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In situ respiration measurements of megafauna in the Kermadec Trench

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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

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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)).

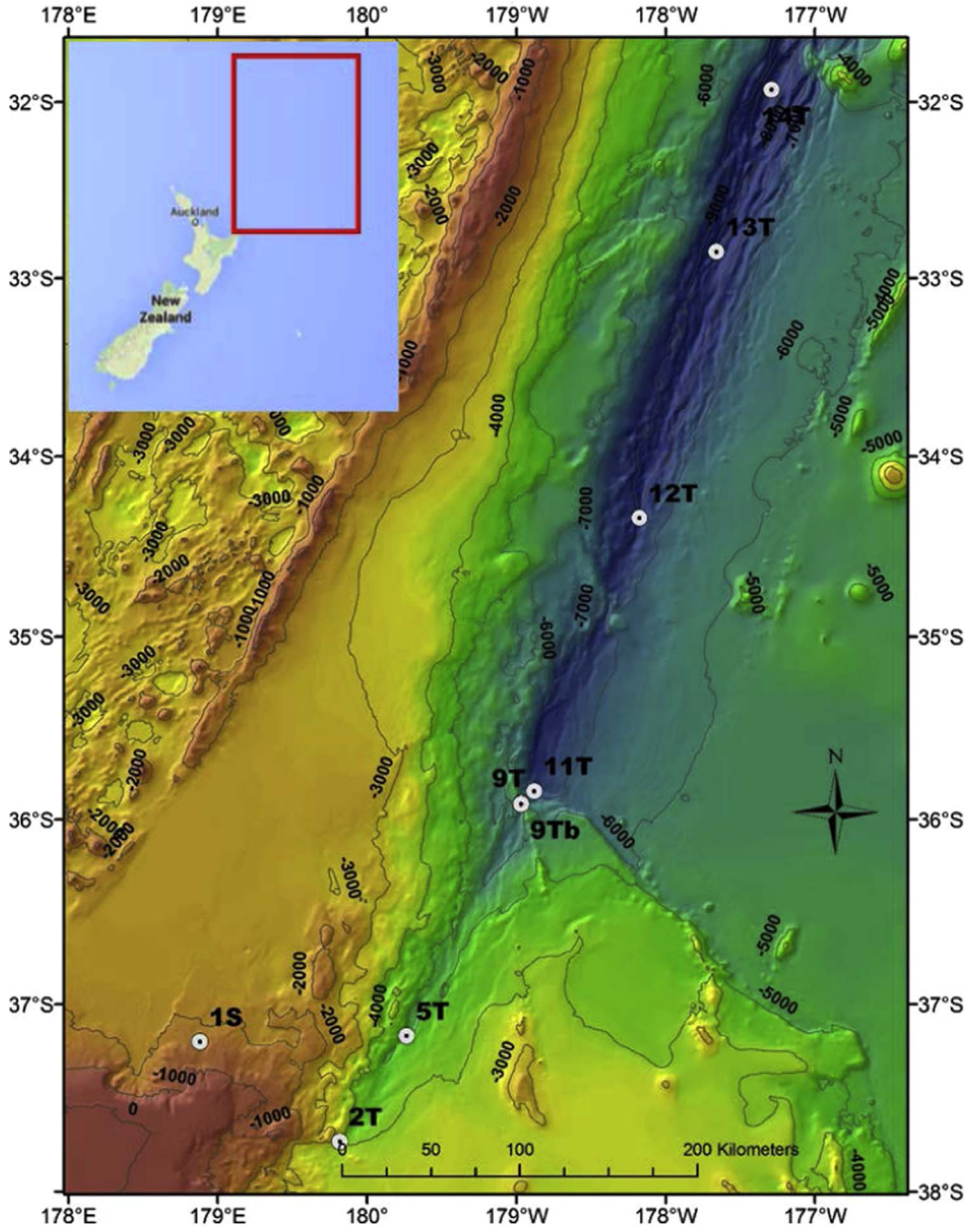

Fig. 1. Map of study area. Inset shows the location of the study area to the North of New Zealand. Station details are given in Table 1.

$$R=(\Delta[O2]xV)/(TxM) \quad (1)$$

To compare hadal animal metabolism to values in the literature, we adjusted values to a common temperature of 2.5 °C using the Q_{10} value of 2.15 as used in Hughes et al. (2011). None of our other experimental organisms can boast the number of published studies to accomplish a similar analysis, thus 2.15 was used for Q_{10} transformations on all experimental rates.

