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RESEARCH ARTICLE

Deep-sea echinoderm oxygen consumption rates and an interclass comparison of metabolic rates in Asteroidea, Crinoidea, Echinoidea, Holothuroidea and Ophiuroidea

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SUMMARY

Echinoderms are important components of deep-sea communities because of their abundance and the fact that their activities contribute to carbon cycling. Estimating the echinoderm contribution to food webs and carbon cycling is important to our understanding of the functioning of the deep-sea environment and how this may alter in the future as climatic changes take place. Metabolic rate data from deep-sea echinoderm species are, however, scarce. To obtain such data from abyssal echinoderms, a novel *in situ* respirometer system, the benthic incubation chamber system (BICS), was deployed by remotely operated vehicle (ROV) at depths ranging from 2200 to 3600 m. Oxygen consumption rates were obtained *in situ* from four species of abyssal echinoderm (Ophiuroidea and Holothuroidea). The design and operation of two versions of BICS are presented here, together with the *in situ* respirometry measurements. These results were then incorporated into a larger echinoderm metabolic rate data set, which included the metabolic rates of 84 echinoderm species from all five classes (Asteroidea, Crinoidea, Echinoidea, Holothuroidea and Ophiuroidea). The allometric scaling relationships between metabolic rate and body mass derived in this study for each echinoderm class were found to vary. Analysis of the data set indicated no change in echinoderm metabolic rate with depth (by class or phylum). The allometric scaling relationships presented here provide updated information for mass-dependent deep-sea echinoderm metabolic rate for use in ecosystem models, which will contribute to the study of both shallow water and deep-sea ecosystem functioning and biogeochemistry.

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Key words: deep sea, ROV, echinoderm, oxygen consumption, metabolism, respiration.

INTRODUCTION

Echinoderms are an important component of deep-sea benthic communities and are found throughout the world's oceans, often dominating benthic megafaunal communities in terms of abundance and/or biomass (Tyler, 1980; Billett, 1991; Ruhl, 2007; Lebrato et al., 2010). When present in large numbers and biomass, echinoderm populations can represent significant stores and users of energy in deep-sea benthic ecosystems (Sibuet and Lawrence, 1981; Walker et al., 1987; McClintock et al., 1990). Their population densities can, though, vary widely in response to climate and food supply (Billett et al., 2001; Ruhl and Smith, 2004; Uthicke et al., 2009).

Echinoderms have functional roles in structuring the chemical and physical features of their habitats, in both shallow-water and deep-sea environments. During feeding and locomotion, echinoderms bioturbate the sediment (Lohrer et al., 2005; Vardaro et al., 2009), displacing particles, increasing sediment heterogeneity and exposing otherwise anoxic sediments to oxygen. As a result, they contribute to the maintenance of overall sediment biodiversity and total benthic oxygen uptake (Smith et al., 2000; Turnewitsch et al., 2000; Vopel et al., 2007; Glud, 2008; Thistle et al., 2008). Echinoderm oxygen consumption rates are typically lower than those found in representatives of other marine invertebrate phyla, such as the crustacea (Webster, 1975; Lawrence and Lane, 1982). Despite this, it has been estimated from extrapolated individual echinoderm oxygen consumption rates that the contribution of echinoderm community respiration to overall total benthic respiration can be important (Piepenburg and Schmid, 1997; Ambrose et al., 2001). Estimates of total benthic oxygen uptake from sediment community oxygen consumption, in areas of high echinoderm abundance and biomass, that exclude the contribution of echinoderm respiration may underestimate actual benthic oxygen flux and carbon demand (Piepenburg and Schmid, 1996; Piepenburg, 2000).

Benthic echinoderm activity also contributes to inorganic and organic carbon cycling, sediment geochemical flux and deep-sea nutrient regeneration (Piepenburg, 2000; Smith et al., 2008; Lebrato et al., 2010). By virtue of their abundance and functional roles, the contribution of echinoderms to long-term deep-sea carbon sequestration and their incorporation within energy budget and carbon cycling models should be further considered and studied (Smith, 1983; Piepenburg, 2005; Ruhl, 2007). Despite their potential importance to deep-sea benthic carbon cycling, however, little information is available regarding deep-sea echinoderm oxygen consumption rates that would facilitate calculation of their contribution to rates of energy and carbon flow in deep-sea food webs (Rowe et al., 2008; Soetaert and van Oevelen, 2009). Such a paucity of information characterises the current knowledge of general deep-sea biodiversity and ecosystem functioning, a situation that has been highlighted as requiring research attention (UNEP, 2007; Danovaro et al., 2008).

Oxygen consumption rate has long been used as a practical measure of an organism's metabolic and organic carbon consumption rate (Schmidt-Nielsen, 1984; Burggren and Roberts, 1991; Brey, 2010), but the collection of such physiological data

from any deep-sea organism is difficult. Organisms brought to the surface from the cold and highly pressurised deep-sea environment without adequate protection can suffer both thermo- and baro-trauma during the transition through the water column to surface ambient temperature and pressure (Hessler, 1972; Macdonald, 1997). Thus, experimental results from deep-sea samples or organisms retrieved to the surface should be considered along with *in situ* physiological measurements (Tengberg et al., 1995; Theron and Sebert, 2003; Dixon et al., 2004). Experiments to investigate deep-sea physiology and ecological processes performed *in situ* under natural environmental conditions are therefore thought to be preferable, where possible (Smith and Baldwin, 1983; Tengberg et al., 1995), and may produce more accurate results than those performed under laboratory conditions (Shirayama, 1995).

The metabolic (oxygen consumption) rates of ectothermic organisms are strongly influenced by two factors: metabolic rate increases exponentially with temperature and scales allometrically with body mass (Schmidt-Nielsen, 1981; Burggren and Roberts, 1991). Within the field of deep-sea physiology, however, metabolic rates of some species have been found to decline with increasing depth but not with declining body mass (Seibel and Drazen, 2007). Detailed investigations of the effect of depth on metabolic rate have been carried out on data sets relating to deep-sea cephalopod molluscs (Seibel, 2007), crustacea (Childress, 1995) and fish (Drazen and Seibel, 2007). With regard to visually dependent deep-sea pelagic organisms, it has been found that metabolic rate declines with water depth in a manner that is independent of mass, temperature and food availability (Seibel, 2007). The visual interactions hypothesis (Childress and Mickel, 1985) suggests how these variations in metabolic rate reflect the energy demands of different ecological niches. Light availability determines the locomotory requirements of sighted pelagic organisms that participate in predator–prey interactions. As light decreases through the water column, so does the vision-related locomotory requirement and the associated metabolic rate of an organism (Childress, 1995; Seibel and Drazen, 2007).

