

# Influence of Infestation by *Labratrema minimus* (Bucephalidae:Digenea) on Oxygen Consumption of Edible Cockle *Cerastoderma edule* (Mollusca: Bivalvia) In Laboratory Conditions

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## Introduction

**Abstract:** Short-term oxygen consumption and filtration rate experiments were conducted to evaluate the response of edible cockle *Cerastoderma edule* when infested by the Digenean trematod *Labratrema minimus*. In this experiment the metabolic activities of bivalves were measured to determine this particular aspect of the host-parasite interaction. We have used the Bucephalidae digenea *Labratrema minimus* infestation as a factor which can alter the metabolic rates of its host: the edible cockle *Cerastoderma edule* from Arcachon bay (France). The results show that specific oxygen consumption of infested cockles decreases in comparison with that of healthy ones. This decrease in specific pumping rate is partly due to increase in the total cockle biomass measured, which is due to the presence of the parasite and can represent 20% of a healthy cockle's O<sub>2</sub> consumption (it can constitute up to 92% of live mass in high infestation intensities (personal observations; 1996) but consume little oxygen. In addition, the disease provoked by infestation can reduce the true metabolic activities. The results show that pumping rate is related to the intensity of the infestation with greater infestation associated with lower oxygen consumption. We also demonstrate that *L. minimus* is capable of oxygen consumption regulation. The consumption rate is maintained below 0.3  $\mu\text{mol O}_2 \text{ min}^{-1} \text{ g}^{-1}$  FDW (Fresh Dry Weight) in all external oxygen concentrations experimented.

**Key Words :** Filtration Rate, *Cerastoderma edule*, Digenea, Host-parasite interactions

## Introduction

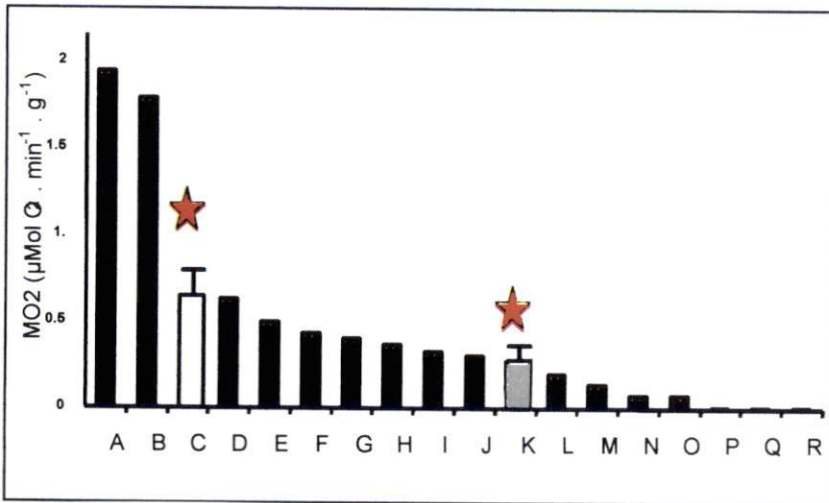
The amount of bivalve's oxygen consumption rate has raised interest for a long time because of their role in food chain as a consumer of primary production. This interest coming for more acknowledgements about particle retention in the bivalve as a pure or applied sciences in aquaculture.

The estimation of oxygen consumption and filtration rate is important from a number of aspects: (i) in feeding where it is an indicator of the animal's reaction to its environment; (ii) in aquaculture, for the prediction of optimal flow of water required and (iii) in estimating the species survival in nature.

Most bivalve molluscs pump water through the pallial cavity by means of ciliated gills, and the mucociliary mechanism of the gill of many bivalves is modified to collect suspended nutritious particles and convey them to the mouth. These animals pump a volume of water in excess to their respiration requirements. However, in suspension feeders, the gill filaments have become greatly elongated and folded on themselves, effectively increasing the exchange surface area. The bivalve pump configuration is made of inhalant and exhalant areas of relatively small sizes, leading to a chamber separated by a large area of gill bearing numerous ciliated slits or pores between gill filaments which act as a series of pumps. The oxygen cost of pumping (Collier, 1959 ; Dejourn, 1972) is one possible method to compare the efficiency of various gills and siphon configurations between bivalves. However, a large variety of other methods have been proposed (Jones & Allen, 1986; Byrne *et al.*, 1990; Eriksen & Iversen, 1997; Bayne *et al.*, 1987; Beninger *et al.*, 1991; Visman, 1990 ; De Villiers *et al.*, 1989). Our knowledge of the physiological responses of bivalves in natural population rarely result from direct observations in the wild but is usually deduced from extrapolations of results obtained in the laboratory. In order to establish the legitimacy of such extrapolations, measurements in high controlled conditions are needed. In spite of many controlled conditions such as temperature, salinity, etc., there is a variety of results among the measures on filtration or respiration rates for a same species in the literature (Figure 1). Thus information about the reasons of the variety of measures is not clearly known. These variations may be the result of physiological modifications in response to factors which may have been ignored, such as the potential effect of parasitism on oxygen consumption. Taking this

factor into account may be important for bivalve modelling studies in which generally the gains and losses of animal are accounted independent from the parasitism factor.

