Mar Biol (2013) 160:2363–2373
DOI 10.1007/s00227-013-2230-8

ORIGINAL PAPER

Metabolism of shallow and deep-sea benthic crustaceans and echinoderms in Hawaii

Suzanne Wilson · John Yeh · Keith E. Korsmeyer · Jeffrey C. Drazen

Received: 29 October 2012 / Accepted: 21 March 2013 / Published online: 4 April 2013

Abstract Little is known about the metabolism of deep-living, benthic invertebrates, despite its importance in estimating energy flow through individuals and populations. To evaluate the effects of depth and broad taxonomic group/locomotory mode, we measured the respiration rates of 25 species of benthic decapod crustaceans and 18 species of echinoderms from the littoral zone to the deep slope of Hawaii. Specimens were collected by hand, trap, or submersible and maintained in the laboratory at temperatures close to ambient temperatures recorded at the time of collection. After acclimatization to laboratory conditions, oxygen consumption was measured for each individual in closed chambers. Overall, crustaceans had higher metabolic rates than echinoderms, and within the crustaceans, caridean shrimps had higher rates than crabs and lobsters. These differences are probably related to locomotory mode and general levels of activity. At in situ environmental temperatures, metabolic rates of deeper-living invertebrates are much lower than those of shallower living species, but this decline is explained by changes in temperature. When the data were compared with similar data sets collected off California and in the Mediterranean, Hawaiian crabs, lobsters, and echinoderms had lower metabolic rates than similar species in the other regions after adjustments for temperature were made. Some of these differences could be methodological. Regional food web models should use broad taxonomic groupings and region-specific data when possible.

Communicated by J. P. Grassle.

S. Wilson · J. Yeh · J. C. Drazen (✉)
Department of Oceanography, University of Hawaii,
1000 Pope Rd., Honolulu, HI 96822, USA
e-mail: jdrazen@hawaii.edu

S. Wilson
Department of Biomedical and Life Sciences,
University of Glasgow, Glasgow, UK

K. E. Korsmeyer
Department of Natural Sciences, Hawaii Pacific University,
Kaneohe, HI, USA

Introduction

The majority of metabolic studies on deep-sea animals have focused on pelagic species, notably fishes, crustaceans, cephalopods, and zooplankton, often in different oceanic regions (Seibel and Drazen 2007). These studies show that after accounting for the known effects of temperature and body mass (Brown et al. 2004; Brey 2010), metabolism in some groups of animals shows dramatic reductions with depth of occurrence. Pressure has little effect on metabolism (Childress 1977; Belman and Gordon 1979; Mickel and Childress 1982; Childress and Thuesen 1993). Instead, the changes have been explained by the visual interaction hypothesis (VIH; Childress 1995; Seibel and Drazen 2007), which suggests that locomotory abilities associated with prey–predator interactions are a main driving factor behind the differences in metabolic rates. In shallow depths, light allows sighted organisms to observe prey and predators from a large distance, necessitating greater locomotory capabilities and associated metabolic rates. The selective pressure for greater locomotory ability is progressively minimized as light rapidly diminishes with depth. Below about 1,000 m sunlight is no longer visible to fishes and invertebrates (Warrant and Locket 2004), and reductions in metabolic rate cease. The VIH is supported by findings that depth-related trends are seen only for sighted pelagic taxa (i.e., fishes, decapods crustaceans, and squid), whereas

non-sighted taxa (i.e., medusae, polychaetes, and chaetognaths) demonstrate no depth trends (Seibel and Drazen 2007). But there is some controversy about this explanation. For instance, copepod respiration rates decline with depth in some studies, and these declines continue past 1,000 m, depending upon how depth is parameterized for the copepods (Ikeda et al. 2006; Childress et al. 2008).

The benthic environment differs from the pelagic in many ways including having more opportunities for camouflage and accumulating sinking detritus that can result in enhanced animal biomass compared with the overlying water column. Benthic animals can hide in a complex habitat rather than relying solely on locomotion to capture prey or evade predators so the VIH does not predict declines in their metabolic rates. However, there are relatively few studies of the metabolism of deep-sea benthic animals. Pelagic studies of metabolism were often possible because short trawls with insulated cod ends were used to capture many specimens quickly and in good condition (Childress 1985). Benthic trawling typically crushes specimens with sediment and rock or asphyxiates them in mud. Studies of benthic invertebrates have shown varying patterns of metabolism with respect to depth (Childress et al. 1990; Company and Sarda 1998; Hughes et al. 2011). A recent comprehensive and data-rich model to predict marine invertebrate metabolism using artificial neural networks (Brey 2010) explained 85 % of the variance, but up to two orders of magnitude in variation remained. Temperature and body mass were clearly important, as were depth of occurrence, phylogeny, and locomotory mode. It was concluded that the high degree of interspecific variation warrants further data collection.

Crustaceans and echinoderms are very diverse and hold fundamentally important positions within benthic ecosystems (Ruhl 2008; Widdicombe and Spicer 2008). Despite their ecological importance, only two studies of benthic crustacean metabolism across a depth gradient have been conducted, one off California (Childress et al. 1990) and the other in the western Mediterranean (Company and Sarda 1998). A handful of measurements of deep-sea echinoderm metabolism have been made (Smith 1983), including one ophiuroid and three holothuroids in a recent study, which also summarized nearly all existing echinoderm data (Hughes et al. 2011). From these studies it is clear that more data are required to further evaluate the factors affecting benthic invertebrate metabolism.

Many environmental factors covary with depth making an analysis of cause and effect difficult. Comparing data from regions with differing conditions and vertical profiles of environmental factors offers a way to disentangle the environmental covariation. For instance, depth-related declines in benthic crustacean metabolism could be evaluated independent of temperature in the Mediterranean because of the isothermal water column (Company and Sarda 1998). Across regions, the influence of food availability was evaluated by comparing metabolism of pelagic squids and crustaceans from eutrophic settings (California) and oligotrophic ones (Hawaii), but no difference in metabolic rates was found (Cowles et al. 1991; Seibel et al. 1997). Regional comparisons of benthic invertebrate data sets have not been made. The islands of Hawaii are located in the center of the oligotrophic North Pacific gyre, so this ecosystem provides an interesting region for comparative study. The islands of Hawaii have a diversity of benthic crustaceans and echinoderms (Clarke 1972; Chave and Malahoff 1994; Vetter et al. 2010), some of which have been commercially exploited to depths of ~600 m (Gooding 1984; Moffitt and Parrish 1992).