Here, we present the oxygen consumption rates obtained from abyssal echinoderms using a novel remotely operated vehicle (ROV)-operated *in situ* respirometer; the first metabolic rate data reported from deep-sea (i.e. bathyal and abyssal) benthic echinoderms for over 25 years. We combined these new data with previously published deep-sea and shallow-water oxygen consumption rate measurements to provide a metabolic rate data set composed of 84 species of echinoderm. The data set was tested to investigate how echinoderm metabolic rate varied with mass or between echinoderm class. Size-dependent echinoderm metabolic rates were then calculated that can be applied to future modelling studies of both shallow-water and deep-sea ecosystem functioning and biogeochemistry. We also then investigated whether the metabolic rate of echinoderms varies with depth.

MATERIALS AND METHODS

Study sites

All deployments of the *in situ* respirometry equipment were made from the RRS James Cook (cruises JC10 and JC36). The equipment was operated *in situ* by the NERC ROV Isis. The deployments occurred within three different submarine canyons in the northeast Atlantic: the Nazaré, Setúbal and Whittard Canyons (Table 1). The Nazaré and Setúbal Canyons (JC10) intersect the western Iberian margin between 38°N and 39°30′N off the coast of Portugal (Arzola et al., 2008). The Whittard Canyon (JC36) intersects the Celtic margin at ~10°45′W (Zaragosi et al., 2000).

Respirometry equipment

The *in situ* respirometry equipment used during JC10, called the benthic incubation chamber system 2 (BICS2), was developed from an original respirometer design by Oceanlab (Aberdeen, UK). In brief, it was composed of two watertight acrylic respirometry chambers housed within an external glass reinforced plastic protective frame with dimensions 1000×580×642 mm. Each chamber had a capacity of 15.29 l. A 6000 m rated optode (Oxygen Optode 3975: Aanderaa Data Instruments AS, Bergen, Norway) was located inside each chamber to measure the oxygen concentration (in μmol O_2 l^{-1}) and temperature (°C) of the enclosed water. A stir bar was installed inside the lid of each chamber to prevent water stratification inside each chamber. The stir bar was powered by ambient water movement of a connected external current meter paddle mechanism. Measurements from the optodes were logged *via* an RS232 link through a custom-built TT8 controller (Oceanlab) to a memory card. The equipment was deployed on an ROV elevator platform. The ROV collected individual echinoderm specimens from the sediment surface using a purpose-built scoop, ‘sieved’ any entrained sediment out of the scoop, placed the echinoderm specimen into one of the respirometry chambers and sealed the chamber by closing the watertight lid.

The later JC36 deployments were made with a third respirometer design, BICS3, which incorporated design improvements following the earlier deployments of BICS2. Each watertight chamber had a 15.38 l capacity and contained an Aanderaa Oxygen Optode 3975 connected to a data logger (XR-420CTDm: RBR Europe Ltd, Stadhampton, Oxfordshire, UK). Each chamber also contained a motor-driven stirrer (K/MT 111; KUM, Kiel, Germany) powered by a lithium AA battery cell contained in a separate anodised aluminium pressure tube. *In situ*, the ROV collected individual echinoderms using a suction sampler with mesh barrier to retain the echinoderm at the front of the nozzle whilst removing any entrained sediment.

Respirometry measurements

Four deployments of BICS2 during JC10 resulted in oxygen consumption data being obtained from two different species of echinoderm (Table 2): the ophiuroid *Ophiura (Ophiuroglypha)*

Table 1. Station data for the JC10 and JC36 *in situ* respirometer deployments in the North East Atlantic

Station no.	Date	Depth (m)	Latitude (N)	Longitude (W)	Canyon location
JC10-090	09/06/07	3534	39°29.821	09°55.984	Nazaré
JC10-106	15/06/07	3497	39°29.809	09°55.753	Nazaré
JC10-119	19/06/07	3507	39°29.831	09°55.820	Nazaré
JC10-143	28/06/07	2226	38°14.362	09°23.629	Setúbal
JC36-015	23/06/09	3645	48°09.612	10°33.816	Whittard
JC36-039	07/07/09	3636	48°09.733	10°33.685	Whittard
JC36-100	22/07/09	3406	48°09.993	10°33.468	Whittard

irrorata concreta (Koehler, 1901) and the synallactid holothurian *Zygothuria lactea* (Théel, 1886). During JC10, because of equipment failure, it was not possible to obtain control measurements of background seawater respiration as only one respirometry chamber was available for use during each deployment. During JC36, two units of BICS3 were available, providing four individual respirometry chambers. The two BICS3 systems were deployed three times (Table 1) and successful control measurements were made during each deployment. The oxygen consumption rates of two additional species of echinoderm were obtained during the JC36 deployments, from the elasipodid holothurians *Benthodytes gosarsi* (Gebruk, 2008) and *Peniagone azorica* (von Marenzeller, 1892).

To limit the effects of any stress associated with the ROV collection procedure on echinoderm oxygen consumption, data sampling started 24 h after the animals had been introduced to the chamber. Data sampling ceased at whichever occurred first: the completion of a further 48 h of data logging, cessation of data logging due to battery discharge, or commencement of elevator (and respirometer) recovery to deck. For the *Z. lactea* oxygen consumption, as the total incubation period was only 13 h in length, the data-sampling period was selected as the last 4 h of incubation prior to elevator retrieval, eliminating the first 9 h during which the rate of oxygen depletion was elevated in comparison.