3. Results

The respirometer was deployed 9 times in the region of the Kermadec trench; one test site at ~1600 m and then at roughly 1000 m increments from 4000 to 10000 m. Aside from the 1500 m test site, consistent changes in oxygen and temperature were seen with depth proceeding from the abyssal to the deepest hadal sites (Table 1). Temperature within the Kermadec trench was 1.16 at 6000 m and increased to 1.83 at 10,000 m via adiabatic heating (Jamieson et al., 2010; Taira et al., 2005). Dissolved oxygen was highest (~205–207 μm) at abyssal depths, with a regular but small amplitude decline to a depth of 9989 m (171 μm).

Specimens ranged in size from 1 to 53 g wet weight (Table 2). Specimens captured at abyssal site were all larger than the hadal specimens except for the ophiuroid. Holothurians captured at 7130 and 8074 m for respiration experiments were 2 g wet weight. The polychaete and anemone were the largest animals incubated at hadal depths, with masses of 6 and 4 g respectively. Ash-free dry weight as a percentage of wet weight ranged from 1.125% to 13.95%. The range of water content among specimens was 55.9–90.4%.

Respiration rates varied by taxa (Table 2). The highest mass specific rate was for the ophiuroid from 4000 m depth and the lowest rates were for the large holothuroids from this same station. The mass specific respiration rates of the hadal holothurians were higher than those from the abyssal station but all of these differences are largely driven by variations in body mass. Presentation of mass specific animal respiration as a function of body mass clearly illustrates this point (Fig. 3). Due to the limited amount of data comparisons between depths cannot be made robustly. However, generally the respiration rates of the ophiuroid, polychaete and abyssal anemones were higher

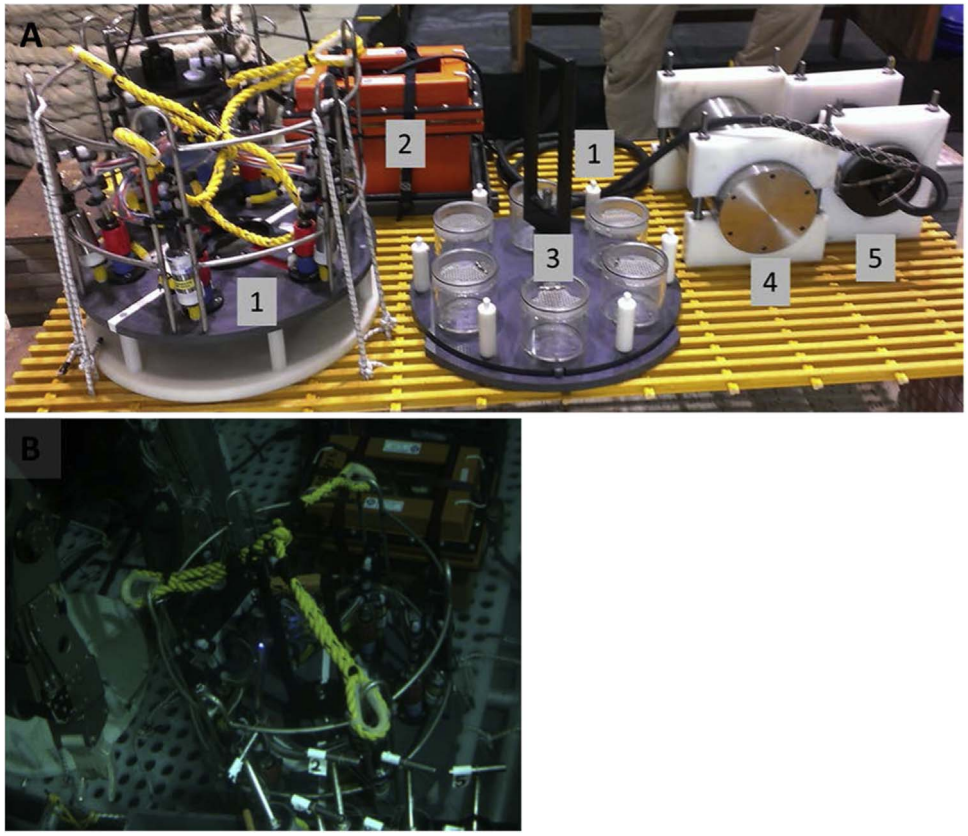

Fig. 2. A. The in-situ respirometer components. 1) The umbilical/manifold which consists of the cable connecting the junction box to the manifold and the optodes and pumps used to conduct the incubations. 2) The deep-sea power and light battery. 3) The chamber assembly carried by the ROV for collection of experimental animals. 4) The pressure housing that regulates power input to the pumps and records dissolved oxygen and temperature data from the optodes. 5) The junction box unifies power and data transmission and distributes to the manifold and pressure housing accordingly. B. The fully assembled respirometer as seen from the HROV Nereus in the Kermadec Trench.

than rates for the holothurians, accounting for the variation in masses (Fig. 3).