Our goal was to characterize the respiration of benthic crustaceans and echinoderms in Hawaii across a depth gradient (0–1,000 m) to evaluate the effects of depth (test the VIH) and to measure differences between broad taxonomic groups/locomotory modes (i.e., walking crabs, swimming shrimp, and crawling echinoderms). We also compare our data set with those from other regions to evaluate the environmental drivers of metabolic rate variation.

Materials and methods

Specimen collection

Shallow-water invertebrates were collected by hand, dip net, and with small baited traps from coral reef and lagoon habitats on the island of Oahu, Hawaii. Invertebrates were quickly transferred back to the laboratory in buckets with continuously aerated water. Deep-water species were collected during two cruises in October 2010 and March 2011 in Hawaii off the island of Oahu using the Hawaii Undersea Research Lab submersible, Pisces V. In October, two dives were performed off the south coast of Oahu at ~250 and ~500 m, and in March, three dives were performed off of the west coast at depths of ~250, ~500, ~1,000 m. During each dive, ambient environmental parameters such as depth, temperature, and salinity were recorded continuously, and all dives occurred along a contour within 50 m of the target depth.

Three methods of collection were used to maximize the number of species collected during the dives. A baited trap (1 m × 0.5 m × 0.3 m) was used to capture more mobile crustaceans. It was placed on the seafloor after reaching the target depth of each dive and retrieved just prior to ascent (4–5 h later). The submersible's manipulator arm was used to capture large, less mobile invertebrates by delicately picking them up and stowing them in an insulated

"biobox." A suction sampler was used to collect more agile crabs and shrimps. Specimens were sucked into a nozzle (diameter = 10 cm) held by the manipulator arm, passed through flexible tubing, and deposited into a cylindrical tank. All three sampling methods used sealable holding areas constructed of PVC that provided insulation while ascending through the thermocline and allowed individuals to remain cold while the sub was at the surface awaiting recovery. Upon retrieval of the submersible (i.e., sub on deck), specimens were immediately transferred to containers of prechilled seawater set to match the temperature at the depth of collection. They were identified to the lowest taxonomic group possible using standard keys, guides, and texts, and with the assistance of specialists.

Specimen maintenance and acclimation

Specimens were maintained in aquaria in temperature-controlled rooms during the course of experiments to simulate natural conditions to the extent possible. Shallow-water species were maintained at 24 °C. Those from 1,000 and 500 m were kept at 5 °C, and those from 250 m were kept at 10 °C. These temperatures approximated average temperatures observed at the time of collection (25.0 °C in shallow water, 15.7 °C at 250 m, 7.2 °C at 500 m, and 4.3 °C at 1,000 m). Seawater was made from artificial sea salt to minimize the potential for contamination by exotic bacteria or pathogens. Salinity was maintained at 34.5 to 35.5 to match the salinities at collection sites. Specimens were acclimated to laboratory conditions for a minimum of 48 h. Shallow species were maintained with a 12-h light/12-h dark photoperiod with regular room lighting. Experimental chambers were loosely covered with dark plastic during experiments to avoid disturbance to the specimens from the surroundings, but their chambers were not completely dark. Species from 250 m had a controlled, dim 12-h light/12-h dark photoperiod. Species from 500 and 1,000 m were kept in complete darkness with the exception of exposure to dim red lights while work was being performed. Past studies of deep-sea animals, including crustaceans, have determined that they have little or no sensitivity to red light (Warrant and Locket 2004; Raymond and Widder 2007). The individuals used in these experiments lived for 1–4 months after capture.

Food was withheld from specimens prior to experiments to avoid the effects of specific dynamic action on metabolic rates. Shallow species were fasted for 24 h before an experimental run, but 96 h or more was used for deep-sea specimens based on previous studies of digestion rates in deep-water animals (Drazen et al. 2007). Only crustaceans that were active and responding to mechanical stimuli were used in experiments. Activity in echinoderms is much harder to monitor and was assessed by movement of the spines and/or tube feet.

Experimental procedure

Cylindrical glass respirometry chambers of varying volumes (0.12–3.8 l) equipped with stirring mechanisms were used for the experiments based on animal size. All individuals were weighed to the nearest 0.1 g after removal from the respirometer. Specimens too big for these chambers, such as lithodid crabs and some echinoids, were placed in large, rectangular, PVC chambers (Drazen et al. 2011). Calibrated oxygen optodes (Aandera 4330 or Thermo Scientific Orion RDO) were used in measuring oxygen content and temperature continuously during each experiment.

The closed respirometry experiments ran for 3–14 h dependent upon the rate of oxygen consumption and chamber size. With the exception of some early experiments, a penicillin–streptomycin antibiotic solution (15 units ml^{-1}) was used to reduce background microbial respiration rates. All experiments were run in the same temperature-controlled rooms the specimens were acclimated in. Chambers were placed in water baths to further stabilize temperatures during the experiments. Temperature fluctuations were 1–1.5 °C in the 24 °C laboratory and 0.5 °C in the cold rooms.

Controls were run for each experiment. Background rates of oxygen consumption were determined in chambers for 1–2 h before specimens were introduced or in chambers alongside an experiment for the same length of time. The oxygen consumption in controls was usually small (<5 %), and this value was subtracted from the corresponding total respiration rate.

