventilatory or irrigatory activity and that a low level of metabolic activity is more easily maintained in the face of falling environmental oxygen concentration than a high level.

The influence of temperature on oxyregulation was to increase the degree of oxygen independence with increasing temperature. This was despite the link of low starting respiration rates with firstly, low temperatures and secondly oxyregulation, when it might have been expected that an inverse relationship, as noted by NEWELL *et al.*, (1978) in the gastropod *Crepidula fornicata*, would exist. A second difference with the results of NEWELL *et al.*, (1978) in regard to temperature was the lack of influence of the environmental or acclimatization temperature, and the relationship between increased temperature and increased oxygen independence could be described adequately using the experimental temperature alone.

The response of *T. fabula* to temperature alone has been well studied (ANSELL *et al.*, 1980; WILSON, 1978) and the lethal limit, depending on the previous thermal history, would appear to be around 25° - 27°C. However, ANSELL, *et al.*, (1980) found a rather lower thermal limit for normal physiological response, as evinced by ability to burrow, and this rather lower normal physiological response limit may be connected to the rather dramatic increase in oxygen independence seen most noticeably in the Marseille experiments. This increased independence may therefore be no more than a consequence of the loss of control over metabolism of the animal at the onset of a heat coma, the thermal limit for which may be lowered in the presence of another stress factor, that of lowered oxygen tension.

TABLE 3. Correlation coefficients for the least squares linear regression of $b_2 \times 10^3$ values versus temperature (Temp, °C), dry flesh weight (wt, mg), initial oxygen uptake rate (start, $\mu\text{l O}_2 \text{ mg}^{-1} \text{ h}^{-1}$), and days held prior to experiment (Days) for Dublin, Marseille and all groups (n = 32, 21 and 53 respectively). *denotes significant at P = 0.05, **significant at P = 0.01.

	Location		
	Dublin	Marseille	All
Temp	-0.200	-0.696**	-0.441**
Wt	0.201	-0.531**	0.059
Start	0.137	0.512**	0.284*
Days	-0.450**	0.138	-0.063

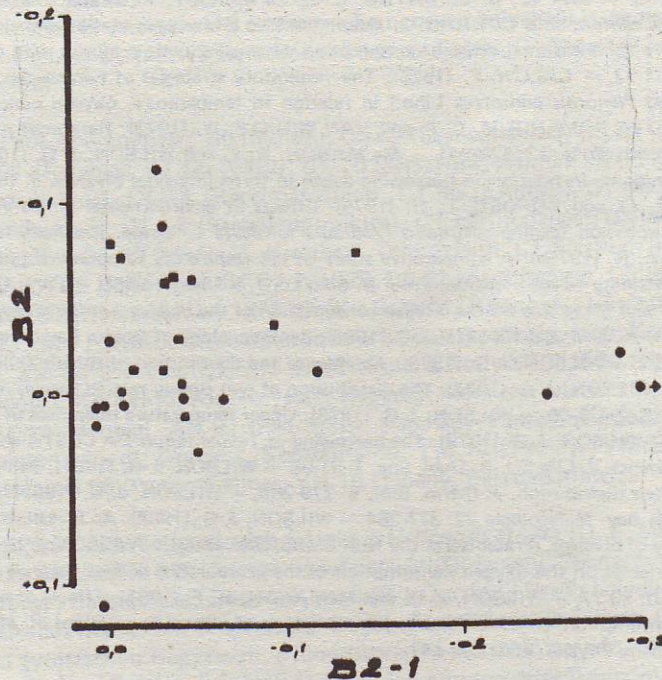


FIG. 3. *T. fabula* $b_2 \times 10^3$ values (B2) plotted against $b_2 \times 10^3$ values of the previous run (B2-1). Notation as Fig. 2.

The very low oxygen uptake rates of the Marseille specimens at 25°C may either have been due to the physiological limit mentioned above, or to the fact that the animals had been collected at temperatures above 20°C, normally considered at, or near, the long-term limit for this species (ANSELL *et al.*, 1980; WILSON, 1978). Neither explanation is wholly satisfactory, as firstly the respiration of the Dublin specimens continued rising, albeit with some check, over the range tested, possibly, as suggested by WILSON (1981), due to bacterial intervention, at the higher temperatures and secondly, the Marseille specimens showed little sign of stress or abnormal response up to 20°C.

The oxygen uptake rates with temperature were consistently higher in the Dublin S-C specimens than the W-C, with those of the Marseille specimens being highest of all at 10°C and intermediate at 15°C and 20°C. In this respect *T. fabula* shows the same pattern of reverse acclimation as *T. tenuis*, which implies a reduction in metabolic demand at times of low food availability and supports the suggestion (WILSON, 1977) that they are filter-feeders rather than deposit feeders.

With regard to *T. fabula* distribution, the results presented here confirm that the thermal niche is rather narrower than that of *T. tenuis*, nor does *T. fabula* appear to have any advantage over *T. tenuis* in oxyregulatory ability. The earlier conclusions of WILSON (1976, 1977, 1978, 1979, 1981) regarding influence of the sediment is confined to the physical composition and its effect on burrowing.