The oxygen consumption rate of each individual echinoderm ($\dot{V}_{O_2}$, μmol $O_2\,h^{-1}$) was calculated from the mean rate of change in the oxygen concentration of the respirometry chamber seawater between the start and end of the data-sampling period ($\Delta O_{2,w}$, μmol $O_2\,l^{-1}\,h^{-1}$) and the volume of the water held inside the respirometry chamber (V_c) minus the water displacement volume of the echinoderm (V_e):

$$\dot{V}_{O_2} = \Delta O_{2,w}\,(V_c - V_e)\,. \quad (1)$$

The mean control background seawater oxygen consumption rate during the three BICS3 deployments during JC36 was 0.643 μmol $O_2\,h^{-1}$, a value comparable to that determined in other studies. For example, Bailey and colleagues recorded a background oxygen consumption rate at 4050–4170 m depth in the Mediterranean of <0.01 ml $O_2\,h^{-1}$ (<0.447 μmol $O_2\,h^{-1}$) (Bailey et al., 2005). The mean JC36 background oxygen consumption rate was subtracted from all of the BICS-derived echinoderm oxygen consumption rates (including those from JC10) to give final individual oxygen consumption rates (Table 2). In order to assess the reliability of the BICS2 and BICS3 measurements, the obtained metabolic rates of the four species of echinoderm were compared with both *in situ* deep-sea and laboratory-based previously published data from ophiuroids and holothurians measured at temperatures ranging between –1.8 and 4°C (Fig. 1). The oxygen consumption rates included in this comparison were temperature normalised *via* Q_{10} temperature coefficient adjustment to 2.5°C (see below).

Comparative metabolic data set

In addition, a single mean data point for each species' oxygen consumption results obtained with BICS2 and BICS3 was incorporated into a large data set consisting of echinoderm metabolic rates obtained from the literature. Published metabolic rate data were primarily available from laboratory-based studies, but some data were derived from other *in situ* studies (see supplementary material Table S1). Data were added to our collated echinoderm dataset if they met the following criteria.

1. The echinoderms used for the metabolic measurements were adults. By restricting the metabolic rate data to adult specimens, any variation in the data set due to ontogenetic stage was eliminated.
2. The experimental temperature for the oxygen consumption measurements (a) was reported in the publication, (b) fell within the temperature range experienced by the echinoderm species in their natural habitat and (c) was the temperature to which the echinoderm had been acclimated.
3. It was possible to obtain from the publication, or to derive *via* conversion calculations, a value for an echinoderm's individual oxygen consumption rate ($\dot{V}_{O_2}$, μmol $O_2\,h^{-1}$).
4. Mass data were provided as wet mass (g).

When oxygen consumption and/or wet mass data were only available from graphs, the data were retrieved after digitisation of the figure and analysis using Engauge Digitizer (http://digitizer.sourceforge.net/).

Previous studies that have investigated the influence of depth on metabolic rate have used a species' minimum depth of occurrence (MDO) as the depth variable (Seibel and Drazen, 2007; Childress et al., 2008). Such data, however, are not available for many echinoderms and, as a result, the depth of echinoderm collection or capture depth (CD) (Ikeda et al., 2006) was used here as the depth variable. If a range of depth values was reported in a publication (e.g. a varied trawl depth), a mean collection depth was computed from the minimum and maximum depth in the range. Where the publication only reported that echinoderms were collected from intertidal areas at low tide, a depth of 1 m was listed as the depth of collection. If the publication only indicated that SCUBA divers were used to collect the echinoderm specimens, a collection depth of 10 m was used.

Table 2. Calculated individual oxygen consumption (metabolic) rates for the deep-sea ophiuroid and holothurian specimens used with the BICS2 and BICS3 *in situ* respirometers

Station no.	Species	Mean temperature (°C)	$\dot{V}_{O_2}$ (μmol $O_2\,h^{-1}$)	Wet mass (g)
JC10-090	*Ophiura irrorata concreta*	2.55	1.764	9.2
JC10-106	*Ophiura irrorata concreta*	2.54	0.538	8.8
JC10-119	*Ophiura irrorata concreta*	2.51	0.607	7.0
JC10-143	*Zygothuria lactea*	4.23	28.281	130.2
JC36-015	*Peniagone azorica*	2.58	1.058	25.6
JC36-015	*Peniagone azorica*	2.58	1.115	76.9
JC36-039	*Peniagone azorica*	2.57	1.424	61.5
JC36-039	*Peniagone azorica*	2.57	1.695	41.0
JC36-039	*Peniagone azorica*	2.57	1.046	51.3
JC36-100	*Benthodytes gosarsi*	2.63	9.544	1192.4
JC36-100	*Benthodytes gosarsi*	2.63	9.794	1107.2

Mean temperature refers to the mean temperature recorded by the oxygen optodes during the data sampling period (see text for further details). $\dot{V}_{O_2}$, oxygen consumption rate. Adjustment for background seawater oxygen consumption rate has been made. BICS, benthic incubation chamber system.

Basal metabolic rates, obtained from resting and starved organisms, are the preferred data for comparisons in physiological studies as opposed to routine or active metabolic data (Makarieva et al., 2008). However, the reviewed echinoderm publications often did not make clear whether an effort had been made to collect standard or basal metabolic data. The collated metabolic data used for comparative purposes should therefore be considered as relating to routine metabolic rates. Other authors have determined that the use of routine metabolic rate data within comparison data sets should not affect overall results (Makarieva et al., 2008).

The total dataset of metabolic rates incorporating both shallow-water and deep-sea echinoderm data was composed of 308 data points from 84 species representing all five classes of echinoderm: the Ophiuroidea (brittle stars and basket stars), Asteroidea (sea stars), Echinoidea (sea urchins), Holothuroidea (sea cucumbers) and Crinoidea (feather stars or sea lilies). The metabolic rate data held in this total dataset was composed of two types: (1) values averaged from a number of individual measurements, for which the individual data were not provided in the corresponding publication, and (2) multiple, unaveraged, individual echinoderm data points listed in the source publication or derived from summary figures. In order to limit the influence within the collated dataset of numerous individual data points for a single species from any single publication, multiple individual data points from one publication corresponding to one experimental temperature were averaged. Where the data points from individuals of a single species in one publication covered a large range of wet masses they were averaged according to the following size categories: 0.1 to <1 g, 1 to <10 g, 10 to <100 g, 100 to <500 g, 500 to <1000 g, 1000 to 1200 g. This produced a final total data set composed of 120 data points from 84 species.