Comparisons were made to the other existing in situ respiration measurements available in the literature (Hughes et al., 2011; Smith, 1983) and generally the rates were similar to those we made at abyssal and hadal depths (Fig. 3). For the ophiuroids our abyssal animal, while having a relatively high rate compared to the other animals we tested, has a considerably lower respiration rate compared to bathyal species of similar size (Smith, 1983). Respiration of the abyssal holothuroids is similar to other abyssal holothuroids (Hughes et al., 2011). However, the four hadal holothurian measurements are somewhat lower than those for bathyal holothurians if one compares deviations from the regression between respiration and mass for all the holothurians (Fig. 3).

4. Discussion

Though it is not possible to evaluate our original hypotheses about the effects of depth on the respiration rates of benthic invertebrates in the Kermadec Trench, this is the first study to measure the respiration rates of hadal animals (to ~8000 m) and one of only a few to measure abyssal animal respiration rates in situ. The data can be compared to measurements of other deep sea megafauna. An excellent study using a similar in situ ROV operated respiration system measured ophiuroid and holothurian respiration at abyssal depths in the North Atlantic (Hughes et al., 2011). Our measurements of hadal and abyssal species are quite similar. This general observation is in keeping with the finding that the movement levels or activity of a hadal holothurian was similar to shallower taxa (Jamieson et al., 2011). Measurements of an ophiuroid, *Ophiopthalamus normani*, respiration made by Smith (1983) was much higher than our single measurement of an ophiuroid at 4049 m on the abyssal plain. Given that nutritional status (e.g. Brockington and Clarke, 2001), growth (e.g. Fraser et al., 2004), and other factors can affect respiration rates in echinoderms, it is premature to speculate as to the reasons for these differences.

Expanding on the work of Hughes et al. (2011) we plotted our

Table 1
Depth of elevator, bottom water dissolved oxygen (DO) and temperature (T), and sample data obtained from 9 deployments of the in situ respirometer.

Site	Deployment date (GMT)	Depth (m)	$[O_2]$ (μm)	T (°C)	Latitude (DM)	Longitude (DM)
1S	12-APR	1578	175	2.80	−37.2010865	178.882473
2T	13-APR	4049	207	1.32	−37.733695	179.81889
5T	21-APR	5025	205	1.07	−37.16967333	−179.73402
9T	1-MAY	6069	199	1.16	−35.91150333	−178.9644967
9Tb	2-MAY	6084	199	1.16	−35.91752333	−178.96607
11T	5-MAY	7140	192	1.33	−35.846925	−178.8788183
12T	6-MAY	8074	185	1.48	−34.34371167	−178.1748133
13T	7-MAY	9175	179	1.68	−32.85133	−177.6595567
14T	8-MAY	9989	171	1.83	−31.93094167	−177.289845

Table 2
Masses and respiration rates (whole animal and mass specific – mean and standard error) of abyssal and hadal organisms collected for incubation experiments. Values are corrected to a standard temperature of 2.5 °C using a Q_{10} value of 2.15 (see text).