In several cases an automated, intermittent-flow style respirometer was used to measure oxygen consumption (Steffensen 1989). This respirometer used a cylindrical acrylic respirometry chamber (1.2 or 2.0 l) submerged in a water bath. The chamber was connected to a pumped recirculation loop that continuously passed water over an oxygen optode and was intermittently flushed with aerated water from the water bath by a second, computer-controlled pump. Closed periods, during which oxygen consumption was determined, ranged from 15–50 min, depending on rates of oxygen consumption and temperature, followed by an open, flushing period of 5–10 min. This closed–open cycle was repeated for up to 43 h. Background rates of oxygen consumption were measured following removal of the animal and subtracted from metabolic rate measurements.

Data analysis

Invertebrates were not restrained in any way so spontaneous activity was possible. Periodic observation found specimens resting, but we consider our measurements to be

of routine rather than resting metabolic rates. Routine mass-specific metabolic rate (μmol O_2 g^{-1} h^{-1}) was measured as the rate of change in oxygen concentration in the chamber over time and divided by the specimen wet mass. The first hour of the experiment, when trial runs suggested elevated oxygen consumption, was excluded. Oxygen in the chambers was rarely <80 μmol l^{-1}, a concentration well above thresholds for metabolic suppression (Childress 1975; Donnelly and Torres 1988; Cowles et al. 1991; Erdman et al. 1991; Company and Sarda 1998). In the few cases where it did, that part of the experiment was not used to estimate respiration rate. When experiments lasted >10 h, multiple estimates of metabolic rate were made and the average taken.

Temperature and body mass have well-documented influences on respiration rates (Brown et al. 2004; Brey 2010). To evaluate factors contributing to the residual variability, such as depth, we used temperature and mass scaling coefficients as in past studies (Drazen and Seibel 2007; Seibel and Drazen 2007; Hughes et al. 2011), adjusting metabolic rates to a median temperature of 10 °C and a mass of 10 g. This mass generally falls within the range of most species in this and other studies (Childress et al. 1990; Company and Sarda 1998; Hughes et al. 2011). We used empirically derived scaling factors when possible (regressions of log-transformed metabolic rate and mass) or used intraspecific averages from the most comprehensive meta-analysis of aquatic invertebrate respiration rates to date, which included 413 species of crustaceans (255 malacostracans) and 79 species of echinoderms (Brey 2010). In Brey's (2010) study the mean mass exponent (b) was −0.278, where metabolic rate $\approx$ $mass^b$, and the mean temperature exponent (c) was −7,726, where metabolic rate $\approx$ $e^{-c/T}$ using absolute temperature (K).

The effect of depth was evaluated by comparing an animal's metabolic rate with its depth of capture, which was facilitated by the depth stratified sampling (shallow, 250, 500, 1,000 m). Many past studies, particularly those focused on pelagic animals, have used the minimum depth of occurrence (Seibel and Drazen 2007). This is the depth below which 90 % of the adult population resides, and it is appropriate when working with animals that undergo diel vertical migrations. In our case, the depth distributions of most of these invertebrates are poorly resolved. This is likely due to the difficulty of sampling steep, rocky volcanic slopes off Hawaii. The Hawaii Undersea Research Laboratory submersible observation database (http://www.soest.hawaii.edu/HURL/animals/; Chave and Malahoff 1994) provides some information on deeper-water animals, so long as the identification of those taxa is relatively simple using photographs and video. However, several species could not be identified and may represent new species. Voucher specimens were preserved in 95 % ethanol (available from corresponding author). For shallow-water species the upper limits to depth are often known but the lower limits are not because most are studied with SCUBA, which is limited to ~40 m depth. It is reasonable to assume that no shallow-water species are found below the permanent thermocline which occurs at ~100 m depth off Hawaii.

The data from our study were compared with several region-specific studies available in the literature. In all cases, the respiration rates from the papers were standardized to 10 °C as for the Hawaii data and evaluated as a function of mass.

Often, the data were not normally distributed and sample sizes for some between-group comparisons were low, so we employed permutational ANOVA and ANCOVA approaches (PERMANOVA, Anderson et al. 2008). These tests were performed using untransformed data and Euclidean distances between samples, approximating conventional ANOVA, except that probabilities were based on permutation (10,000 iterations) of the data set rather than assumptions of normality.

Results

Metabolic rates were measured for 25 species of benthic decapod crustaceans and 18 species of echinoderms collected from depths of 0.5–1,000 m (Table 1). The crustaceans were distributed across five infraorders representing a variety of crabs (Brachyura and Anomura), lobsters (Achelata, Polychelida), and shrimps (Caridea). The echinoderms were distributed across three classes representing sea stars (Asteroidea), urchins (Echinoidea), and sea cucumbers (Holothuroidea). For a few individuals, repeat measurements were made and these agreed within 20 %. In two cases the replicates were in simple, closed and intermittent-flow respirometers with the same level of agreement. These replicate values were averaged for the individual for all subsequent analysis. Metabolic rates ranged from very low rates of 0.02–0.05 μmol O_2 g^{-1} h^{-1} (~5–10 °C) for some large echinoids and a holothuroid, and >20 μmol O_2 g^{-1} h^{-1} for a few of the small shallow-water shrimps (22–24 °C).

After correcting for temperature, the mass-specific metabolic rates of the crustaceans and echinoderms showed significant negative relationships with body mass, interspecifically (Fig. 1; $p < 0.01$). About one order of magnitude in variability was evident across the range of masses

Table 1 Shallow- and deep-water benthic crustaceans and echinoderms from Hawaii showing the number of specimens whose metabolic rates were determined, their capture depth, wet weight (WW, mean and range), ambient temperature, metabolic rate, and metabolic rate normalized to 10 °C and 10 g WW