The metabolic rates comprising the final data set had been collected at experimental temperatures ranging from –1.8 to 29.0°C, covering almost the entire range of temperatures over which echinoderms are found (–2 to 35°C) (Lawrence, 1987b). In order to compare the data obtained at different temperatures, metabolic rate values were normalised to 12°C, the median temperature value within the total data set. Temperature normalisation was made using the following Q_{10} adjustment (Schmidt-Nielsen, 1981), where R_2 is the temperature-normalised individual metabolic rate (μmol O_2 h^{-1}) at the normalisation temperature (T_2, °C), and R_1 is the experimentally derived individual metabolic rate (μmol O_2 h^{-1}) at the reported experimental temperature (T_1,°C):

$$R_2 = R_1 \times Q_{10}^{(T2 - T1)/10} . \quad (2)$$

The Q_{10} value used for normalisation was calculated from the mean of published Q_{10} values also collated during the literature review (Table 3). Values were included in the Q_{10} dataset where the acclimatised temperature of the echinoderm was reported in the publication and included within the temperature range from which the Q_{10} value was computed. Eleven publications provided 28 Q_{10} values, normally distributed with a range from 1.16 to 3.99 and a mean ± standard error value of 2.15±0.13.

Statistical analysis

The relationship between body mass (M) and metabolic rate (R) is generally described by the power function $R=aM^b$ where a is a normalisation constant independent of size and temperature and b is a scaling coefficient or exponent representing the slope of the plot of M against R on logarithmic coordinates (Schmidt-Nielsen, 1984; Cech, 1990). The scaling coefficients between the individual echinoderm oxygen consumption rates and mass were determined from the slope of a least squares linear regression (model I) following logarithmic transformation of both variables. In order to remove the influence of body size from the data set so that a comparison of

Table 3. Q_{10} data collated from the literature, derived from wet mass metabolism relationships

Species	Q_{10}	Temperature range (°C)	Class	References
Acanthaster planci	1.89	25–27	Asteroidea	Yamaguchi, 1974
Acanthaster planci	2.14	27–29	Asteroidea	Yamaguchi, 1974
Acanthaster planci	1.64	29–31	Asteroidea	Yamaguchi, 1974
Allocentrotus fragilis	1.22	6–9	Echinoidea	Ulbricht and Pritchard, 1972
Antedon b. bifida	2.20	8–18	Crinoidea	Warnock and Liddell, 1985
Hemipholis elongata	2.60	13–24	Ophiuroidea	Christensen and Colacino, 2000
Nemaster rubiginosa	2.17	27–30	Crinoidea	Warnock and Liddell, 1985
Ophiactis resiliens	2.62	15–25	Ophiuroidea	Pentreath, 1971
Ophionereis fasciata	2.47	15–25	Ophiuroidea	Pentreath, 1971
Ophiopteris antipodum	2.22	15–20	Ophiuroidea	Pentreath, 1971
Sterechinus neumayeri	2.54	–1.7 to 0.6	Echinoidea	Brockington and Clarke, 2001
Sterechinus neumayeri	2.99	–1.7 to 0.9	Echinoidea	Brockington and Clarke, 2001
Strongylocentrotus droebachiensis	1.36	4–14	Echinoidea	Siikavuopio et al., 2008
Strongylocentrotus droebachiensis	1.46	4–14	Echinoidea	Siikavuopio et al., 2008
Strongylocentrotus droebachiensis	1.17	4–14	Echinoidea	Siikavuopio et al., 2008
Strongylocentrotus franciscanus	3.45	12–15	Echinoidea	Ulbricht and Pritchard, 1972
Strongylocentrotus franciscanus	2.18	15–18	Echinoidea	Ulbricht and Pritchard, 1972
Strongylocentrotus intermedius	1.84	5–10	Echinoidea	Sedova, 2000
Strongylocentrotus intermedius	1.76	10–15	Echinoidea	Sedova, 2000
Strongylocentrotus intermedius	2.07	15–20	Echinoidea	Sedova, 2000
Strongylocentrotus nudus	2.57	10–20	Echinoidea	Ohsaki, 2001
Strongylocentrotus purpuratus	3.99	15–20	Echinoidea	Farmanfarmaian and Giese, 1963 (cited in Farmanfarmaian, 1966)
Strongylocentrotus purpuratus	2.78	10–15	Echinoidea	Farmanfarmaian and Giese, 1963 (cited in Farmanfarmaian, 1966)
Strongylocentrotus purpuratus	2.25	6–9	Echinoidea	Ulbricht and Pritchard, 1972
Strongylocentrotus purpuratus	1.16	12–15	Echinoidea	Ulbricht and Pritchard, 1972
Strongylocentrotus purpuratus	1.74	15–18	Echinoidea	Ulbricht and Pritchard, 1972
Strongylocentrotus purpuratus	2.06	6–13	Echinoidea	Webster, 1972 (cited in Lawrence and Lane, 1982)
Strongylocentrotus purpuratus	1.77	13–23	Echinoidea	Webster, 1972 (cited in Lawrence and Lane, 1982)

The mean Q_{10} value of 2.15 (0.13 s.e.) obtained from this data set was used to normalise the echinoderm metabolic rates included in this study.

Table 4. Summary of metabolic rates, wet masses and depths collated during this study and incorporated into the final data set

Class	No. of species	No. of data points	Temperature (°C)	Depth (m)	Mass (g)	$\dot{V}_{O_2}$ at 12°C (μmol O_2 h^{-1})
Asteroidea	20	26	–1.8 to 25	1–100	1.3–334.7	0.24–78.19
Crinoidea	9	13	8–29	10–315	0.3–54.1	0.34–35.57
Echinoidea	22	36	–1.8 to 28	1–4115	3.1–954	0.54–215.89
Holothuroidea	17	26	–1.2 to 25	1–3645	0.6–1149.8	0.58–375.17
Ophiuroidea	16	19	0–24	1–3650	0.2–13.9	0.09–21.13

Depth refers to the collection depth of the echinoderm specimens, mass refers to the wet mass of the echinoderms, and temperature refers to the experimental temperature at which oxygen consumption measurements were taken. The individual oxygen consumption rates ($\dot{V}_{O_2}$) have been normalised to 12°C by Q_{10} adjustment (see text).

metabolic rates with depth and temperature could be performed, the Q_{10}-normalised individual metabolic rate was adjusted to mass-specific metabolic rate ($\dot{M}_{O_2}$) for a standard 15 g echinoderm, using the scaling coefficient (b) derived during the power regressions. The 15 g standard mass was chosen, as it was close to the median individual wet mass in the final data set of 14.6 g.