Site	Phylum, class	Taxon	Wet weight (g)	% Water	Respiration rate (μmol-O_2 h^{-1})	2.5 °C	Mass specific respiration rate (μmol-O_2 g^{-1} h^{-1})	2.5 °C
2T	Echinodermata, Holothuroidea	*Bathyplotes* sp.	14	90.4	0.34 ± 0.017	0.38	0.025 ± 0.0006	0.027
	Echinodermata, Holothuroidea	*Abyssocucumis abyssorum*	53	86.1	0.57 ± 0.038	0.62	0.011 ± 0.0004	0.012
	Cnidaria, Anthozoa	Actinostolidae	24	81.8	1.40 ± 0.17	1.53	0.058 ± 0.007	0.064
	Cnidaria, Anthozoa	Hormathiidae	24	55.9	1.33 ± 0.029	1.45	0.055 ± 0.001	0.060
	Echinodermata, Ophiuroidea	*Ophiolimna* sp.	1	76.9	0.22 ± 0.015	0.25	0.22 ± 0.016	0.25
11T	Echinodermata, Holothuroidea	*Elpidia glacialis kermadecensis*	2	76.5	0.16 ± 0.077	0.17	0.078 ± 0.038	0.086
	Echinodermata, Holothuroidea	*Elpidia glacialis kermadecensis*	2	70.1	0.13 ± 0.038	0.14	0.063 ± 0.019	0.069
	Annelida, Polychaeta	*Macellicephala* sp.	6	68.5	0.60 ± 0.16	0.66	0.100 ± 0.027	0.110
12T	Echinodermata, Holothuroidea	*Elpidia glacialis kermadecensis*	2	67.9	0.13 ± 0.015	0.14	0.063 ± 0.007	0.068
	Echinodermata, Holothuroidea	*Elpidia glacialis kermadecensis*	2	74.1	0.22 ± 0.038	0.24	0.11 ± 0.019	0.12
	Cnidaria, Anthozoa	Actinostolidae	4	78.8	0.23 ± 0.017	0.25	0.058 ± 0.004	0.063

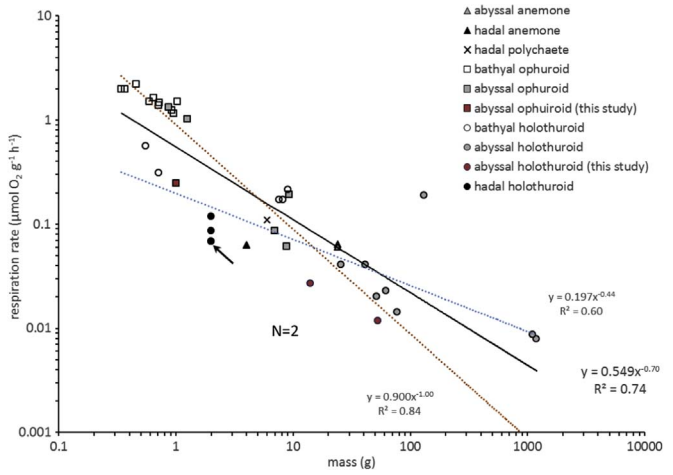

Fig. 3. In situ respiration rates as a function of animal mass for abyssal and hadal megafauna including other in situ measurements from the literature (Smith, 1983; Hughes et al., 2011). All values are standardized to 2.5 °C. Regressions are for all data (solid line), all ophiuroids (orange line) and all holothuroids (blue line). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

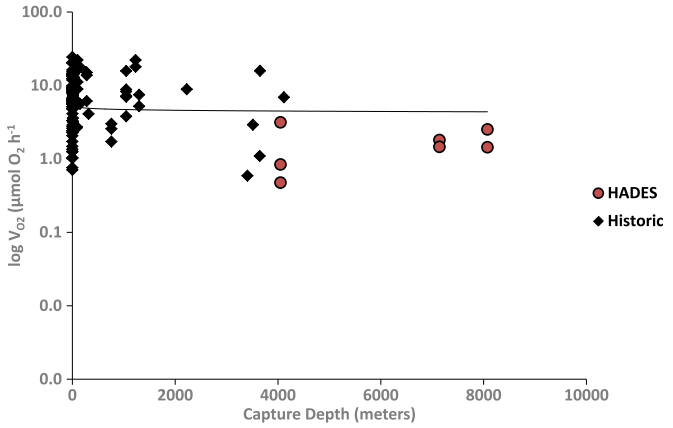

Fig. 4. Echinoderm metabolic rate (V_{O2}) as a function of Capture Depth. Data comes from the collated data and new rates as reported in Hughes et al. (2011) (Historic) and those generated by this study (HADES). Data from our work was transformed to be comparable by standardizing to a echinoderm class specific weight of 15 g and for a temperature of 12 °C.

echinoderm respiration rates against capture depth (Fig. 4). Like the Hughes et al. (2011) echinoderm data our rates were normalized for a standard 15 g wet weight and for a temperature of 12 °C. Our abyssal rates fall below the regression line but are comparable to the rates reported by Hughes et al. (2011). Interestingly of the rates that fall below the line at abyssal depths, the two values closest to the regression line belong to ophiuroids. However the Hughes et al. (2011) value came from a much larger specimen than ours, 8.3 g compared to 1 g.