In the present study, *in vitro* measurement of respiration rates of *C. edule* were carried out in healthy animals and on individuals parasited with *L. minimus*. Respiration measurements were performed on the individuals using a method involving collection and adaptation of animals prior to the measurements. In addition, the oxygen consumption of the parasitic mass only was measured and the two oxygen consumption rates were compared. Such comparisons have never been performed so far.



**Figure 1:** A comparison between the oxygen consumption values for bivalve molluscs as it could be seen in different references. The big variety of measurements could be explained by parasitism factor that is neglected. A : *Dreissena polymorpha* (Garton & Haag, 1991), B : *D. polymorpha* (Dorgelo & Smeenk, 1988), C : healthy *Cerastoderma edule* (this work), D : *Mytilus edulis* (Hamburger *et al.*, 1983), E : *Mya truncata* (Bernard & Noakes, 1990), F : *Clinocardium nuttallii* (Bernard & Noakes, 1990), G : *Crassostrea gigas* (Bernard & Noakes, 1990), H : *M. edulis* (Bernard & Noakes, 1990), I : *Saxidomus giganteus* (Bernard & Noakes, 1990), J : *Chlamys hastata* (Bernard & Noakes, 1990), K : *C. edule* parasited by *Labratrema minimus* (this work), L : *Yoldia traciaeformis* (Bernard & Noakes, 1990), M : *Solemya reidi* (Bernard & Noakes, 1990), N : *C. edule* (Smaal, 1998), O : *Perna canaliculus* (Marsden & Weatherhead, 1998), P : *M. edulis* (Vismann, 1990), Q : *Anodonta cygnea* (Massabuau *et al.*, 1991), R : *Corbicula fluminea* (Tran, 1997).

## Materials and Methods

Oxygen and filtration rates of cockles were measured separately. The groups used for both measurements came from the same site of Péréire, in Arcachon bay (Figure 2). This site is located in the eastern part of the bay of Arcachon (south west of France,  $44^{\circ}40'$  N ;  $1^{\circ}10'$  W) and is protected by the Barnet sand banks. Previous samplings performed to establish the spatial distribution of cockles in the bay have shown that the cockles of this site are infested with *L. minimus* only and not by other Digenea species (Javanshir, 1999).

