Deep–Sea Research I 118 (2016) 30–36

Contents lists available at ScienceDirect

Deep–Sea Research I

journal homepage: www.elsevier.com/locate/dsri

In situ respiration measurements of megafauna in the Kermadec Trench

Clifton C. Nunnally*, Jason R. Friedman, Jeffrey C. Drazen

University of Hawai'I at Manoa, Department of Oceanography, 1000 Pope Road, Honolulu, HI 96822, USA

ARTICLE INFO

Keywords:
Respiration
Hadal
Holothurian
Polychaete
Anemone
Kermadec Trench
In situ
Metabolism

ABSTRACT

The aim of this paper is to measure metabolic rates of megafauna living in depths greater than 6000 m. Echinoderms, actinarians and a polychaete were captured by remotely operated vehicle (ROV) and inserted into respiration chambers in situ at depths of 4049 m, 7140 m and 8074 m in the region of the Kermadec Trench SW Pacific Ocean. Hadal research has moved into a new frontier as technological improvements now allow for a meticulous investigation of trench ecology in depths greater than 6000 m. The development of an in situ respirometer for use in these studies was deployed in the Kermadec Trench to obtain the first ever rates of basal metabolic rates of hadal megafauna. Typical deep-sea experiments of individual animal physiology must deal with covarying factors of pressure, temperature, light and food supply in this study investigated the effects of pressure and increased food supply on overall animal metabolism. In the Kermadec Trench, holothurian respiration rates (n=4), 0.079 ± 0.011 (mean ± SE) μmol-O_2 g^{-1} h^{-1}, were higher than those captured at abyssal depths (n=2), 0.018 ± 0.002 μmol-O_2 g^{-1} h^{-1}, in the same region ($p < 0.001$). When Q_{10} adjusted to a common temperature of 2.5 °C trench holothurian respiration rates ranged between 0.068 and 0.119 μmol-O_2 g^{-1} h^{-1}. Anemone respiration rates were remarkably similar between abyssal and hadal specimens, 0.110 and 0.111 μmol-O_2 g^{-1} h^{-1}, respectively. Our results on echinoderm respiration when corrected for temperature and mass fall below the slope regression when compared with other in situ measurements at shallower ocean depths.

1. Introduction

Hadal (depths greater than 6000 m) investigations have focused primarily on examining the diversity and in some cases relative abundances of the trench fauna. These studies have identified declines in diversity and suggest that meiofaunal (Danovaro et al., 2002; George and Higgins, 1979; Itoh et al., 2011), megafaunal (Beliaev, 1989) and holothurian (Hansen, 1956; Wolff, 1960) abundances increase with depth. The trenches represent the deepest ~45% of the oceans and increasing hydrostatic pressures may limit the species that have evolved the capacity to live there. Increased abundance of some taxa may exist due to increased food supply from channeling of detritus, downslope transport of sediment, and turbidity flows from seismic activity (reviewed in Jamieson et al., 2010). Indeed accumulation of organic carbon in trenches may actually increase as the distance from surface production increases (Ichino et al., 2015; Itou, 2000; Oguri et al., 2013).

Little research has yet begun to explore hadal food webs and carbon budgets. An important component of such research is understanding trophic linkages. The diets of a few fauna such as amphipods have been investigated with a variety of biomarkers (Blankenship and Levin, 2007; Kobayashi et al., 2012; Perrone et al., 2003). Another important component is determining the energy usage or metabolic rates of individual taxa or faunal groups. Metabolic rates can be used to construct models of the flow of energy and materials in an ecosystem (Childress and Thuesen, 1992; Christiansen et al., 2001; Smith, 1992; Smith et al., 2001). In the deep sea, energetic demands can be extrapolated from data on shallow living animals by using models of the mass and temperature dependence of metabolic rate (Mahaut et al., 1995), or they are based on a handful of measurements of representative taxa (Ambrose et al., 2001; Piepenburg and Schmid, 1996; Smith, 1992; Smith et al., 2001). It remains unclear whether the energetic demands/metabolism of the trench fauna can be extrapolated from work on shallower living animals.