Anemones are rarely used as organisms for respiration experiments in the deep-sea thus few comparisons can be made. Ex situ incubations of anemones recovered in a trawl from 477 m in the Gulf of Mexico and incubated at 8.5 °C (Nunnally unpublished data) when corrected for temperature of 2.5 °C had respiration rates of 0.049 and 0.051 μmol-O_2 g^{-1} h^{-1} at 111 and 140 g, slightly lower than those measured in situ in this study.

The measured rate of the large polynoid polychaete captured and incubated by the in situ respirometer was comparable with in situ experiments of pelagic polychaetes (Thuesen and Childress, 1993). Thuesen and Childress (1993) measured the respiration rates of five pelagic mid-water polychaete species captured at 1 ATM and incubated at 5 °C. Their results showed a high respiration rate of 3.928 μmol O_2 g^{-1} h^{-1} for *Tomopteris pacifica* and a low of 0.068 μmol O_2 g^{-1} h^{-1} for *Poebius meseres*. Our value of 0.094 μmol O_2 g^{-1} h^{-1} is near the median of their 5 measured species. However the biomasses of the three pelagic species measured were much smaller than the benthic polynoid we captured, 0.02–1.2 g compared to 6 g. The largest of which had the lowest oxygen consumption rate. Predator-prey dynamic in the pelagic realm would dictate a fast moving 'errant' polychaete which would have a nominally high metabolism. Although very little is known of the life history and ecology of the polynoid polychaete in our study, it is relatively large and was observed moving quickly over the sediments from ROV Nereus and baited lander footage. These observations suggest that it is a carnivore and would thus have a functional need for high activity and an elevated metabolic rate.

The estimation of megafaunal density in trenches is based on historical expeditions using a combination of grabs, trawls and photographs and is incredibly difficult to do (Beliaev, 1966; Beliaev and Brueggeman, 1989; Lemche et al., 1976). Recent modelling efforts have sought to correlate biological information with geological morphology of the Kermadec Trench in an effort to predict benthic biomass (Ichino et al., 2015) but this does not differentiate amongst size classes. The relationship of bacterial biomass to that of the various size classes of benthic metazoan fauna is also unknown in trenches, making it

perilous to predict megafauna biomass based on total benthic biomass. For that reason, we used historical estimates of megafaunal density and biomass (most commonly holothurians) to estimate the total amount of carbon respired by megafauna at 7 and 8 km within the Kermadec Trench. Trawl records of megafaunal biomass (Beliaev, 1966; Beliaev and Brueggeman, 1989) in the Kermadec range from 0.4 to 0.6 g m^{-2}. Estimated biomass from the photographic evidence of Lemche et al. (1976), which surveyed an estimated areas of 6000 m^2 in the Palau, New Britain, Bougainville and New Hebrides trenches, was equivalent to 1.0 g m^{-2}. Using these estimates of megafaunal biomass and our calculated holothurian respiration rates adjusted for mass (which among our subjects was always 2 g wet weight) and a suitable respiratory quotient of 0.8 (Piepenburg and Schmid, 1996) we estimated megafaunal carbon turnover due to respiration at these depth in the Kermadec Trench ranged between 0.02 and 0.5 mg-C m^{-2} y^{-1}. Our crude estimate encompasses the estimates of ophiuroid and holothurian communities of 0.029 mg-C m^{-2} y^{-1} (Ruhl et al., 2013) and 0.47 mg-C m^{-2} y^{-1} Smith (1983) made at shallower depths of 4.1–4.8 and 1.3 km respectively. Our estimates of total community respiration are necessarily lacking because the megafaunal density estimates are based on one study from 40 years earlier (Lemche et al., 1976). Ruhl et al. (2013) clearly demonstrates that this is a major caveat as taxa dominance can play a role in total respiration, likely making our values underestimates as we have included only holothurians in our community estimate. Still it is surprising that hadal megafaunal community respiration would be similar to that at much shallower depths.

5. Conclusions

Prior food web models of deep-sea habitats have been defined by the amount of information they lack (Rowe et al., 2008). Carbon utilization that occurs due to the respiration of fish and megafauna is a consistently lacking variable. Some work has provided in situ rates of fish (Drazen and Seibel, 2007; Drazen and Yeh, 2012; Drazen et al., 2011; Drazen, 2002; Smith and Hessler, 1974) and invertebrate respiration (Hughes et al., 2011; Smith, 1983; Wilson et al., 2013) including this study that helps close this gap in our knowledge. The current works provides data that brings us closer to estimates of megafauna carbon demand though clearly better estimates of their density within trenches are needed. As there are likely few biological pathways for carbon to leave the trench, the continued study of trenches must seek to include a reliable estimate of biomass and metabolic rates for the epibenthic and infaunal communities to determine the overall mass of carbon sequestered in biological forms.