Species	*n*	Capture depth (m)	Mass (g)	Temperature (°C)	Metabolic rate (μmoles O_2 g^{-1} h^{-1})	Metabolic rate 10 °C & 10 g
Crustaceans						
Achelata						
Arctides regalis	3	25	62.0 (37–77.0)	23.9	0.78 ± 0.03	0.36 ± 0.02
Parribacus antarcticus	1	25	72.8	23.1	1.43	0.74
Scyllarus aurora	1	250	36.5	11.4	0.37	0.46
Anomura						
Chirostylidae	1	500	1.2	4.9	0.62	0.56
Lithodes longispina	2	1,000	312.8 (177–448.1)	5.5	0.47 ± 0.02	1.85 ± 0.29
Munida sp. 1	3	250	3.4 (2–6.2)	7.5	0.76 ± 0.09	0.71 ± 0.21
Munida sp. 2	2	500	2.0 (0.8–3.3)	4.6	0.29 ± 0.14	0.29 ± 0.06
Munida sp. 3	2	1,000	1.5 (0.9–2.1)	4.9	0.44 ± 0.08	0.41 ± 0.0
Paguridae	1	250	0.5	5.8	0.33	0.21
Brachyura						
Cancer macropthalmus	1	500	15.1	5	0.17	0.31
Carpilius convexus	1	1	123.3	26.1	1.23	0.57
Carpilius maculatus	1	1	52.9	27	0.33	0.11
Liomera sp.	5	1	5.4 (2.2–11.1)	25.8	2.26 ± 1.13	0.44 ± 0.22
Paramola japonica	1	250	49	12.4	0.54	0.66
Pilodius areolatus	1	3	4.2	23.9	2.77	0.61
Platypodia eydouxii	2	1	14.1 (13.7–14.5)	25.3	2.69 ± 0.79	0.72 ± 0.16
Thalamita crenata	5	1	17.1 (7.6–46.1)	23	3.33 ± 3.68	1 ± 0.95
Caridea						
Alpheus sp.	1	1	0.58	24.6	6.76	0.89
Heterocarpus ensifer	15	500	4.2 (0.8–9.4)	5.3	1.69 ± 0.37	1.96 ± 0.5
Heterocarpus laevigatus	5	500	47 (26–72)	5.9	0.5 ± 0.12	1.12 ± 0.26
Palaemon pacificus	11	1	0.36 (0.03–0.7)	24.1	21.98 ± 10.4	1.91 ± 0.39
Plesionika sp.	1	500	1.98	4.7	1.19	1.28
Saron marmoratus	6	3	3.97 (0.7–9.5)	23.2	4.29 ± 2.19	0.85 ± 0.16
Stenopus hispidus	1	1	0.09	22.2	26.05	2.26
Polychelida						
Homeryon asper	1	1,000	55.5	6	0.29	0.69
Echinoderms						
Asteroidea						
Henricia robusta	1	1,000	47.4	5.7	0.08	0.19
Henricia pauperrima	1	500	52	5.3	0.16	0.40
Mediaster ornatus	10	500	44.4 (15.9–85.4)	5.9	0.07 ± 0.03	0.15 ± 0.04
Tamaria scleroderma	3	250	10.5 (8.2–12.6)	10.3	0.15 ± 0.02	0.15 ± 0.01
Echinoidea						
Acanthocidaris hastigera	1	250	121	10.3	0.12	0.23
Aspidodiadima hawaiiensis	7	500	13.2 (10.5–16.7)	4.8	0.12 ± 0.03	0.21 ± 0.05
Aspidodiadima sp.	2	250	20 (17.9–22.1)	10.6	0.24 ± 0.02	0.28 ± 0.03
Echinometra mathaei	4	1	13.4 (5.1–20.3)	21	0.69 ± 0.57	0.25 ± 0.19
Histocidaris variabilis	1	500	248.5	5.3	0.07	0.28
Micropyga sp. white	1	250	14.6	10	0.17	0.18
Micropyga tuberculata	6	250	237.3 (81.5–400)	10.3	0.1 ± 0.07	0.22 ± 0.11
Stereocidaris hawaiiensis	2	500	106 (75.8–135)	5.5	0.05 ± 0	0.13 ± 0.01

Table 1 continued

Species	*n*	Capture depth (m)	Mass (g)	Temperature (°C)	Metabolic rate (μmoles O_2 g^{-1} h^{-1})	Metabolic rate 10 °C & 10 g
Stylocidaris calacantha	2	250	66.0 (62–70.1)	11.3	0.05 ± 0	0.07 ± 0
Stylocidaris rufa	2	250	65.4 (28.4–102.4)	11.4	0.02 ± 0	0.03 ± 0.01
Tripneustes gratilla	4	1	168.4 (85.2–390.5)	21	0.23 ± 0.09	0.16 ± 0.05
Holothuroidea						
Actinopyga mauritiana	2	1	296.4 (107.4–485)	21	0.24 ± 0.1	0.19 ± 0.03
Holothuria atra	2	1	591 (320–862)	21	0.04 ± 0.01	0.05 ± 0.02
Mesothuria sp.	1	500	45.2	6.6	0.06	0.14

for each group. Crustacean metabolic rate was significantly higher than for echinoderms (ANCOVA, $p < 0.001$), which is evident from the very different intercepts, yet similar slopes in the regression with body mass (Fig. 1a vs. b). Within the crustaceans, the shrimps (Caridea) had significantly greater metabolic rates than the other groups (Fig. 1; ANCOVA, $p < 0.01$). In addition, the influence of mass on metabolic rate was greater for the carideans (scaling exponent of −0.36) compared with the crabs and lobsters (−0.15). There was also much more variation in rates at any given size among the crabs and lobsters. For the echinoderms, among the three classes, there were no significant differences in the relationship between mass and metabolic rate (ANCOVA, $p > 0.05$).

The relationship between wet body mass and metabolic rate was evaluated for all species for which at least five individuals were measured. Six significant relationships were found ($p < 0.05$; Table 2). Mass-specific scaling exponents ranged from −0.22 to −0.43 for three shrimps and were quite large for three echinoids ranging from −0.43 to −1.4. However, the range of mass for the echinoid *A. hawaiiensis* was very small (Table 1), which reduces confidence in the absolute value (Table 2).