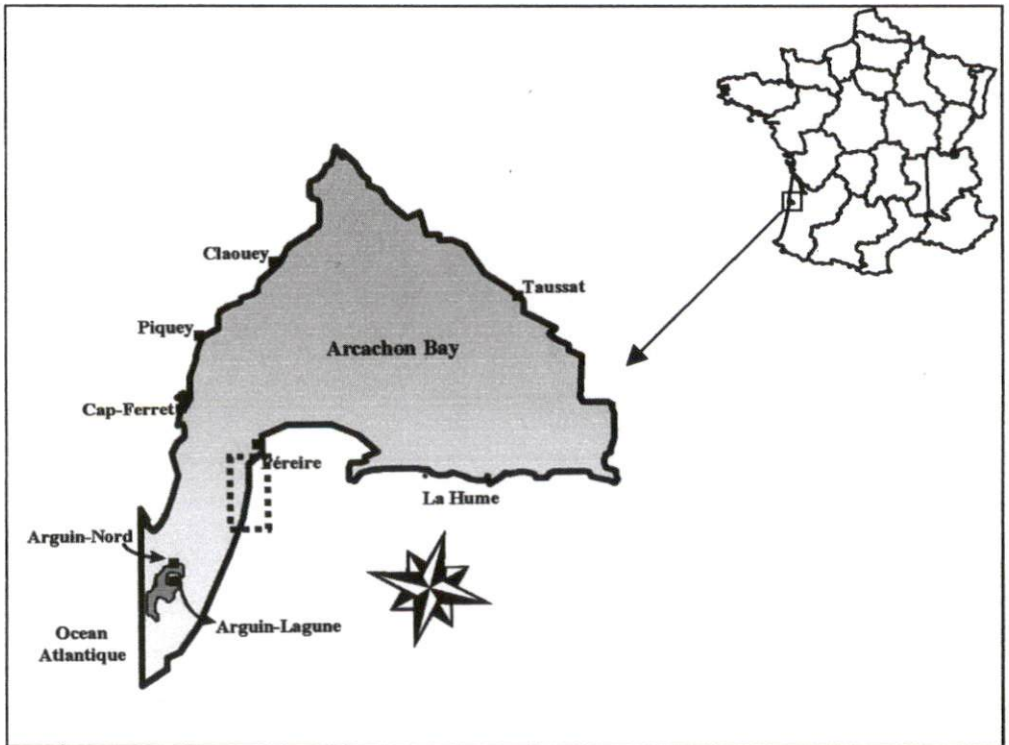


Figure 2: The Arcachon Bay and Péréire station in the southeast

After collection, the animals were brought to the laboratory, washed with filtered sea water in order to eliminate the epibionts and then maintained individually in 250 ml containers in order to select cockles infested by *L. minimus*. Infested cockles were identified by following the cercariae liberation. Individuals of the two groups of infested and healthy cockles were then marked and maintained in filtered sea current water during 48 hr. to allow clearance of the gut contents and acclimatization to laboratory conditions. Temperature was maintained at  $20 \pm 1^\circ\text{C}$ . Two groups of cockles (healthy and infested) were selected with the closest possible mean size and brought into the oxygen consumption glass chamber of 75 ml Vol. (Figure 3). The water entering this chamber consisted of filtered sea water ( $0.45 \mu\text{m}$ ), saturated with oxygen in normoxia conditions ( $\text{PO}_2 = 21 \text{ kPa}$ ), and was conducted through stainless steel pipes of 0.5 mm diameter. The pumping was generated with a Braun-Melsungen pump at a constant rate of  $300 \mu\text{l min}^{-1}$ . The position of cockles in the chamber was designed to resemble that found in natural condition in the sediment. This was achieved by using an oyster culture net of 5mm mesh size, as shown in Figure 3. Each experiment on a single cockle lasted for 16 minutes during which, four samples of 5 ml of water from the entry and exit pipes were re-sampled with a glass syringe. The oxygen concentration of each sample (entrance or exit) was then measured using an oxygen electrode (Clark Radiometer E 5046, modified in laboratory for these measurements, its precision being 0.01 kPa). Each time, the measurement was repeated four times from sub samples 1 ml volume each. The results presented are the averages of the four measurements. Oxygen consumption measures were converted into  $\text{Mo}_2$  unit ( $\mu\text{mol. O}_2 \text{ min}^{-1}$ ), following to equation proposed by Dejours (1981):

$$\text{MO}_2 = V \cdot \alpha_w \text{O}_2 \cdot (\text{PeO}_2 - \text{PsO}_2)$$

In which,

$MO_2$  : oxygen consumption per time ( $\mu\text{mol. min}^{-1}$ )

$V$  : water entrance flux in the chamber ( $\text{ml. min}^{-1}$ )

$\alpha wO_2$  : oxygen solubility coefficient in sea water ( $\mu\text{mol., L}^{-1}. \text{kPa}^{-1}$ ),  
(11,12 in our case)

$PeO_2$  &  $Pso_2$ ): oxygen partial pressure in input and output water of the chamber (kPa)

After each measurement the cockle was dissected. The parasitic tissues containing sporocysts of *L. minimus* were delicately separated from cockle tissues. The fresh weight of each of these separated tissues was immediately measured with a  $10^{-4}$  g precision scale. The dry weight was measured after 48 h in a  $50^\circ\text{C}$  oven.

In addition, oxygen consumption of *L. minimus* parasitic mass was examined in normoxia ranging from 14 to 21 kPa. In this case, all of the sporocysts containing eggs, developing and developed cercariae were extracted from cockle tissues. Then, they were suspended in 5 ml oxygen saturated filtered sea water within a glassware syringe following the method described in Quetin & Mickel (1987). After 10 minutes (lethal time for exhausting oxygen concentration) oxygen measurement was done by injecting vertically 1 ml of suspending liquid into the oxygen electrode. This injection was not abrupt but lasted during 2 minutes. Injections were repeated 4 times, and the water with sporocysts suspension was renewed 4 times after each measurement. At each time, the entire parasitic mass was examined in this manner. The oxygen consumption of this mass was calculated from equation, (Jørgensen, 1990):

$$MO_2 \cdot B^{-1} = V \cdot \alpha wO_2 \cdot (PO_2 \text{ at } t_0 - PO_2 \text{ at } t \text{ 10 min}) \cdot B^{-1}$$

Where,

$MO_2$ : the oxygen consumption per time unit ( $\mu\text{mol. min}^{-1}$ )

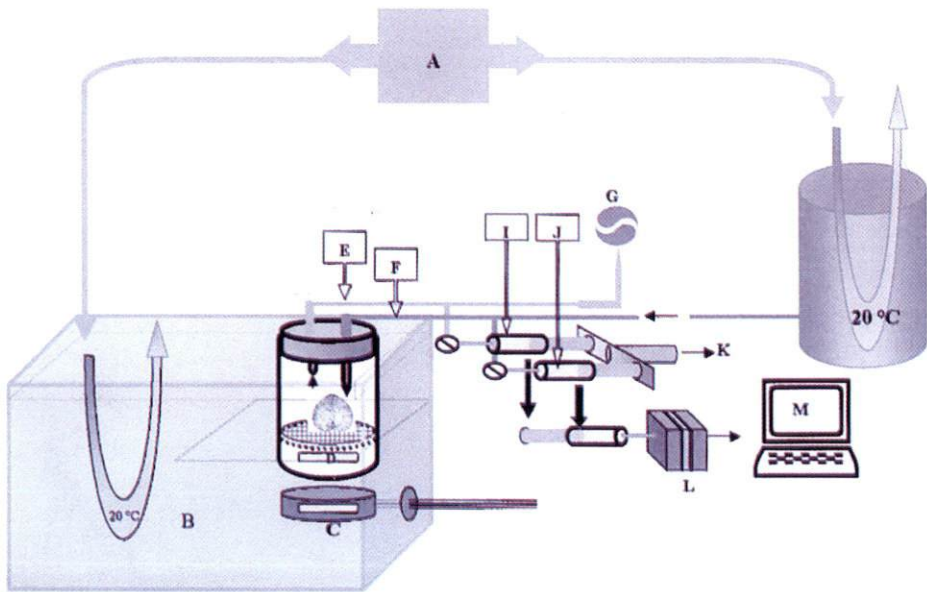
B: dry weight of parasitic mass (g)