Pelagic fish, crustaceans and cephalopod metabolism in the deep-sea is predicted to vary with light levels, and thus depth to about 1000 m, and the nature of predator prey interactions (Childress, 1995; Seibel and Drazen, 2007). In the dimly lit and sparsely populated deep-sea, predators and prey do not interact as frequently or over as large a distance, relaxing the need for locomotory capacity which reduces metabolism. This argument is supported by the fact that sighted taxa exhibit depth-related metabolic declines but non-visual groups such as

* Corresponding author. Current address: Louisiana Universities Marine Consortium (LUMCON), 8124 Highway, Chauvin, LA 70344, United States.
E-mail addresses: cnunn@hawaii.edu, cnunnally@lumcon.edu (C.C. Nunnally).

http://dx.doi.org/10.1016/j.dsr.2016.10.009
Received 22 January 2016; Received in revised form 13 October 2016; Accepted 19 October 2016
Available online 26 October 2016

holothurians do not (Hughes et al., 2011; Seibel and Drazen, 2007). In contrast, recent data on non-visual copepods found declines from the epipelagic to the abyssopelagic (Ikeda et al., 2006; Wilson et al., 2013). The role of food supply in governing the evolution of individual basal metabolic rates has largely been discounted (McClain et al., 2012; Seibel and Drazen, 2007) but a variety of animals respond to low rations by depressing routine metabolism (Christiansen and Diel-Christiansen, 1993; Sullivan and Smith, 1982; Yang and Somero, 1993) suggesting at least some effect intraspecifically. Past studies suggest that pressure does not greatly affect metabolic rates (Belman and Gordon, 1979; Childress, 1977; Meek and Childress, 1973) though there are clearly many examples of molecular adaptation to ensure cellular activity and the depth limits of different groups are likely constrained by their physiological adaptations to pressure (Yancey et al., 2014). In previous studies it has been difficult to separate the covarying effects of food supply, temperature, light, and pressure on metabolic rates. Thus in situ measurements of hadal respiration rates could provide a test both for the effects of pressure and that of increased food availability, while keeping other factors of light, and temperature constant.

Hadal ecological studies have entered a new era of investigation due to advances in submersible vehicles and full-ocean depth rated instruments. The development of hadal Remotely Operated Vehicles (ROV) such as Kaiko (Kyo et al., 1995) and Nereus (Bowen et al., 2009) have provided the ability to explore the hadal environment in a reactive manner and to precisely make measurements, take samples, and conduct experiments. Here, we use a full-ocean depth *in situ* respirometer, manipulated by Hybrid Remotely Operated Vehicle (HROV) Nereus, within the Kermadec Trench, to measure hadal animal metabolism for the first time. Our objective was to test echinoderms and abundant megafauna found commonly in the hadal realm for variations in overall respiration as depth and ostensibly food supply increased within the Kermadec Trench (Ichino et al., 2015; Itou et al., 2000)(Fig. 1). Lack of suitable dives during the expedition did not provide us with the expected abundance of respiration measurements. However, we do compare our limited measurements to bathyal and abyssal species and provide data that can ultimately be used to compose hadal carbon budgets and food web models.