Depth did not have a significant influence on metabolic rate after temperature and mass were accounted for (Table 3). This was also true within each taxonomic group (Fig. 2). A significant difference was observed in the temperature and mass standardized rates between the caridean shrimps and the other crustaceans (ANOVA, $p < 0.01$). Given the lack of significant differences between the crab and lobster infraorders, we grouped these crustaceans and evaluated depth effects but found none (ANOVA, $p > 0.05$). In comparing standardized rates between echinoderms and crustaceans, the latter have higher metabolic rates (Fig. 2). Mean crustacean metabolic rate at 10 g and 10 °C was 0.84 ± 0.59 μmol O_2 g^{-1} h^{-1} compared with 0.18 ± 0.09 μmol O_2 g^{-1} h^{-1} for echinoderms.

To evaluate environmental drivers of metabolic rate, we compared our data with other region-specific studies. Childress et al. (1990) and Company and Sarda (1998) present data on benthic decapod crustaceans in two discrete locations (California and the Spanish Mediterranean, respectively) and across depths. Webster (1975) reported respiration rates for a number of shallow-water echinoderms from California. Webster's measurements from other areas were omitted from the comparison because they were few in number.

Differences in temperature-standardized metabolic rates between regions were found for both crustaceans and echinoderms. The mean respiration rates of Hawaiian crustaceans were significantly lower than those of crustaceans from either of the other regions (ANCOVA, $p < 0.001$; Fig. 3). When shrimps were evaluated separately from the rest, there were no significant differences among regions (ANCOVA, $p > 0.05$). The difference between Hawaii and the other regions was driven by data for non-caridean and penaid crustaceans (mostly crabs and lobsters). The Hawaiian crabs and lobsters had significantly lower metabolic rates than those from either the Mediterranean or California (ANCOVA, $p < 0.001$). Further examination of the data suggests that the difference in metabolic rates between California and Hawaii is a consequence of the very high respiration rates of the shallow-water species in California. When the shallow-water crabs and lobsters were compared with those in Hawaii, there was a significant difference ($p < 0.01$) while there was no difference in metabolic rates between the deep-living species ($p > 0.05$; all species with MDO >100 m or capture depth ≥250 m). Although there was not a significant decline in metabolism with depth in the Childress et al. (1990) study, the highest metabolic rates of crabs and lobsters at any given size were for shallow-water species (Fig. 3b). Similar to the results for the crustaceans, the metabolic rates of California echinoderms were significantly higher than those from Hawaii (ANCOVA, $p < 0.001$; Fig. 3d).