V: volume of suspension at  $t_0$  (ml)

$\alpha_w O_2$ : oxygen solubility coefficient in sea water which is related to salinity and temperature ( $\mu\text{mol.}, \text{L}^{-1} \cdot \text{kPa}^{-1}$ ), (11,12 in our case)

$PO_2$  at  $t_0$  &  $t_0 + 10 \text{ min}$  oxygen partial pressure at the beginning and at the end of the 10 minutes incubation (ml).

Biometric measurements and fresh and dry weight of this mass were then performed.



**Figure3** : Respiration measurement unit. A & B: thermostatic baths of 20 °C, G: peristaltic pump that eject the seawater through E tube. C & D are stirrer with its magnet Bar. Each sample (I & J) is ejected through the stainless steel tubes (E & F) from measurement chamber that is suspended in thermostatic bath. In the chamber the cockle is situated on an oyster culture, 5 mm mesh size filet. Finally oxygen content of each sample was measured by radiometer (L).

## Results

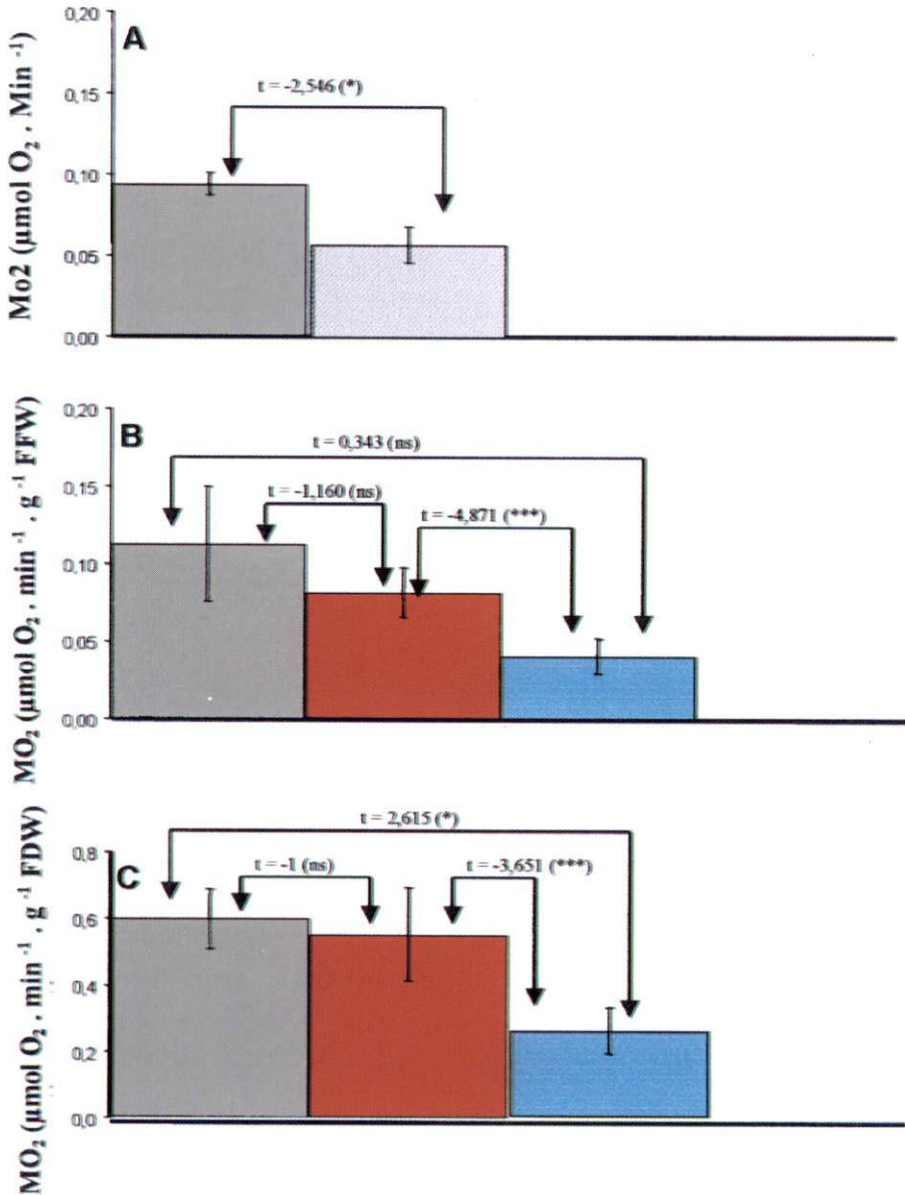
The mean size of infested cockles were 28.9 mm and the healthy ones 29.0 mm ( $P > 0.05$ ). The weight of extracted parasitic mass was 0.171 g Dry Weight (DW) in infested cockles. The weight of healthy cockles (0.189 g) DW was differ from infested ones (0.138 g) DW, parasitic mass removed but there was no significant difference between these values ( $t = -1.55$ ;  $p > 0.05$  ;  $df = 21$ ). Contrarily DW of infested cockles 0.31 g, was of 40% higher than that of healthy ones (0.19 g ,  $\sigma : 0.02$ ) T test.

