C. R. Biologies 335 (2012) 261–270

Contents lists available at SciVerse ScienceDirect

Comptes Rendus Biologies

www.sciencedirect.com

Physiology/Physiologie

First respiration estimates of cold-seep vesicomyid bivalves from *in situ* total oxygen uptake measurements

Première estimation des taux de respiration des bivalves Vesicomyidae des sources de fluides froids, par des mesures in situ de flux d'oxygène

Carole Decker *, Jean-Claude Caprais, Alexis Khripounoff, Karine Olu *

IFREMER Centre de Brest, Unité Étude des Écosystèmes Profonds, 29280 Plouzané, France

ARTICLE INFO

Article history:
Received 3 November 2011
Accepted after revision 6 March 2012
Available online 24 April 2012

Keywords:
Vesicomyid bivalves
Total oxygen uptake
Methane flux
Respiratory rate
Benthic chamber
Cold-seep

ABSTRACT

Vesicomyid bivalves are one of the most abundant symbiont-bearing species inhabiting deep-sea reducing ecosystems. Nevertheless, except for the hydrothermal vent clam *Calyptogena magnifica*, their metabolic rates have not been documented, and only assessed with *ex situ* experiments. In this study, gathering benthic chamber measurements and biomass estimation, we give the first *in situ* assessment of the respiration rate of these bivalves. The giant pockmark Regab, located at 3160 m depth along the Congo-Angola margin, is a cold-seep site characterised by dense assemblages of two species of vesicomyids: *Christineconcha regab* and *Laubiericoncha chuni* with high dominance of *C. regab*. Two sites with dense aggregates of vesicomyids were selected to measure total oxygen uptake (TOU), and methane fluxes using IFREMER's benthic chamber CALMAR deployed by the ROV *Quest 4000* (MARUM). Photographs were taken and bivalves were sampled using blade corers to estimate density and biomass. Total oxygen uptake was higher at Site 2 compared to Site 1 (respectively 492 mmol.m^{-2}.d^{-1} and 332 mmol.m^{-2}.d^{-1}). However, given vesicomyid densities and biomass, mean oxygen consumption rates were similar at both sites (1.9 to 2.5 μmol.g total dry mass^{-1}.h^{-1} at the Site 1 and 1.8 to 2.3 μmol.g total dry mass^{-1}.h^{-1} at Site 2). These respiration rates are higher than published *ex situ* estimates for cold-seep or hydrothermal vent bivalves. Although methane fluxes at the base of sulphide production were clearly higher at Site 2 (14.6 mmol.m^{-2}.d^{-1}) than at Site 1 (0.3 mmol.m^{-2}.d^{-1}), they do not seem to influence the respiration rates of these bivalves associated to sulphide-oxidizing symbionts.

Mots clés :
Bivalves Vesicomyidae
Flux total d'oxygène
Flux de méthane
Taux de respiration
Chambre benthique
Sources de fluides froids

RÉSUMÉ

Les bivalves Vesicomyidae sont l'une des familles d'espèce symbiotrophiques dominantes dans les écosystèmes réducteurs profonds. Cependant, à l'exception de l'espèce hydrothermale *Calyptogena magnifica*, leur métabolisme est peu connu et uniquement estimé à partir d'expérimentations ex situ. Dans cette étude, le taux de respiration de ces bivalves est estimé in situ pour la première fois, à l'aide d'une cloche benthique manipulée par un ROV et de la quantification de leur biomasse. Le pockmark géant Regab, localisé à 3160 m de profondeur le long de la marge Congo-Angolaise, est un site d'émission de fluides froids caractérisé par des agrégats denses de bivalves Vesicomyidae des espèces *Christineconcha regab* qui domine, et *Laubiericoncha chuni* plus rare. Deux sites ont été

* Corresponding authors.
E-mail addresses: carole.decker@ifremer.fr (C. Decker), karine.olu@ifremer.fr (K. Olu).

1631-0691/$ – see front matter © 2012 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.
doi:10.1016/j.crvi.2012.03.002

sélectionnés pour mesurer le flux total d'oxygène et le flux de méthane avec la cloche benthique CALMAR (IFREMER) manipulée par le ROV *Quest 4000* (MARUM). Des photographies des agrégats ainsi que des prélèvements quantitatifs ont été réalisés pour estimer la densité et la biomasse de bivalves. Le flux total d'oxygène est plus élevé sur le Site 2 que sur le Site 1 (respectivement 492 mmol.m^{-2}.j^{-1} et 332 mmol.m^{-2}.j^{-1}). Cependant, en prenant en compte la densité de bivalves et leur biomasse, le taux moyen de consommation d'oxygène est similaire sur les deux sites (1,9 to 2,5 μmol.g poids sec $total^{-1}$.h^{-1} au Site 1 et 1,8 to 2,3 μmol.g poids sec $total^{-1}$.h^{-1} au Site 2). Ces valeurs sont supérieures à celles publiées sur des estimations ex situ de taux de respiration de bivalves hydrothermaux. Bien que les flux de méthane, à la base de la production de sulfure, soient plus élevés sur le Site 2 (14,6 mmol.m^{-2}.j^{-1}) que sur le Site 1 (0,3 mmol.m^{-2}.j^{-1}), ils ne semblent pas influencer le métabolisme des bivalves associés à des bactéries symbiotiques sulfo-oxydantes.