We used analysis of variance (ANOVA) and analysis of covariance (ANCOVA) with *post hoc* Tukey tests to analyse the relationships between echinoderm metabolic rate, depth and temperature. Significance was tested at the 95% confidence level. All analyses were carried out using the Minitab (version 15; www.minitab.com) or Sigmaplot (version 11.0; www.sigmaplot.com) statistical packages.

RESULTS

In situ oxygen consumption measurements

Oxygen consumption measurements were obtained during cruise JC10, in the Nazaré and Setúbal Canyon systems, from three specimens of the ophiuroid *O. concreta irrorata* at abyssal depths and one specimen of the holothurian *Z. lactea* at bathyal depth. During cruise JC36, in the Whittard Canyon, oxygen consumption measurements were obtained from abyssal depths from five specimens of the holothurian *P. azorica* and two specimens of the holothurian *B. gosarsi* (Table 2).

Echinoderm metabolic data set and comparison

The echinoderm collection depths for the previously published metabolic rate values ranged from 1 to 4115 m, the deepest data point being derived from *Echinocrepis* sp. metabolic rates (B. D. Wigham, D. M. Bailey and D. O. B. Jones, unpublished) determined during trial deployments of the initial Oceanlab BICS design (Jamieson et al., 2005). Wet masses in the final data set varied over four orders of magnitude and the individual oxygen consumption rates over three (Table 4). The echinoid genus *Strongylocentrotus* was most commonly represented within all of the echinoderm classes, with six different *Strongylocentrotus* species providing 36 data points (see supplementary material Table S1).

The mean wet masses of the five echinoderm classes differed significantly from each other (ANOVA, F=25.326, P<0.001). Pairwise Tukey tests indicated that the differences in the mean wet masses between the Echinoidea (81.52 g), Asteroidea (47.12 g) and Holothuroidea (202.90 g) classes were not significant, nor were they between the Crinoidea (7.28 g) and Ophiuroidea (2.64 g) classes. The Ophiuroidea and Crinoidea mean wet masses, however, were both significantly different from those for each of the other three classes (all significantly different where P<0.001, apart from between the Asteroidea and Crinoidea where P<0.05).

The scaling coefficient, b, representing the slope of the linear regressions between log wet mass and log $\dot{V}_{O_2}$ for each echinoderm class (Table 5), ranged from 0.68 (ophiuroids) to 0.90 (asteroids), and all were highly significantly different from zero (P<0.001; Fig. 2). The slopes of the scaling relationships between each class were found to be significantly different from each other (ANCOVA, F=3.72, P<0.05). Pairwise Tukey tests, however, only indicated that the slope of the holothurian regression was significantly different from those for the ophiuroids (t=3.177, P<0.05) and crinoids (t=–3.491, P<0.05), whilst all other paired class scaling relationship combinations were not significantly different.

To investigate the application of scaling power 'laws' (see Discussion) to the echinoderm data set, the deviation from 1, 3/4 and 2/3 of the regression slopes between the temperature-normalised metabolic rates and mass was tested. None of the class-specific metabolic scaling relationships were significantly different from 3/4 and only the echinoid relationship was significantly different from 2/3 (t=2.469, P<0.05). The overall echinoderm slope ($0.9646M^{0.70}$) was significantly different from zero (t=18.03, P<0.001) and 1 (t=–1.98, P<0.05). It was not significantly different from 2/3 (t=2.47, P=n.s.) or 3/4 (t=1.39, P=n.s.).

Echinoderm metabolic rates were standardised to an echinoderm mass of 15 g using each class-specific scaling coefficient to enable a mass-independent comparison of metabolic rate with temperature and collection depth. As expected for ectothermic organisms, metabolic rate varied highly significantly with temperature (ANOVA, F=35.627, P<0.001). The mass- and 12°C-normalised metabolic rates of the final data set showed no change with collection depth CD (Fig. 3, $\dot{V}_{O_2}=7.395CD^{0.018}$, P=n.s.), the slope of the regression being not significantly different from zero. The mass-specific metabolic rates of each echinoderm class were also investigated independently with respect to collection depth, and none were found to vary significantly with depth.

DISCUSSION

In situ deep-sea echinoderm respiration

The unprotected retrieval of deep-sea specimens to the surface of the ocean exposes such organisms to altered pressure and temperature. Physiological and biochemical systems are sensitive to both pressure

Table 5. Metabolic scaling coefficient, b, for each echinoderm class and for the phylum as a whole, as derived from the final dataset of metabolic rates (see Fig. 2)

Class	Scaling coefficient, b	s.e. of regression slope	95% confidence interval	
Asteroidea	0.90	0.14	0.62	1.19
Crinoidea	0.74	0.11	0.49	1.00
Echinoidea	0.85	0.07	0.70	1.00
Holothuroidea	0.81	0.10	0.60	1.02
Ophiuroidea	0.68	0.17	0.32	1.04
Echinodermata	0.70	0.04	0.62	0.78