Figure 4 shows the three different types of comparisons of oxygen consumption rates between infested animals and healthy ones used in this experiment as is recommended in the literature.

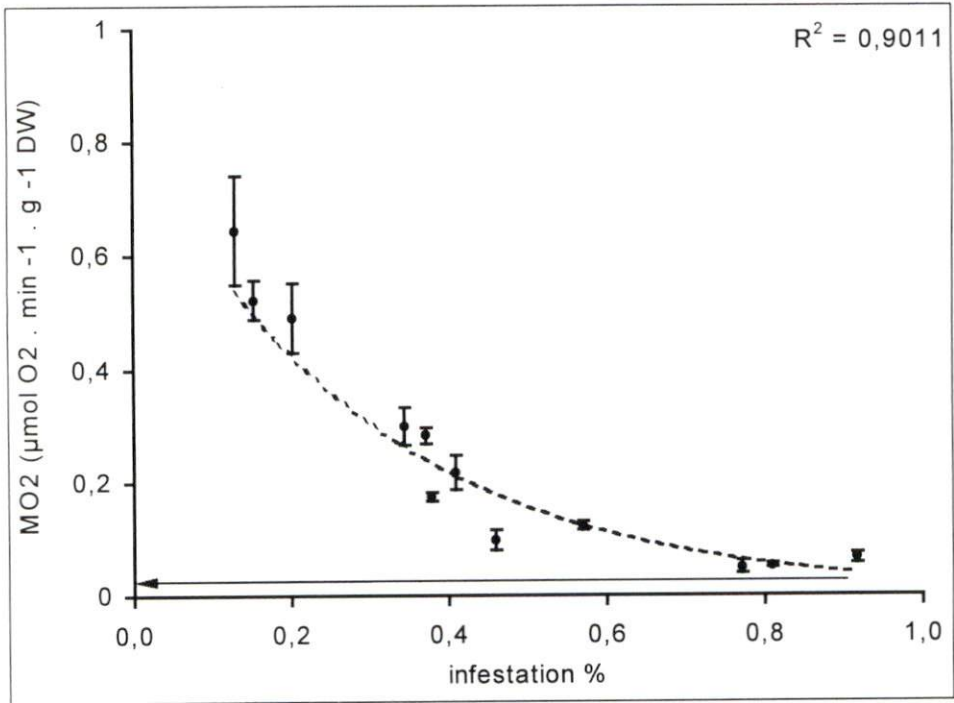
- (i) Comparison of fresh weight (FW)
- (ii) Comparison of dry weight (DW), the most commonly used in literature
- (iii) Comparison of animal size.

The results indicate that the oxygen consumption rate of a 29 mm healthy cockle is greater than that of an infested cockle (Figure 3A). Although we have seen above that the healthy cockles have a higher weight than the infested ones (parasitic mass removed). It is noticeable from Figure 3B and 3C that the oxygen consumption of cockle per gram weight is independent from the parasite presence. Thus the weakest oxygen consumption of a cockle can be related to its lesser body weight. The host oxygen consumption is also related to infestation intensity as shown on Figure 5.





**Figure 4:** A comparison between oxygen consumption values of infested (red column) cockles, healthy cockles (grey column) and parasitic mass (blue column) expressed in three different ways : (A): per cockle, B : per fresh flesh weight and (C) per day flesh weight. White area: healthy cockle, horizontal rays: per parasite mass removed cockle weight and vertical rays: parasite respiration. The bars show standard error of average.