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References

Ambrose, W.G., Clough, L.M., Tilney, P.R., Beer, L., 2001. Role of echinoderms in benthic remineralization in the Chukchi Sea. Mar. Biol. 139 (5), 937.
Beliaev, G.M., 1989. Deep–sea Ocean Trenches and Their Fauna. Nauka, Moscow, Russia.
Belman, B.W., Gordon, M.S., 1979. Comparative studies on the metabolism of shallow-water and deep-sea marine fishes. V. Effects of temperature and hydrostatic pressure on oxygen consumption in the mesopelagic *Melanostigma pammelas*. Mar. Biol. 50 (3), 275–281.
Blankenship, L.E., Levin, L.A., 2007. Extreme food webs: foraging strategies and diets of scavenging amphipods from the ocean's deepest 5 km. Limnol. Oceanogr. 52 (4), 1685–1697.
Bowen, A.D., Yoerger, D.R., Taylor, C., McCabe, R., Howland, J., Gomez-Ibanez, D., Kinsey, J.C., Heintz, M., McDonald, G., Peters, D., Young, C., Buescher, J., Fletcher, B., Whitcomb, L.L., Martin, S.C., Webster, S.E., Jakuba, M.V., 2009. The nereus hybrid underwater robotic vehicle. Underw. Technol. 28 (3), 79–89.
Brockington, S., Clarke, A., 2001. The relative influence of temperature and food on the metabolism of a marine invertebrate. J. Exp. Mar. Biol. Ecol. 258, 87–99.
McClain, C.R., Allen, A.P., Tittensor, D.P., Rex, M.A., 2012. Energetics of life on the deep seafloor. Proc. Natl. Acad. Sci. U. S. A..
Childress, J.J., 1977. Effects of pressure, temperature and oxygen on the oxygen-consumption rate of the midwater copepod *Gausia princeps*. Mar. Biol. 39 (1), 19–24.
Childress, J.J., 1995. Are there physiological and biochemical adaptations of metabolism in deep-sea animals? Trends Ecol. Evol. 10 (1), 30–36.
Childress, J.J., Thuesen, E.V., 1992. Metabolic potential of deep-sea animals: regional and global sclaes. In: Rowe, G.T., Pariente, V. (Eds.), Deep-Sea Food Chains and the Global Carbon Cycle. Kluwer Academic, Dordrecht (Netherlands), 217–236.
Christiansen, B., Diel-Christiansen, S., 1993. Respiration of lysianassoid amphipods in a subarctic fjord and some implications on their feeding ecology. Sarsia 78 (1), 9–15.
Christiansen, B., Beckmann, W., Weikert, H., 2001. The structure and carbon demand of the bathyal benthic boundary layer community: a comparison of two oceanic locations in the NE-Atlantic. Deep Sea Res. Part II: Top. Stud. Oceanogr. 48 (10), 2409–2424.
Danovaro, R., Gambi, C., Della Croce, N., 2002. Meiofauna hotspot in the Atacama Trench, eastern South Pacific Ocean. Deep Sea Res. Part I: Oceanogr. Res. Pap. 49 (5), 843–857.
Drazen, J.C., Seibel, B.A., 2007. Depth-related trends in metabolism of benthic and benthopelagic deep-sea fishes. Limnol. Oceanogr. 52 (5), 2306–2316.
Drazen, J.C., Yeh, J., 2012. Respiration of four species of deep-sea demersal fishes measured in situ in the eastern North Pacific. Deep-Sea Res. I 60, 1–6.