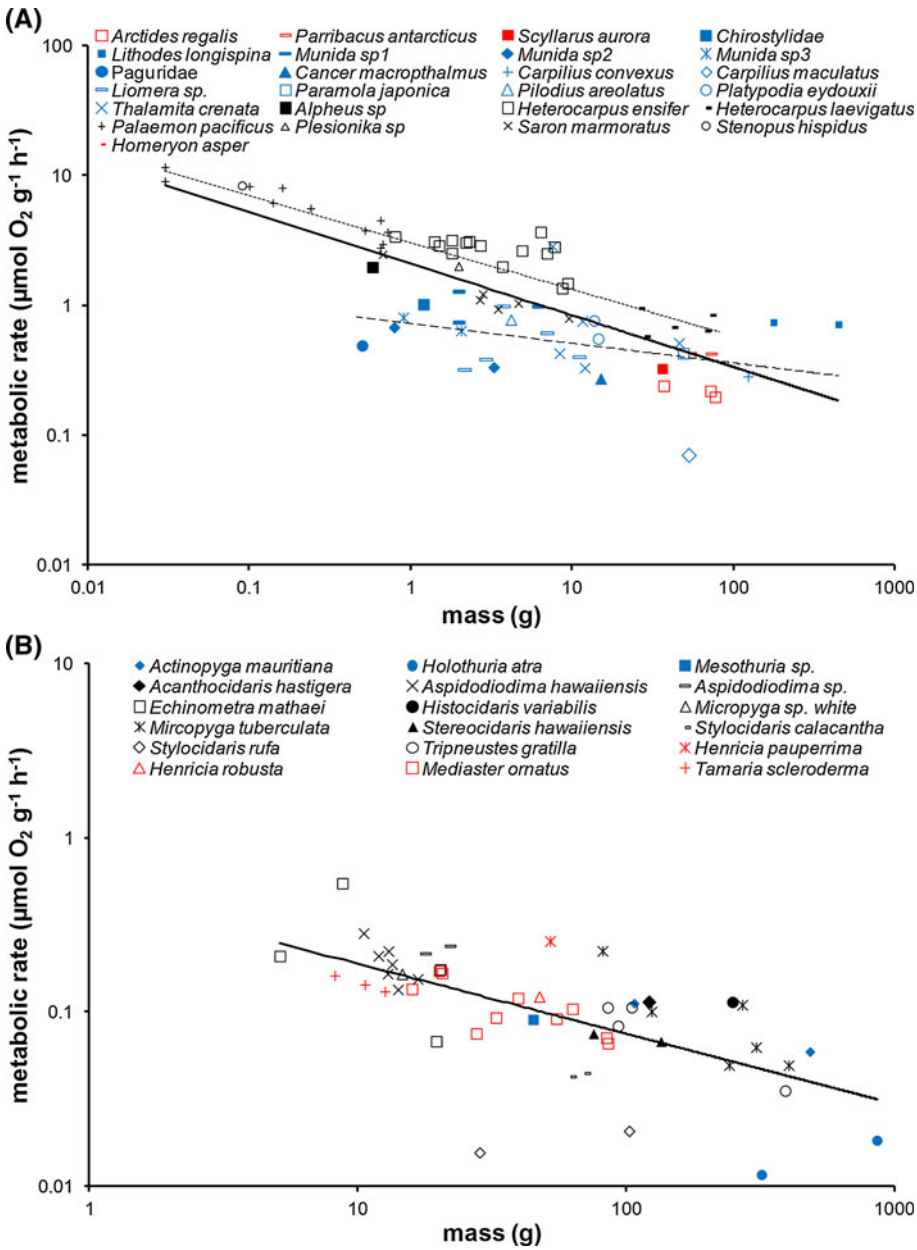

Fig. 1 Temperature-corrected (10 °C) metabolic rates as a function of mass in (**a**) benthic crustaceans including shrimps (*black symbols*), crabs (anomurans and brachyurans in *blue* to simplify presentation) and lobsters (*red*), and in (**b**) echinoderms including asteroids (*red*), holothuroids (*blue*), and echinoids (*black*). *Solid lines* are regressions for all data (crustacean $MR = 2.09x^{-0.40\pm0.04}$, $r^2 = 0.56$; echinoderm $MR = 0.477x^{-0.40\pm0.06}$; $r^2 = 0.44$; error is SE). *Dotted* regression in **a** is for carideans ($MR = 3.04x^{-0.36\pm0.03}$; $r^2 = 0.79$) and *dashed* regression is for all other crustaceans ($MR = 0.723x^{-0.15\pm0.06}$; $r^2 = 0.15$)

Table 2 Significant mass scaling relationships for individual species (log(MR10) = a + b(±SE)* log(mass (g)), MR10 = metabolic rate adjusted to 10 °C [see "Methods"]) and Pearson correlation coefficients (*r*) and *p* values

Species	*n*	a	b	*r*	*p*
Heterocarpus ensifer (C)	15	0.528	−0.219 ± 0.084	−0.5874	0.02
Palaemon pacificus (C)	11	0.49	−0.371 ± 0.049	−0.9304	<0.001
Saron marmoratus (C)	6	0.276	−0.431 ± 0.065	−0.9574	0.01
Mediaster ornatus (A)	10	−0.31	−0.428 ± 0.128	−0.7622	0.01
Aspidodiadima hawaiiensis (E)	7	0.844	−1.404 ± 0.466	−0.8028	0.03
Micropyga tuberculata (E)	6	0.822	−0.816 ± 0.263	−0.8404	0.04

C Caridea, *A* Asteroidea, *E* Echinoidea

Table 3 Results of two factor (taxonomic group and depth) PERMANOVA performed on metabolic rate adjusted to a common size (10 g) and temperature (10 °C)

Source	*df*	SS	MS	Pseudo-F	*p*	Unique perms
Crustaceans						
Taxonomic group	4	3.7405	0.93514	3.5918	0.04	9,954
Depth	3	0.69234	0.23078	0.88641	0.47	9,956
Group × depth	3	5.34E−02	1.78E−02	6.84E−02	0.98	9,952
Residual	14	3.645	0.26035			
Total	24	8.2796				
Echinoderms						
Taxonomic group	2	1.69E−02	8.45E−03	0.83018	0.47	9,959
Depth	3	1.74E−02	5.79E−03	2.0274	0.34	8,892
Group × depth	2	4.37E−03	2.19E−03	0.21466	0.81	9,951
Residual	10	0.10181	1.02E−02			
Total	17	0.13553				

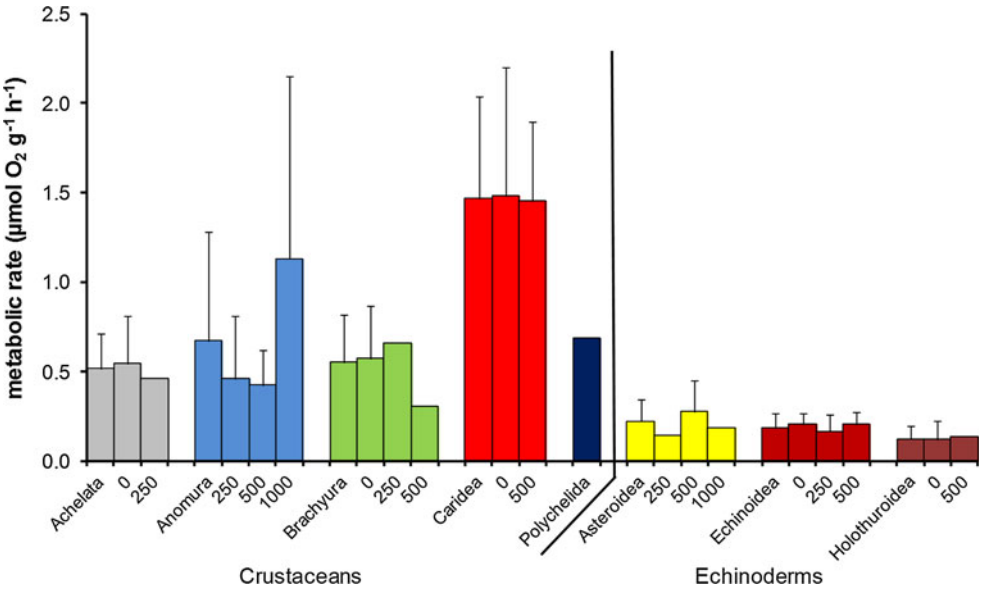

Fig. 2 Mean metabolic rate (standardized to 10 °C and 10 g—see "Methods") for groups of crustaceans and echinoderms. First column is average for group and subsequent columns are averages for species within each depth (when present). All echinoderms have significantly lower metabolic rates than all crustaceans ($p < 0.05$). Within crustaceans, Caridea have a significantly higher metabolic rate than other groups of crustaceans ($p < 0.05$)

Discussion

Hawaiian, benthic invertebrate metabolic rates were variable but scaled with body mass as in previous studies. Seibel and Drazen (2007) found a scaling exponent of -0.28 ± 0.03 for mass-specific metabolic rate for all benthic crustaceans, slightly lower than in the present study. In this study, the magnitude of the overall scaling exponent was increased by the inclusion of caridean shrimps, which had the smallest masses and the highest mass-specific metabolic rates. The carideans showed a stronger relationship between metabolic rate and mass than the crabs and lobsters. This difference may be because the latter group was more diverse in lifestyle and body plan, including munida squat lobsters and large, long-legged lithodid crabs. The interspecific scaling exponent for echinoderm metabolic rates (−0.40) agrees well with the value of −0.39 determined by Seibel and Drazen (2007), but was somewhat larger than the value of −0.30 in the review by Hughes et al. (2011), perhaps as a result of the greater sample size and range of masses in that study. Overall, our results suggest that, even after accounting for the effects of temperature and mass, there is a great deal of variability in metabolic rate, particularly among crustaceans (Fig. 1).