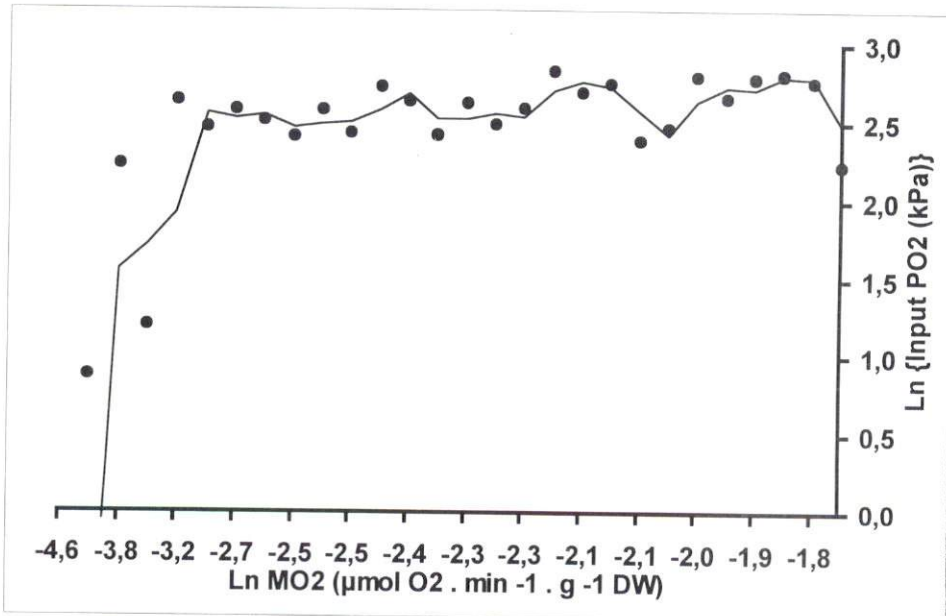
**Figure 5:** Relation between oxygen consumption rate and infestation ratio (parasitic mass/ cockle weight). This figure shows that above 92% infestation (the red line) the host enter in a lethal stage following to decrease of oxygen consumption.

The greater the parasitic mass, the lesser the oxygen consumption per gram body weight. This consumption approaches values near to  $0.01 \mu\text{mol}$  when 92% of body weight is infested with the parasitic mass. It can be estimated that beyond this proportion of parasitic weight, the cockle reaches a lethal stage with almost all of its body mass infested with *Labratrema minimus*.

The results of parasitic mass oxygen consumption show that, contrary to what is commonly accepted in the literature, where, trematods have not any aerobic metabolism (Cassier *et al.*, 1998), the oxygen consumption of the Digenean trematods is not null. Here, we observe that *L. minimus* consumes  $0.11 \mu\text{mol O}_2 \cdot \text{g}^{-1} \text{DW}$ , which approximately represents 20% of the cockle oxygen consumption. It is clear that the parasitic mass extracted from cockle body was not a uniform mass and consisted of sporocystes, cercariae and perhaps a few cockle internal tissues.

And a large proportion belonged to *L. minimus* active live mass. This result shows that the parasitic mass may represent up to 92% of cockle dry weight. A negative correlation between infestation intensity and respiration rate was observed during the experiments. These data show that the more the cockle is infested, the weaker is its oxygen absorption.

The distribution of points of  $\text{Mo}_2$  consumed per dry weight unit of *L. minimus* intensity show that the parasitic mass has an oxygen regulator capacity (Fig. 6). The oxygen consumption of parasite can't increase above a limit whatever is the  $\text{Peo}_2$  level and the threshold remains at  $0,32 \mu\text{mol O}_2 \cdot \text{g}^{-1}$ . A relation between  $\text{PO}_2$  input (kPa) and  $\text{Mo}_2$  show that the parasitic mass of *L. minimus* regulates its oxygen consumption even if oxygen consumption increases (Fig. 6).



**Figure 6:** (Ln × Ln) Points distribution of *L. minimus* mass respiration measurements. It could be observed that *L. minimus* needs oxygen to arrive in a platform that limit its consumption at  $0,32 \mu\text{mol O}_2 \cdot \text{g}^{-1} \text{DW}$ .

## Discussion

In this study we have used the breathing physiology of bivalves as a comparison in the responses to interactions with host-parasite ecology. We have focused on the aerobic metabolism–ventilation activity and parasitism interactions, which has not been considered so far in literature for bivalve respiration and filtration rate studies.

All cockles used in this study were transported to the laboratory 1 to 2 days before the experiment started. Knowing that the collection of animals can be stressful, sufficient recovery period must be allowed prior for optimising the respiration rate. We have used this stress as a stimulant to aggravate the potential differences between infested and healthy individuals. Transport stress is known as a strong filtration (and equally respiration) stimulus for the aquatic organisms (McMahon, 1985; Truchot, 1992; Legeay & Massabuau, 1999). Our results showed that with the same body size, infested cockle consumes less oxygen than a healthy one in controlled conditions. The study shows that the difference is essentially due to the difference between parasitic mass and cockle mass. (with a same size, infested cockle has a weight higher than a healthy one). Equally, we have shown that a suspension of *Labratrema minimus*, which is considered to have anaerobic metabolism (Grassé *et al.* 1970), consumes oxygen. Although these parasites do not live in a very high oxygenated conditions, because the oxygenation state within a bivalve is at the weak values like the cases of *Modiolus demissus* (Booth & Mangum, 1978), *Anodonta cygnea* (Massabuau *et al.*, 1991), and *Corbicula fluminea* (Tran, 1997), but it can represent 20 % of its host oxygen consumption. It has an oxygen consumption regulation system and it needs an oxygen concentration between 2 to 4 kPa. Thus, no matter the surrounding oxygen concentration is, it needs up to 4 kPa oxygen concentration in its media. This oxygen concentration is required to maintain the parasitic mass in sporocystic stage.