Drazen, J.C., Yeh, J., Friedman, J.R., Condon, N., 2011. Metabolism and enzyme activities of hagfish from shallow and deep water of the Pacific Ocean. Comp. Biochem. Physiol. 159, 182–187.
Drazen, J.D., 2002. Energy budgets and feeding rates of *Coryphaenoides acrolepis* & *armatus*. Mar. Biol. 140 (4), 677–686.
Fraser, K.P., Peck, L.S., Clarke, A., 2004. Protein synthesis, RNA concentrations, nitrogen excretion, and metabolism vary seasonally in the Antarctic holothurian Heterocucumis steineni (Ludwig 1898). Physiol. Biochem. Zool. 77 (4), 556–569.
Beliaev, G.M., 1966. Hadal Bottom Fauna of the World Ocean. Israel Program for Scientific Translations, Academy of Sciences of the USSR.
Beliaev, G.M., Brueggeman, P.L., 1989. Deep Sea Ocean Trenches and Their Fauna.
George, R.Y., Higgins, R.P., 1979. Eutrophic Hadal Benthic Community in the Puerto Rico Trench. Ambio Spec. Rep. 6, 51–58.
Hansen, B., 1956. From depths exceeding 6000 m. Galathea Report: Scientific Results of the Danish Deep-sea Expedition round the World. vol. 33(2), pp.1950–1952.
Hughes, S.J.M., Ruhl, H.A., Hawkins, L.E., Hauton, C., Boorman, B., Billett, D.S.M., 2011. Deep-sea echinoderm oxygen consumption rates and an interclass comparison of metabolic rates in Asteroidea, Crinoidea, Echinoidea, Holothuroidea and Ophiuroidea. J. Exp. Biol. 214 (15), 2512–2521.
Ichino, M.C., Clark, M.R., Drazen, J.C., Jamieson, A., Jones, D.O.B., Martin, A.P., Rowden, A.A., Shank, T.M., Yancey, P.H., Ruhl, H.A., 2015. The distribution of benthic biomass in hadal trenches: a modelling approach to investigate the effect of vertical and lateral organic matter transport to the seafloor. Deep Sea Res. Part I: Oceanogr. Res. Pap. 100, 21–33.
Ikeda, T., Sano, F., Yamaguchi, A., Matsuishi, T., 2006. Metabolism of mesopelagic and bathypelagic copepods in the western North Pacific Ocean. Mar. Ecol. Prog. Ser. 322, 199–211.
Itoh, M., Kawamura, K., Kitahashi, T., Kojima, S., Katagiri, H., Shimanaga, M., 2011. Bathymetric patterns of meiofaunal abundance and biomass associated with the Kuril and Ryukyu trenches, western North Pacific Ocean. Deep Sea Res. Part I: Oceanogr. Res. Pap. 58 (1), 86–97.
Itou, M., 2000. A large flux of particulate matter in the deep Japan Trench observed just after the 1994 Sanriku-Oki earthquake. Deep Sea Res. I 47, 1987–1998.
Itou, M., Matsumura, I., Noriki, S., 2000. A large flux of particulate matter in the deep Japan Trench observed just after the 1994 Sanriku-Oki earthquake. Deep Sea Res. Part I: Oceanogr. Res. Pap. 47 (10), 1987–1998.
Jamieson, A.J., Fujii, T., Mayor, D.J., Solan, M., Priede, I.G., 2010. Hadal trenches: the ecology of the deepest places on Earth. Trends Ecol. Evol. 25 (3), 190–197.
Jamieson, A.J., Kilgallen, N.M., Rowden, A.A., Fujii, T., Horton, T., Lörz, A.N., Kitazawa, K., Priede, I.G., 2011. Bait-attending fauna of the Kermadec Trench, SW Pacific Ocean: evidence for an ecotone across the abyssal–hadal transition zone. Deep Sea