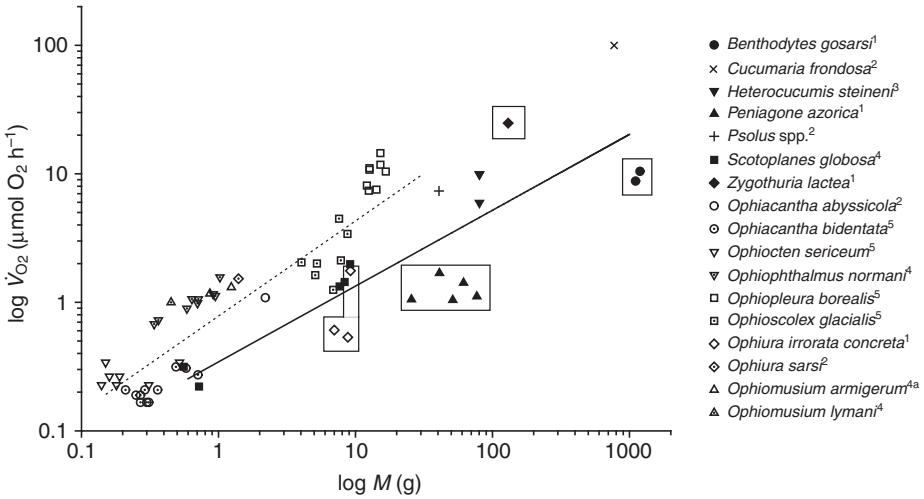

Fig. 1. Comparison of individual metabolic rates ($\dot{V}_{O_2}$) as a function of wet mass (M) of ophiuroid and holothurian species, obtained at their normal habitat temperature between –1.8 and 4.0°C, with those from the deep-sea species investigated in this study (boxed) obtained using *in situ* BICS2 and BICS3 respirometers (2.51–4.23°C). All individual metabolic rates have been Q_{10} adjusted to 2.5°C using a Q_{10} of 2.15. The solid line and markers indicate the linear regression for the holothurian metabolic rates ($\dot{V}_{O_2}=0.344M^{0.5901}$, $R^2=0.6485$, $P<0.001$); the dashed line and open markers indicate the linear regression for the ophiuroid metabolic rates ($\dot{V}_{O_2}=0.7808M^{0.6559}$, $R^2=0.7403$, $P<0.001$). Superscript letters indicate data from: [1]this study, [2]Hargrave et al. (Hargrave et al., 2004), [3]Fraser et al. (Fraser et al., 2004), [4]Smith (Smith, 1983) and [5]Schmid (Schmid, 1996). [a]*Ophiomusium armigerum* is now accepted as *Ophiosphalma armigerum* (Stöhr and Hansson, 2009).

and temperature changes (Somero, 1998). Temperature influences the weak chemical bonds that maintain protein formation, functioning and subunit aggregation, enzyme–ligand complex integrity and lipid-based physical structures (Somero et al., 1983). Pressure influences the volume of both gas- and water-filled spaces, with alterations in pressure having consequences to biological functioning ranging from the molecular level to that of the whole organism (Somero, 1991). Both pressure and temperature changes therefore result in the dissociation of weak acids and bases, denatured proteins and altered lipid fluidity (Somero, 1991; Mozhaev et al., 1996). Enzyme catalytic rate and regulation, osmotic regulation, transmembrane transport and ion flux, nerve resting potentials and synaptic transmission are hence strongly affected by pressure and temperature changes (Somero et al., 1983; Somero, 1991; Somero, 1992; Siebenaller and Garrett, 2002).

Although some deep-sea species can be collected in a suitable physiological state to allow experimental investigations to proceed (Childress et al., 1990; Thuesen and Childress, 1993; Treude et al., 2002), the decompression process has been found to introduce artefacts into physiological measurements and experimental results obtained from deep-sea organisms retrieved to the surface. Decompression is well known to affect gas-filled organs of organisms such as fish, which exhibit swim bladder overinflation and exophthalmia (Wilson and Smith, 1985; Rogers et al., 2008). The decompression of deep-sea organisms has been found to cause molecular changes (Dixon et al., 2004), transmembrane ion flux inhibition (Somero, 1991), cardiovascular and nervous system perturbation (Mickel and Childress, 1982; Gibbs, 1997), convulsions (Shillito et al., 2008), oxygen consumption rate changes (Bailey et al., 1994; Cottin et al., 2008), paralysis (Macdonald, 1997) and death (Hessler, 1972; Treude et al., 2002). Reliable and accurate physiological research using deep-sea organisms recovered to the surface hence requires the use of specialist retrieval equipment that enables the organisms to be maintained at both *in situ* temperature

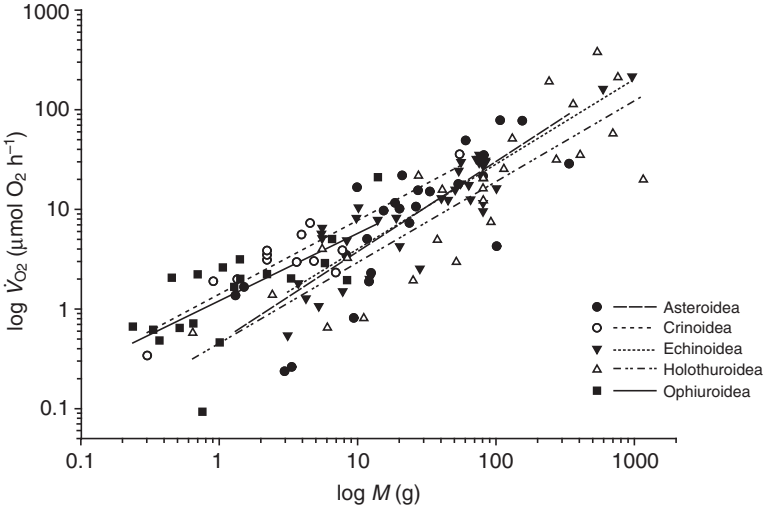

Fig. 2. Metabolic rates ($\dot{V}_{O_2}$) of the five echinoderm classes as a function of wet mass (M) as collated in the final echinoderm metabolic rate data set (see text). Scaling relationships are in the form $\dot{V}_{O_2}=aM^b$ where a is a normalisation constant and b is a scaling coefficient representing the slope of the relationship between $\dot{V}_{O_2}$ and M. The metabolic rates of all five echinoderm classes are highly significantly correlated with mass ($P<0.001$): Asteroidea ($0.472M^{0.90}$, $R^2=0.636$), Crinoidea ($1.414M^{0.74}$, $R^2=0.792$), Echinoidea ($0.564M^{0.85}$, $R^2=0.796$), Holothuroidea ($0.456M^{0.81}$, $R^2=0.730$), Ophiuroidea ($1.215M^{0.68}$, $R^2=0.481$). All metabolic rates have been normalised to 12°C using a Q_{10} adjustment of 2.15. Sources of all data can be found in supplementary material Table S1.