For a host-parasite interaction, the cockle must pump the water in order to fulfill its needs and the needs of parasites lodging in it. If we assume this hypothesis, then the parasite cockles must have an oxygen consumption and filtration rates higher than the healthy ones due to the parasitic mass added. But we have shown that this conjugated mass has oxygen requirements lower than healthy cockle tissue which does not exceed 20% of oxygen needs. This interaction seems to be progressive as the sporocysts developed. Our results also show that in high

infestation with *L. minimus* (up to 90% of FDW), oxygen consumption approaches to  $0,05 \mu\text{mol O}_2 \cdot \text{min}^{-1} \cdot \text{g}^{-1} \text{DW}$  which is a very few value compared to normal specific oxygen consumption rate of healthy ones. The respiration below this value may be lethal to host comparing to its high oxygen consumption in healthy conditions. Also as we have seen that the parasitic mass has an oxygen consumption regulator property, and decrease in oxygen consumption in high infested cockles could lead them into a lethal state. The parasitism notion was not taking into account in previous studies about bivalve filter feeding or modelling related to bivalve filtration rates. Based on our information, it is the first approach to problem of parasites influence on the pumping rate and it shows the difference of behaviour between two groups in the same conditions when the parasitism is considered as a factor. A comparison of our data with many of those in literature shows that variety could not be estimated when parasitism is not considered as an influencing factor.

Otherwise, results of filtration rate experiments show that the parasite cockles have a pumping rate weaker than the healthy ones. The decrease in pumping rate is with a limitation in variety of filtration scale. This result shows that the cockles parasite with *Labratrema minimus* have handicap per adaptation to laboratory conditions compared to the healthy ones. The latter have pumped the water comfortably in a large choice contrary to the parasite ones. Accepting that the collection of animals from their natural habitat and their transport to the laboratory are stress factors (Theed, 1963 ; Widdows, 1985 ; Legeay & Massabuau, 1999), unpublished results showed that the parasited cockles were also indifferent to this stress.

A comparison between both experiments of oxygen consumption as well as filtration rate measurements, predict that the two actions are related in the *C. edule*. It pumps the water in order to capture the nutrient particle and insures its oxygen requirements. These two related factors are thus rather weaker in the parasited cockles. These decreases are highly related to their parasitic states because both groups of animals (healthy and parasited) were used in exactly similar conditions. As it has been shown, the high parasitism with *Labratrema* leads to a state in which the host's party from oxygen absorption become lower and lower.

In conclusion, we consider parasitism as the main factor in pumping rate and oxygen consumption in bivalves.

## References

- Bayne, B.L., Hawkins, A.J.S. and Navarro, E. , 1987. Feeding and digestion by the mussel *Mytilus edulis* L. (Bivalvia: Mollusca) in mixture of silt and algal cells at low concentrations. *J. Exp. Mar. Biol. Ecol.*, Vol. 111, pp.1-22.
- Beninger, P. G. ; Le Pennec, M. and Donval, A. , 1991. Mode of particle ingestion in five species of suspension-feeding bivalve molluscs. *Mar. Biol.*, **108**:255-261.
- Bernard, F.R. and Noakes, D.J. , 1990. Pumping rates, water pressures, and oxygen use in eight species of marine bivalve molluscs from British Columbia. *Can. J. Fish. Aquat. Sci.* **47**:1302-1306.
- Booth, C.E. and Mangum, C.P. , 1978. Oxygen uptake and transport in the lamellibranch mollusc *Modiolus demissus*. *Physiol. Zool.*, **51**:17-32.
- Byrne, R.A. ; Gnaiger, E. ; McMahon, R.F. and Dietz, T.H. , 1990. Behavioral and metabolic responses to emersion and subsequent reimmersion in the freshwater bivalve *Corbicula fluminea*. *Biol. Bull.*, **178**:251-259.
- Cassier, P. ; Brugerolle, G. ; Combes, C. ; Grain, J. and Raibaut, A. , 1998. Le parasitisme. Un équilibre dynamique. Masson, 365 P.
- Collier, A. , 1959. Some observations on the respiration of the American oyster, *Crassostrea virginica* (Gmelin). *Publ Inst. Mar. Sci. Univ. Tex.* **6**:92-108.
- Dejours, P. , 1972. Comparison of gas transport by convection among animals. *Respir. Physiol.* **14**:96-104.
- Dejours, P. , 1981. Principales of comparative respiratory physiology. Elsevier, 265 P.
- Devilliers, C.J. ; Allanson, B.R. and Hodgson, A.N. , 1989. The effect of temperature on the filtration rate of *Solen cylindraceus* (Hanley) (Mollusca : Bivalvia). *S. Afr. J. Zool.* **24**:11-17.
- Dorgelo, J. and Smeenk, J.W. , 1988. Contribution to the ecophysiology of *Dreissena polymorpha* (Pallas) (Mollusca: Bivalvia): growth, filtration rate and respiration. *Verh int Verein Limnol.*, **23**:2202-2208.