The differences in metabolic rate among the broad taxonomic groups most likely relate to locomotory mode and capacity, which are linked to visual abilities in megafaunal animals. Vision allows for rapid movement in response to predators and prey detected at a distance,

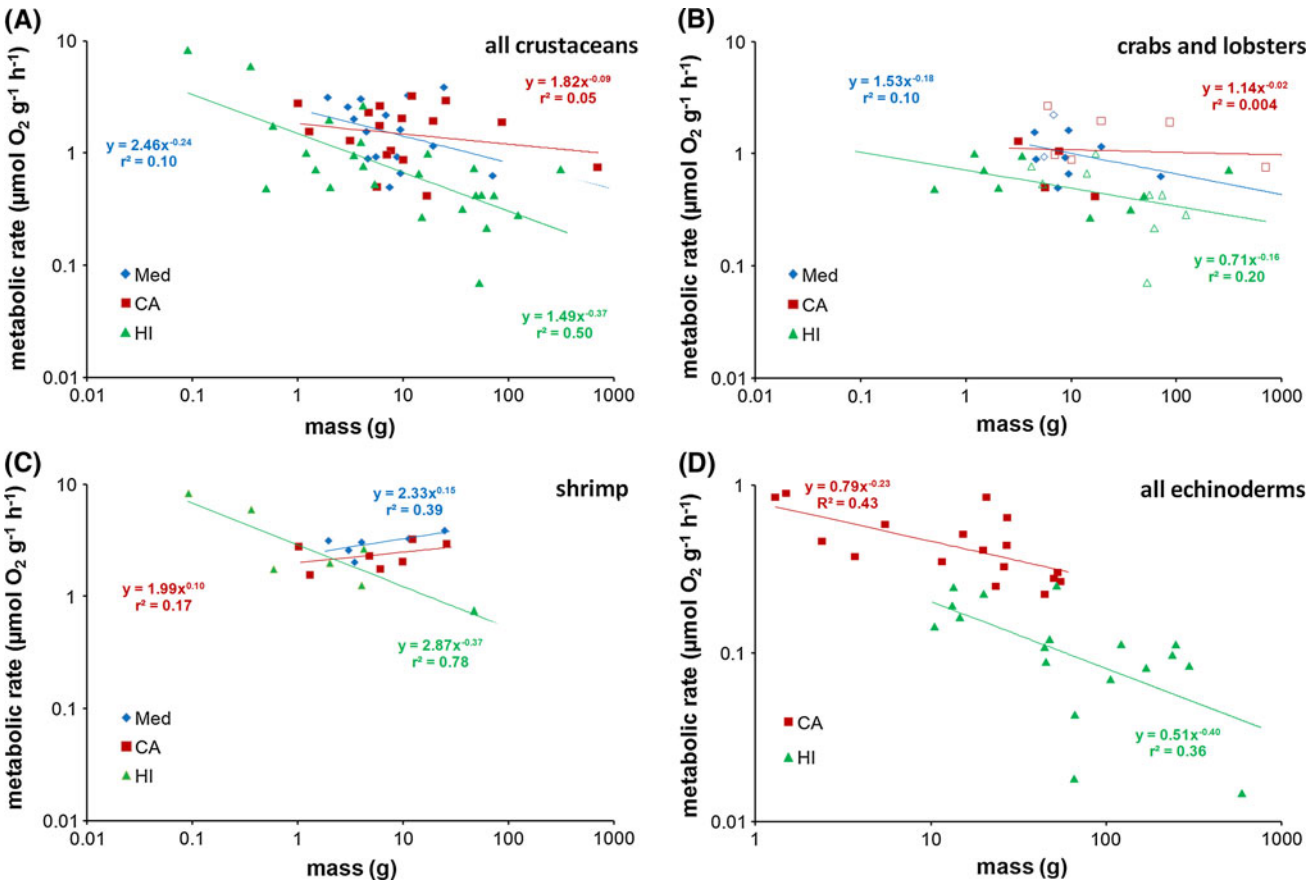

Fig. 3 Temperature-corrected (10 °C) metabolic rates as a function of body mass and habitat region for **a** all crustaceans, **b** crabs and lobsters only (*open symbols* are shallow species with MDO <100 m or capture depth <250 m), **c** shrimps only, and **d** all echinoderms. *Med* Mediterranean, *CA* California, *HI* Hawaii. Data from Mediterranean (Company and Sarda 1998) and California (Webster 1975; Childress et al. 1990) from the literature

requiring greater locomotory capacity (Seibel and Drazen 2007), whereas animals with limited mobility may rely only on tactile senses. Brey (2010) found that locomotory mode was a substantial factor explaining invertebrate metabolic rates. Likewise in the present study, the echinoderms (crawling invertebrates without image forming visual ability) had significantly lower metabolic rates than the crustaceans, agreeing with observations of their lower activity in situ (Smith et al. 1993; Chave and Malahoff 1994). In contrast, the caridean shrimps, including the deep-living *Heterocarpus* spp., often swim in the water column (Gooding et al. 1988) and had the highest metabolic rates. Previous studies have also found that carideans, and some penaid shrimps, have the highest metabolic rates among crustaceans (Childress et al. 1990; Company and Sarda 1998). In contrast with the shrimps, most crabs and lobsters are strictly benthic, crawling or walking across the seafloor, and have lower metabolic rates. Similar patterns of metabolic rate and locomotory activity are observed between benthic and benthopelagic fish species (Drazen and Seibel 2007).