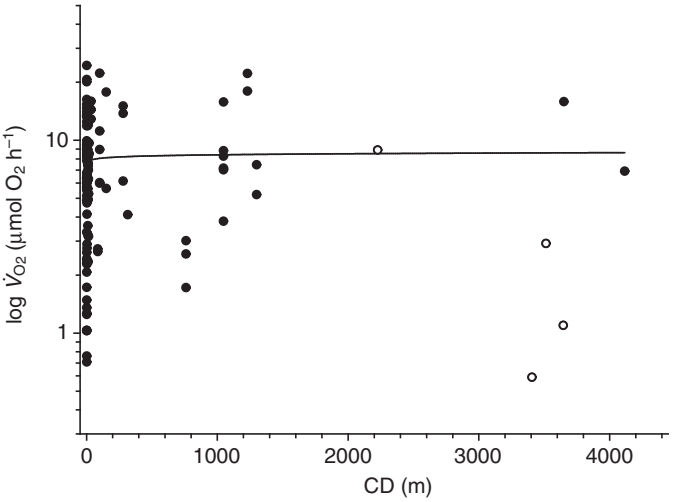

Fig. 3. Echinoderm metabolic rate ($\dot{V}_{O_2}$) as a function of collection depth (CD). Data (N=120) have been normalised to a standard echinoderm mass of 15 g using the echinoderm class-specific scaling coefficients (see text) and to a temperature of 12°C using a Q_{10} value of 2.15. No significant change in metabolic rate with depth is observed ($\dot{V}_{O_2}$=7.395CD$^{0.018}$, R^2=0.006, P=n.s.). Open circles represent data from this study. Data sources can be found in supplementary material Table S1.

and *in situ* pressure (Gibbs, 1997; Shillito et al., 2008). Alternatively, physiological investigations and measurements should be performed *in situ* at depth.

The current *in situ* echinoderm metabolic rate data are the first to be collected with the BICS2 and BICS3 respirometry equipment and only a small number of replicates for each species were obtained. However, a comparison with other data from deep-sea (bathyal and abyssal) echinoderm species (Smith, 1983), shallow water Antarctic species (Fraser et al., 2004) and continental shelf and bathyal Arctic species (Schmid, 1996; Hargrave et al., 2004) indicates that the measured individual metabolic rates appear broadly comparable to those of cold shallow-water and deep-sea species (Fig. 1).

The three *O. irrorata concreta* oxygen consumption rates obtained with BICS2 ranged from 0.61 to 1.76 µmol O_2 h^{-1}. The highest rate is comparable to those from the Arctic species *Ophioscolex glacialis* (Schmid, 1996) and to those obtained via *in situ* respirometry at 1300 m depth from specimens of the holothurian *Scotoplanes globosa* (Smith, 1983). The oxygen consumption rates obtained from the *P. azorica* and *B. gosarsi* specimens with BICS3 are low for their size compared with the other holothurian rates (illustrated by the position of the data points below the line of least squares regression on Fig. 1). Both of these holothurian species are members of the Elasipodida order which, whilst showing greatest modification of their tube feet and papillae for oxygen uptake, do not have respiratory trees (Lawrence, 1987b). As such, compared with other holothurians, these species may have a reduced ability to deliver oxygen directly into the body interior and this may have led to the observed lower oxygen consumption rates. The single *Z. lactea* oxygen consumption rate, obtained using BICS2, is higher than that of *B. gosarsi* and *P. azorica*, perhaps reflecting the fact that it was calculated from data obtained within 13 h of the holothurian being manipulated by the ROV. The *Z. lactea* oxygen consumption rate, however, is in line with those obtained from the holothurians *Cucumaria frondosa*, *Psolus* spp. (Hargrave et al., 2004) and *Heterocucumis steineni* (Fraser et al., 2004).

Metabolic rate variability

High intra- and inter-specific variability is typical in metabolic rate measurements of aquatic and marine ectotherms (Patterson, 1992), including bivalves (Peck and Conway, 2000), copepods (Thuesen et al., 1998), gelatinous zooplankton (Bailey et al., 1994), medusae (Thuesen and Childress, 1994), pelagic worms (Thuesen and Childress, 1993) and squid (Seibel, 2007; Rosa et al., 2009). The data set presented here also indicates such variation in the metabolic rate measurements of the echinoderms. This variability could come from many sources. Echinoderm metabolic rate is known to alter in response to salinity (Talbot and Lawrence, 2002), pH (Farmanfarmaian, 1966), partial pressure of oxygen (Shick, 1983; Spicer, 1995; Christensen and Colacino, 2000), seasonal growth (Lawrence and Lane, 1982; Fraser et al., 2004), feeding status (Vahl, 1984; Brockington and Clarke, 2001; Idrisi et al., 2003), nutritional quality of food (Otero-Villanueva et al., 2004), reproductive status (Giese et al., 1966; Féral and Magniez, 1988) and lifestyle (e.g. epifaunal *versus* infaunal) (Lawrence, 1987a).

During collation of the full data set, it was not possible to control for all of the variables listed above. One or more of the variables salinity, pH, oxygen tension, reproductive status and level of seasonal growth were often not commented upon within a publication. Not all publications confirmed that metabolic rate measurements had been taken from starved individuals or, because of the nature of the study (e.g. burrowed infaunal species), feeding status could not be controlled for. These variables explain a proportion of the variability in the collated data set once size and temperature are controlled for. Variability in the data set is also explained by the different respirometry techniques (Lawrence, 1987a) that have been used over the seven decade span of the literature from which data were obtained.

Metabolism and depth

The decline in metabolic rate with depth found in fish, crustacea and squid with visual capabilities is attributed to reduced requirements for locomotor ability as visual predator–prey interactions decline with decreasing light availability (Childress and Mickel, 1985). Correspondingly, such a depth-related trend has not been observed in deep-sea non-visual pelagic organisms, or benthic visual taxa that can find refuge from predation on the sea floor, including crustacea, cephalopods, fish and medusae (Childress et al., 1990; Thuesen and Childress, 1994; Thuesen et al., 1998; Seibel and Childress, 2000; Seibel and Drazen, 2007). As the benthic and bentho-pelagic echinoderm lifestyle, at any depth, is not dependent on visual-locomotor interactions with prey or predators, the visual interactions hypothesis predicts that there should be no decline in echinoderm metabolic rate with depth after accounting for size and temperature (Childress and Mickel, 1985; Seibel and Drazen, 2007). However, in comparison to the comprehensive reviews of fish, crustacean and cephalopod metabolic rates with depth (Childress, 1995; Seibel, 2007; Seibel and Drazen, 2007), equivalent investigations of echinoderm metabolic rates have previously been characterised by a paucity of data from deep-sea specimens. The new metabolic rate data obtained with the BICS2 and BICS3 respirometers during this study have therefore contributed greatly in removing this constraint. The results from the final data set in this study indicate that at neither the class nor the phylum level did echinoderm metabolic rate vary with depth.