- Eriksen, N.T. and Iversen, J.J.L. , 1997. On-line determination of respiration rates of aquatic organisms in a mono-phase oxystat at steady-state dissolved oxygen tension. *Mar. Biol.*, **128**:181-189.
- Garton, D.W. and Haag, W.R. , 1991. Heterozygosity, shell length and metabolism in the European mussel *Dreissena polymorpha*, from a recently established population in Lake Erie. *Comp. Biochem. Physiol.*, **99**: 45-48.
- Grassé, P.P. ; Poisson, R.A. and Tuzet, O. , 1970. Zoologie. I. Invertébrés. 2e éd.,
- Hamburger, K. ; MØhlenberg, F. ; Randlov, A. and Riisgard, H.U. , 1983. Size, oxygen consumption and growth in the mussel *Mytilus edulis*. *Mar. Biol.*, **75**:303-306.
- Hawkins, A.J.S. ; Navarro, E. and Iglesias, J.I.P. , 1990. Comparative allometries of gut-passage time, gut content and metabolic faecal loss in *Mytilus edulis* and *Cerastoderma edule*. *Mar. Biol.* **105**:197-204.
- Javanshir, A. , 1999. Effets de quelques parasites (Digenea) sur la dynamique des populations et la physiologie respiratoire de la coque *Cerastoderma edule* (Mollusque: Bivalve) dans le bassin d'Arcachon. Thèse de doctorat de l'Université Paris , 6, 102 P.
- Jørgensen, C.B. , 1990. Bivalve filter feeding: hydrodynamics, bioenergetics, physiology and ecology. Olsen & Olsen, Fredensborg, 140 P.
- Legeay, A. and Massabuau, J.C. , 1999. Blood oxygen requirements in resting crab *Carcinus maenas* 24 hours after feeding. *Can. J. Zool.*
- McMahon, B.R. , 1985. Functions and functioning of crustacean hemocyanin. *In*: Respiratory pigments in animals. Relation structure function. J. (Eds. N. Lamy; J.P. Truchot and R. Gilles). Springer, New York, pp.35-58.
- Marsden, I.D. and Weatherhead, M.A. , 1998. Effects of aerial exposure on oxygen consumption by the New Zealand mussel *Perna canaliculus* (Gmelin, 1791) from an intertidal habitat. *J. Exp. Mar. Biol. Ecol.*, **230**: 15-29.
- Massabuau, J.C. ; Burtin, B. and Wheathly, M. , 1991. How is O<sub>2</sub> consumption maintained independent of ambient oxygen in mussel *Anodonta cygnea*?. *Respiration Physiology*, **83**:103-114.

- Quetin, L.B. ; Mickel, T.J. and Childress, J.J. , 1987. A method for simultaneously measuring the oxygen consumption and activity of pelagic crustaceans. *Comp. Biochem. Physiol.* **59 A**: 263-266.
- Schulte E.H. , 1975. Influence of algal concentration and temperature on the filtration rate of *Mytilus edulis*. *Mar. Biol.*, **30**:331-341.
- Smaal, A.C. , 1998. Food supply and demand of bivalve suspension feeders in a tidal system. Thèse de doctorat, Université de Groningen. 237 P.
- Theede, H. , 1963. Experimentelle Untersuchungen über die Filtrationleistung der Meeresmuschel *Mytilus edulis* L. *Kielę Meeresforschungen.*, **19**:20-41.
- Tran, D. , 1997. Influence de l'oxygénation de l'eau et de l'activité respiratoire sur les mécanismes de bioaccumulation du cadmium chez le bivalve d'eau douce *Corbicula fluminea*. DEA Université Bordeaux 1, 23 P.
- Truchot, J.P. , 1992. Respiratory function of arthropod hemocyanins. *In* : *Advances in Comparative and Environmental Physiology*, (ed.C.P. Mangum). Springer, Heidelberg, Vol. 13, pp.378-410.
- Vismann, B. , 1990. Field measurements of filtration and respiration rates in *Mytilus edulis* L.: an assessment of methods. *Sarsia*, **75**:213-216.
- Ward, J.E. , 1986. Effects of the ectoparasite *Boonea (Odostomia) impressa* (Say) (Gastropoda: Pyramidellidae) on the growth rate, filtration rate and valve movements of the host *Crassostrea virginica* (Gmelin). *J. Exp. Mar. Biol. Ecol.*, **99**:163-180.
- Widdows, J.P. , 1985. *Physiological Procedures. The effects of stress and pollution on marine animals.* (ed. B.L. Bayne). Praeger Publishers. New York, pp.161-178
- Willemsen, J. , 1952. Quantities of water pumped by mussels *Mytilus edulis* and cockles *Cardium edule*. *Arch. Néerl. Zool.*, **10**:153-159.
- Winter, J. , 1969. On the influence of food concentration and other factors on filtration rates and food utilization in the mussels *Arctica islandica* and *Modiolus modiolus*. *Mar. Biol.* **4**:87-135.