Res. Part I: Oceanogr. Res. Pap. 58 (1), 49–62.
Kobayashi, H., Hatada, Y., Tsubouchi, T., Nagahama, T., Takami, H., 2012. The Hadal Amphipod Hirondellea gigas possessing a unique cellulase for digesting wooden debris buried in the deepest seafloor. PLoS ONE 7 (8), e42727.
Kyo, M., Hiyazaki, E., Tsukioka, S., Ochi, H., Amitani, Y., Tsuchiya, T., Aoki, T., Takagawa, S., 1995. The sea trial of 'KAIKO' the full ocean depth research ROV. OCEANS '95. MTS/IEEE. In: Challenges of Our Changing Global Environment. Conference Proceedings., pp. 1991–1996.
Lemche, H., Hansen, B., Madsen, F.J., Tendal, O., Wolff, T., 1976. Hadal life as analysed from photographs. Vidensk. Medd. Dan. Naturhistorisk Foren. 139, 263–336.
Mahaut, M.L., Sibuet, M., Shirayama, Y., 1995. Weight-dependent respiration rates in deep-sea organisms. Deep Sea Res. Part I: Oceanogr. Res. Pap. 42 (9), 1575–1582.
Meek, R.P., Childress, J.J., 1973. Respiration and the effect of pressure in the mesopelagic fish *Anoplogaster cornuta* (Beryciformes). Deep Sea Res. 20 (12), 1111–1118.
Oguri, K., Kawamura, K., Sakaguchi, A., Toyofuku, T., Kasaya, T., Murayama, M., Fujikura, K., Glud, R.N., Kitazato, H., 2013. Hadal disturbance in the Japan Trench induced by the 2011 Tohoku–Oki earthquake. Sci. Rep., 3.
Perrone, F.M., Croce, N.D., Dell'anno, A., 2003. Biochemical composition and trophic strategies of the amphipod Eurythenes gryllus at hadal depths (Atacama Trench, South Pacific). Chem. Ecol. 19 (6), 441–449.
Piepenburg, D., Schmid, M.K., 1996. Distribution, abundance, biomass, and mineralization potential of the epibenthic megafauna of the Northeast Greenland shelf. Mar. Biol. 125 (2), 321–332.
Rowe, G.T., Wei, C., Nunnally, C., Haedrich, R., Montagna, P., Baguley, J.G., Bernhard, J.M., Wicksten, M., Ammons, A., Briones, E.E., Soliman, Y., Deming, J.W., 2008. Comparative biomass structure and estimated carbon flow in food webs in the deep Gulf of Mexico. Deep Sea Res. Part II: Top. Stud. Oceanogr. 55 (24–26), 2699–2711.
Ruhl, H.A., Bett, B.J., Hughes, S.J.M., Alt, C.H.S., Ross, E.J., Lampitt, R.S., Pebody, C.A., Smith, K.L., Billett, D.S.M., 2013. Links between deep-sea respiration and community dynamics. Ecology 95 (6), 1651–1662.
Seibel, B.A., Drazen, J.C., 2007. The rate of metabolism in marine animals: environmental constraints, ecological demands and energetic opportunities. Philos. Trans. R. Soc. Lond. B 362 (1487), 2061–2078.
Smith, K.L., Jr., 1983. Metabolism of two dominant epibenthic echinoderms measured at bathyal depths in the Santa Catalina Basin. Mar. Biol. 72 (3), 249–256.
Smith, K.L., Jr., 1992. Benthic boundary layer communities and carbon cycling at abyssal depths in the central North Pacific. Limnol. Oceanogr. 37 (5), 1034–1056.
Smith, K.L., Hessler, R.R., 1974. Respiration of benthopelagic fishes: in situ measurements at 1230 m. Science 184 (4132), 72–73.
Smith, K.L., Jr., Kaufmann, R.S., Baldwin, R.J., Carlucci, A.F., 2001. Pelagic-benthic coupling in the abyssal eastern North Pacific: an 8-year time-series study of food supply and demand. Limnol. Oceanogr. 46 (3), 543–556.
Sullivan, K.M., Smith, K.L., Jr., 1982. Energetics of sablefish, *Anoplopoma fimbria*, under laboratory conditions. Can. J. Fish. Aquat. Sci. 39 (7), 1012–1020.
Taira, K., Yanagimoto, D., Kitagawa, S., 2005. Deep CTD casts in the challenger deep, mariana trench. J. Oceanogr. 61 (3), 447–454.
Thuesen, E.V., Childress, J.J., 1993. Respiration rate, enzymatic activity and chemical compositions of some deep-sea worms, particularly *Nectonnemertes mirabilis* (Nemertea; Hoplonemertinea) and *Poebius meseres* (Annelida; Polychaeta). Deep Sea Res. I 40 (5), 937–951.
Wilson, S., Yeh, J., Korsmeyer, K.E., Drazen, J.C., 2013. Metabolisn of shallow and deep-sea benthic crustaceans and echinodermsm in Hawaii. Mar. Biol. 160, 2363–2373.
Wolff, T., 1960. The hadal community, an introduction. Deep Sea Res. 6, 95–124.
Yancey, P.H., Gerringer, M.E., Drazen, J.C., Rowden, A.A., Jamieson, A., 2014. Marine fish may be biochemically constrained from inhabiting the deepest ocean depths. Proc. Natl. Acad. Sci. U. S. A. 111 (12), 4461–4465.
Yang, T.-H., Somero, G.N., 1993. The effects of feeding and food deprivation on oxygen consumption, muscle protein concentration and activities of energy metabolism enzymes in muscle and brain of shallow living (*Scorpaena guttata*) and deep-living (*Sebastolobus alascanus*) scorpaenid fishes. J. Exp. Biol. 181, 213–232.