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ÖSSZEFOGLALÁS

A Dublin-öbölben és Marseille mellett gyűjtött *Tellina fabula* példányok oxigénfogyasztását mértük a hőmérséklet és a csökkentett oxigénnyomás függvényében. Az eredmények alapján megállapítható, hogy a légzési stressz a vártnál alacsonyabb hőmérsékleten jelentkezett. A stressz fokozódik, ha a nyomás is alacsony. A vizsgálati eredményeket a faj ökológiai és elterjedési viszonyaival összevetve tárgyaljuk.

REFERENCES

- ANSELL, A. D., BARNETT, P. R. O., BODOY, A. and MASSE, H. (1980): Upper temperature tolerances of some European molluscs. 1. *Tellina fabula* and *T. tenuis*. Mar. Biol. 58: 33-39. — BAYNE, B. L. (1967): The respiratory response of *Mytilus perna* L. (Mollusca, Lamellibranchia) to reduced environmental oxygen. Physiol. Zool. 40: 307-313. — BAYNE, B. L. (1971): Oxygen consumption by three species of lamellibranch mollusc in declining oxygen tension. Comp. Biochem. Physiol. 40A: 1065-1085. — BAYNE, B. L. (1973): The responses of three species of bivalve mollusc to declining oxygen tension at reduced salinity. Comp. Biochem. Physiol. 45A: 793-806. — BAYNE, B. L., BAYNE, C. J., CAREFOOT, T. C. and THOMSON, R. J. (1976): The physiological ecology of *Mytilus californianus* CONRAD. 2. Adaptations to low oxygen tension and air exposure. — BURKY, A. J. (1977): Respiration chambers for measuring oxygen consumption of small aquatic molluscs with Clarke-type polarographic electrodes. Malacol. Rev. 10: 71-72. — CALOW, P. (1975): The respiratory strategies of two species of freshwater gastropods (*Ancylus fluviatilis* MÜLL. and *Planorbis contortus* Linn.) in relation to temperature, oxygen concentration, body size, and season. Physiol. Zool. 48: 114-129. — MANGUM, C. P. and VAN WINKLE, W. (1973): Responses of aquatic invertebrates to declining oxygen conditions. Amer. Zool. 13: 529-541. — Mc MAHON, R. F. and WILSON, J. G. (1981): Seasonal respiratory responses to temperature and hypoxia in relation to burrowing depth in three intertidal bivalves. J. therm. Biol. 6: 267-277. — NEWELL, R. C., JOHNSON, L. G. and KOFOED, L. H. (1978): Effects of environmental temperature and hypoxia on the oxygen consumption of the suspension feeding gastropod *Crepidula fornicata* L. Comp. Biochem. Physiol. 59A: 175-182. — TAYLOR, A. C. and BRAND, A. R. (1975a): A comparative study of the respiratory responses of the bivalves *Arctica islandica* (L.) and *Mytilus edulis* L. to declining oxygen tension. Proc. R. Soc. Lond. B 190: 443-456. — TAYLOR, A. C. and BRAND, A. R. (1975b): Effects of hypoxia and body size on the oxygen consumption of the bivalve *Arctica islandica* (L.). J. exp. mar. Biol. Ecol. 19: 187-196. — WALKER, A. J. M. and REES, E. I. S. (1980): Benthic ecology of Dublin Bay in relation to sludge dumping. Fauna. Fish. Invest. Ire. Ser. B. 22. — WILSON, J. G. (1976): Abundance and distribution of British Tellinidae. Ph. D. Thesis, University of Glasgow, Glasgow. — WILSON, J. G. (1977): The distribution of two closely related species of Tellina, *T. tenuis* and *T. fabula*. Prog. Underwat. Sci. N. S. 2: 35-46. — WILSON, J. G. (1978): Upper temperature tolerances of *Tellina tenuis* and *Tellina fabula*. Mar. Biol. 45: 123-128. — WILSON, J. G. (1979): The burrowing of *Tellina tenuis* DA COSTA and *Tellina fabula* GMELIN in relation to sediment characteristics. J. Life Sci. R. Dubl. Soc. 1: 91-98. — WILSON, J. G. (1981): Temperature tolerances of circatidal bivalves in relation to their distribution. J. therm. Biol. 6: 279-286. — WILSON, J. G. (1982): Distribution, biomass and production of bivalves in Dublin Bay. Malacologia 22: 377-384. — WILSON, J. G. (1983): An investigation into the factors affecting the oxyregulatory capability of bivalves. (Presented at the 18th EMBS, Oslo 1983). — WILSON, J. G. and DAVIS, J. P. (1984): The effect of environmental variables on the oxygen consumption of the protobranch bivalve *Nuncula turgida* (LECKENBY and MARSHALL). J. Moll. Stud., 50: 73-77. — WILSON, J. G. and McMAHON, R. F. (1981): Effects of high environmental copper concentration on the oxygen consumption, condition and shell morphology of natural populations of *Mytilus edulis* L. and *Littorina rudis* MATON. Comp. Biochem. Physiol. 70C: 139-147.

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