2. Materials and methods

2.1. In situ respirometer

The respirometer consisted of five main components that allow for in situ measurement of oxygen consumption anywhere in the ocean. These were the pressure housing, junction box, Deep-Sea Power and Light (DSPL) battery, umbilical/manifold and the chamber assembly (Fig. 2A). The pressure housing, a titanium cylinder, contained data recorders and a voltage regulator that modulated the flow rates of stirring pumps. Adjustable flow rates allowed us to deploy the respirometer with both large (0.97 L) and small (0.60 L) chambers that could be swapped out depending on the assumed target animal size. Tests measured total volume turnover of less than one minute using an injected dye to calibrate homogenous but gentle mixing. The junction box is an oil filled volume that incorporated the electrical and data feed of the pressure housing, the power supply from the battery which was distributed through the umbilical cable. A 5 m umbilical cable served as the conduit for all functions necessary for the incubation of animals within the chamber assembly. The long length allowed ample manipulative space for respirometer assembly after being placed onto the elevator platform. The manifold dispersed data feeds and power to each oxygen optode/pump pair that made up the instrument package of the individual incubation chambers. The chamber assembly consisted of two parts, the collection chambers and the lid assembly. The incubation chambers were sealed once the two halves are joined and locked together by the ROV. Viton o-rings were using on the chambers to ensure a tight seal that would prevent leaks. Once assembled the oxygen optode (Aanderaa) recorded dissolved oxygen and temperature values at specified intervals (30 s) and the submersible pump (SeaBird) ensured adequate water flow to ensure a homogenous water volume. The respirometer was deployed using an elevator which delivered the pressure housing, junction box, battery and the lid assembly to the seafloor. The delivery of the in situ respirometer with the elevator eliminated extra ROV bottom time freeing it for more dive tasks. The incubation chambers were carried to the seafloor on the instrument tray of the HROV Nereus. Stainless steel trap doors with a spring mechanism were held open until an animal was deposited into a chamber using the Nereus slurp gun. The traps doors were perforated with large holes that prevented animals from reaching the optode or pumps when closed and also allowed the pump to circulate and mix the chamber water.

2.2. Animal collection

All but the chambers of the respirometer were deployed on a hadal elevator (instrument package, battery, and pressure housing) prior to HROV Nereus dives. Nereus, carrying the rosette of animal chambers, used its suction sampler to collect suitable animals (echinoderms, anemones and polychaetes), place them in individual chambers and close the trap-door lids as it proceeded towards the elevator site. At the elevator the respirometer was assembled beginning experiments (Fig. 2B), free from the motion and activity of the ROV. The first 2–3 h of each experiment were not used to allow the animals to adjust to the chamber. Once regular oxygen declines began, data was considered suitable for analysis. Experiments ranged in duration from 14 to 35 h. At the end of incubations animals were retrieved upon recovery of the elevator at the surface. Collection of animals and experiments were performed between April 11 and May 4, 2014 (Table 1). Unfortunately the number of planned experiments was curtailed by the loss of the HROV Nereus on May 9, 2016 due to catastrophic implosion of the vehicle at 10,000 m.

Replicate measurements were made by dividing the linear consumption of oxygen into equal time segments and calculating the resulting rate. Each in situ set of experiments were accompanied by a control experiment that measured oxygen consumption in an empty incubation chamber. This value was used to account for microbial respiration in the ambient bottom water.

2.3. Tissue processing

Animals were weighed wet after recovery using a motion compensated scale and submerged in seawater to determine displacement volume using a graduated cylinder. Tissue samples were collected from each incubated organism by dissecting a large piece of the body wall of holothurians or the entire cross section for other animals and frozen in cryo-vials in liquid nitrogen and stored at −80 °C. In the lab, tissue was weighed wet placed into pre-combusted tin foil wells and dried for 48 h at 60 °C to obtain dry weight. Samples were then combusted for 4 h at 550 °C and weighted for the remaining tissue as ash. Ash free dry weight was calculated by subtracting the remaining tissue from the dried value.

2.4. Mass specific respiration rates and Q_{10} adjustments for temperature

Respiration was calculated by dividing the change in dissolved oxygen ($\Delta[O_2]$) within the experimental water volume (V) by the time (T) of the incubation. All chamber volumes were corrected for the animal by assuming a density of 1 ml per gram. Mass specific respiration rates are then calculated by dividing by the mass of the animal (M) (Eq. (1)).