This confirms the results of previous studies that have used smaller echinoderm data sets. Smith found that the metabolic rates of two species of deep-sea ophiuroids were comparable to those of shallow-living species at comparable temperatures (Smith,

1983), and Seibel and Drazen found no difference between shallow-water and deep-sea echinoderm metabolic rates (Seibel and Drazen, 2007). Although Brey (Brey, 2010) reported a small, but significant, decline in the metabolic rates of echinoids and asteroids with depth, we found no decline in metabolic rate with depth in any of the echinoderm classes. In comparison to Brey's asteroid data, our data set included data from an additional three species of asteroid but did not extend the depth variable for this class. Although the same number of echinoid species was included in our echinoid data set, the addition of the *Echinocrepis* sp. *in situ* data from 4115 m extended our data set for this class into abyssal depths.

An additional consequence of the paucity of data on deep-sea echinoderms is that the current study used echinoderm capture depth to parameterise the depth variable, which is in contrast to that used in the body of literature concerning fish, crustacean and cephalopod metabolic declines with depth. The literature concerning these last organisms uses MDO to parameterise the depth variable, defined as the shallowest depth below which 90% of the individuals in a population live (Childress and Nygaard, 1973). MDO is preferentially used in studies concerning these pelagic organisms to ensure that the metabolic rates of species that migrate vertically are therefore always analysed in the shallower part of their overall depth distribution (Childress et al., 2008). Data concerning the MDO of the majority of the echinoderm species were absent from the literature, and it was therefore not possible to account for the depth variable in this manner. However, whilst adult echinoderm species found at continental shelf to abyssal depths are vertically distributed, forming distinct faunal zones (Billett, 1991; Howell et al., 2002), there is little evidence to suggest that adult deep-sea echinoderms are capable of significant vertical migration.

Metabolic scaling

Within the power function $R=aM^b$, the scaling coefficient b has been subject to extensive investigation because of its application to various levels of biological organisation and modelling (West et al., 1997; Agutter and Wheatley, 2004; Brown et al., 2004; Whitfield, 2004), and because its value with regard to whole-organism metabolic rate often falls near to 3/4 (b=0.75) (Schmidt-Nielsen, 1984; Savage et al., 2004). The scaling pattern of this relationship is often referred to as the '3/4-power law' or 'Kleiber's law' after its first proponent (Kleiber, 1932; Savage et al., 2004; Glazier, 2006). An alternative value of 0.67 for the scaling coefficient, based on the 2/3 surface-to-volume scaling relationship, has also been proposed (Dodds, 2001; White and Seymour, 2005; White et al., 2006).

Numerous publications present theories for and against the universal validity of each of these scaling exponents and their relevance to applications of metabolic scaling (Hochachka et al., 2003; Agutter and Wheatley, 2004; Brown et al., 2004; Clarke, 2004; Glazier, 2005). Recent work has acknowledged that variation in the value of b exists between different phyla, between large and small mammals of the same taxa and between ectotherms and endotherms (Farrell-Gray and Gotelli, 2005; White et al., 2007; Capellini et al., 2010; Kolokotrones et al., 2010). There is, as yet, no consensus opinion on whether these variations are deviations from a general scaling law or whether there is in fact no such law (Agutter and Wheatley, 2004). Glazier suggests that b varies between 2/3 and 1, representing the two extremes of idealised boundary constraints where metabolic rate either scales with surface area (2/3) or scales with mass or volume limits (1) (Glazier, 2010). The different body forms and varied anatomical, morphological and behavioural adaptations of the five echinoderm classes all determine the oxygen consumption capacities of different echinoderm species (Shick, 1983; Warnock and Liddell, 1985; Lawrence, 1987b; Patterson, 1992), so variation amongst the classes might be expected. Such variation was also found by Lawrence and Lane when they compared the means of a number of interspecific echinoderm scaling constants (Lawrence and Lane, 1982).

In our study, we found that most slope coefficients could not be differentiated from 2/3, 3/4 or 1. The only exceptions are that the echinoid slope 95% confidence interval was greater than 2/3 and the overall echinoderm slope less than 1 (Table 5). None of the scaling coefficients were found to be significantly different from 3/4, which would be expected should the scaling relationships be based on the scaling of resource-transport networks with mass (West et al., 1997; Gillooly et al., 2001). The results also support previous findings that ectothermic organisms exhibit highly variable scaling coefficients between taxa, and that a universal allometric scaling exponent for ectotherm taxa embeds considerable variation (Agutter and Wheatley, 2004; White et al., 2007).

CONCLUSION

The data obtained from the ophiuroids and holothurians at abyssal and bathyal depths with BICS2 and BICS3 (as well as with the initial BICS design) increase the number of benthic deep-sea echinoderm species from which *in situ* measurements of metabolic rate have been obtained from three (Smith, 1983) to eight. The inclusion of these data in the echinoderm metabolic rate data set, which incorporates both shallow-water and deep-sea respiration rates, reveals that there is no change in echinoderm respiration rate with depth, in agreement with the predictions of the visual interactions hypothesis. The calculated allometric scaling relationships represent updated values for mass-dependent deep-sea echinoderm respiration rates compared with those included within previously published data sets (Mahaut et al., 1995; Seibel and Drazen, 2007).

Estimating the roles of echinoderms in food webs and their contribution to carbon cycling is important to enable understanding of how climate change may alter the functioning of the deep-sea environment in the future. The application of the size-dependent echinoderm respiration rates (at both the class and the phylum level) determined here can be used in ecosystem models to help improve estimates of both shallow water and bathyal and abyssal deep-sea ecosystem functioning and biogeochemistry. However, as the numerical dominance of echinoderms (holothurians) within deep-sea communities even extends to the hadal depths of the ocean (Beliaev, 1989; Herring, 2002), the current data now available for echinoderm metabolic rate still only span less than half of their full depth range. As data are obtained from samples found at still greater depths, further important insights into deep-sea echinoderm physiology could be obtained.

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