1. Introduction

Vesicomyid bivalves are one of the most abundant chemosynthetic faunal species inhabiting deep-sea reducing ecosystems, including hydrothermal vents, whale falls and cold-seep ecosystems [1–3]. About 100 vesicomyid species are described worldwide mainly at bathyal and abyssal depths [4,5], and colonise the great majority of cold-seep sites. Vesicomyid bivalves live in symbiosis with sulphide-oxidising bacteria located in their gills [6,7]. These symbionts produce organic compounds used by bivalves for their nutrition and, in turn, the bivalve hosts supply their symbionts with oxygen, carbon dioxide and sulphide. Oxygen and carbon dioxide are directly available in the ambient seawater and are transported through the inhalant siphon to gills and the bacteria therein. Sulphide comes from the sediment and goes through the foot into the haemolymph and is thus transported to the gill [8]. Their metabolism is indirectly based on methane anaerobic oxidation (AOM) [9] producing sulphide used as energy source by the vesicomyid symbionts.

Metabolic rates of vesicomyids are not well known. Three studies on oxygen consumption rates have been performed *ex situ* measurements on hydrothermal vent vesicomyids in stainless steel vessels to maintain *in situ* pressure conditions during the experiment [8,10,11]. Arp et al. [8] assessed oxygen consumption rates in *Calyptogena magnifica* Boss and Turner, 1980 [12], and observed values were as high as those from shallow-water bivalves. Two other smaller species, *Calyptogena elongata* Dall, 1916 [13] and *Calyptogena pacifica* Dall, 1891 [14], show much lower oxygen consumption rates (average 0.2 μmol.g wet weight $[\text{without shell}]^{-1}h^{-1}$ [11]). Only one *in situ* measurement of oxygen consumption rate has been performed on *C. magnifica* on the Galapagos rift, giving an average rate of 0.4 μmol.g wet $weight^{-1}$.h^{-1} [11].

The first *in situ* measurements of methane, oxygen and carbon fluxes were carried out in several deep-sea environments using benthic chambers [15–18]. However, these devices deployed from the surface cannot specifically target selected biogenic habitats in highly heterogeneous environments such as cold-seeps or hydrothermal vents. A relatively new approach is to deploy benthic chambers with submersibles. These devices have been used at seeps to measure both methane and oxygen fluxes, to assess the role of microbial activity, especially anaerobic oxidation of methane [19,20], and the role of macrofauna, particularly through symbioses [20–22] in the regulation of seabed methane emissions (benthic biological filters). Differences in total oxygen uptake (TOU) have been observed between active seeps and "normal" sediments (from 2 to 20 times higher in active seeps) [20,21] and among seep habitats [20,22,23], revealing higher fluxes in macrofauna clusters than in microbial mats on Håkon Mosby mud volcano (HMMV) [22]. In these papers, TOUs have been measured *in situ* by autonomous or ROV-manipulated chambers in microbial mats, vesicomyid beds, siboglinid or ampharetid polychaete fields. Only one *in situ* oxygen uptake estimation on vesicomyid bivalves has been obtained with a benthic chamber deployed from the surface, remotely guided for habitat selection, but without estimation of the density and biomass of individuals [20]. TOUs also vary according to advective methane fluxes and show a negative relationship across the HMMV ecosystem [22].

The giant Regab pockmark off Gabon, located at 3160 m depth along the Congo-Angola margin, is characterised by dense assemblages of vesicomyids, mytilids and escarpids distributed along a gradient of methane concentrations decreasing from the centre to the periphery [24]. Two species of vesicomyids – *Christineconcha regab* Cosel & Olu, 2009 [4,25] and *Laubiericoncha chuni* Cosel & Olu, 2008 – are found in the pockmark, where *C. regab* largely dominates. The giant pockmark was re-visited by the ROV *Quest 4000* (MARUM, University Bremen, Germany) in 2008. We selected several vesicomyid beds in the centre and at the south-west border of the active area to: (1) perform *in situ* benthic fluxes measurements to estimate vesicomyid respiratory rates; and (2) compare TOU on clam beds of various density with different methane levels along this cold-seep ecosystem.

2. Materials and methods

2.1. Study site

The giant pockmark Regab (800 m wide and 15 m deep) was discovered in 2001 at 3160 m depth along the Congo-Angola margin [24]. Dense assemblages of symbiont-bearing species including Bathymodioinae, Escarpiidae and Vesicomyidae have been observed along a NE-SW axis