After correcting for mass and temperature, depth was not a significant factor in explaining metabolic rates in benthic invertebrates off Hawaii. Off California, caridean shrimps showed a significant decline in metabolism with depth, though other benthic crustacean groups did not (Childress et al. 1990). Alternatively, in the Mediterranean, the metabolism of the strictly benthic crustaceans (mostly crabs and lobsters) declines with depth, but not in the swimming caridean and penaid shrimps (Company and Sarda 1998). Declines are not seen in benthic fishes (Drazen and Yeh 2012), echinoderms (Hughes et al. 2011; present data), and as suggested by the present result, most benthic crustaceans. However, those benthic-associated species that spend time swimming above the seafloor would be expected to show metabolic declines with depth, as has been found for swimming malacostracans with vision (Brey 2010) and swimming carideans (Seibel and Drazen 2007). Although this study did not find a decline in metabolic rate with depth in the carideans off of Hawaii, only three species of deep-water shrimps were examined and these were all captured at 500 m depth (Table 1). The

use of capture depth (Hughes et al. 2011) as opposed to minimum depth of occurrence (e.g., Donnelly and Torres 1988; Childress 1995; Seibel and Drazen 2007) may also have affected our comparisons but not likely to any great extent. In the present study for the carideans, where our results contrast with previous studies (Seibel and Drazen 2007; Brey 2010), depth distributions are known due to commercial fisheries. *Heterocarpus ensifer* and *Heterocarpus laevigatus* have minimum depths of 270 and 500 m, respectively (Gooding 1984; Hawaii Undersea Research Laboratory, unpub data). This small difference from a capture depth of 500 m does not alter the results qualitatively.

The reasons for lower benthic crustacean and echinoderm metabolic rates in Hawaii compared with similar studies off California or in the Mediterranean could be the result of several factors. Brey (2010) noted substantial differences in metabolic rates of the same species across studies in his meta-analysis and considered between investigator effects to be a significant source of variability. However, the metabolic rates for shrimp are similar across all three studies (Fig. 3b) suggesting that there was no systematic bias due to method differences. Indeed, all three studies captured specimens and performed closed respirometry on temperature-acclimated individuals in similar fashion. We cannot rule out procedural differences, though, because much of the data in Childress et al. (1990) for shallow-water species in California were compiled from the literature and the differences in metabolic rates between Hawaii and California are explained by the shallow-water groups alone. For the echinoderm comparisons, Webster (1975) ran his respirometry experiments for 2 h, much shorter than most of ours. Stress elevates metabolic rates, particularly at the beginning of experiments. Longer duration experiments allow for handling stress to be minimized.

We also explored the possibility that our approach to temperature standardization led to the regional differences. There is wide variation in species-specific temperature effects on marine invertebrates (Brey 2010), and it is often the case that species from different regions inhabit different temperature regimes. For the crustaceans, the differences in metabolic rate were found between shallow-living species, which in Hawaii were kept at $\sim$25 °C. Thus, if the temperature correction applied was too severe, it would inappropriately depress the metabolic rates of these specimens compared to others where respiration was measured closer to 10 °C. Thus, we applied more moderate temperature corrections ($Q_{10} \sim 1.8$), but the differences between regions were still significant (ANCOVA; $p < 0.01$; data not shown).

Food availability has been used to explain reduced activity levels (Collins et al. 1999) and metabolic rates (Dalhoff 2004) and it differs among the regions compared. California has a eutrophic upwelling zone with high primary production compared with Hawaii, which is located in an oligotrophic central gyre (Karl and Lukas 1996). Productivity levels in the Mediterranean are intermediate (Longhurst 1998). Despite these differences, no difference was found in metabolic rates of pelagic crustaceans and squids between Hawaii and the California current; rather, the metabolic rates of crustaceans were higher in Hawaii in waters to about 400 m (Cowles et al. 1991; Seibel et al. 1997). In the present study, the Hawaiian echinoderms and shallow-water crabs and lobster species, living in a more oligotrophic setting than the other regions, had lower metabolic rates. However, no differences were found for the shrimps or deep-water crab and lobster species. In addition, food as a driver of metabolism has been discounted on evolutionary and energetic grounds (Seibel and Drazen 2007). In short, selection should act to reduce the metabolic costs of an animal in any environment. More food does not result in higher metabolic rates because a higher metabolic rate alone does not confer any selective advantage.

This study is the first to examine the metabolic rates of many species of benthic invertebrates across depths in a tropical region. At in situ environmental temperatures the metabolism of deeper-living invertebrates is much lower than that of shallow-living species, but this decline can be explained by changes in temperature alone, and this appears to be the case for most benthic invertebrates (Seibel and Drazen 2007; Brey 2010). Our results confirm that taxonomic group has a large bearing on average metabolic rates (Brey 2010), and it is probably linked to locomotory pattern as well as physiological differences. In addition, the Hawaiian crabs, lobsters, and echinoderms had lower metabolic rates than similar species in other ocean regions. While the reasons for these differences may include methodology, environmental drivers may also be important. The implications of these findings are that for approximating metabolism for food web and energy budgets, the benthic fauna should be broken down into at least broad taxonomic groups and region-specific data should be used if at all possible.

Acknowledgments Thanks to Erica Aus, Nicole Condon, Chris Demarke, Anela Choy, Jason Friedman, William Misa, and Cordelia Moore for help at sea and in the laboratory. Ethan Capone and Cassandra Drazen assisted with collection of shallow-water species. Chris Kelley provided depth information from the NOAA, Hawaii Undersea Research Laboratory (HURL) database. Chris Mah, Robert Moffitt, Les Watling, and Kareen Schnabel helped with specimen identification. We thank the submersible crew of HURL for their outstanding attitude and ability to achieve our science objectives. Thanks also to the captain and crew of the RV Ka'imikai-o-Kanaloa. This research was supported by grants from NSF-OCE (#0727135) and NOAA-HURL to J. C. Drazen. Support to K. E. Korsmeyer was provided by the Hawaii Pacific University Trustee's Scholarly Endeavors Program.

References

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E Ltd, Plymouth

Belman BW, Gordon MS (1979) Comparative studies on the metabolism of shallow-water and deep-sea marine fishes. 5. Effects of temperature and hydrostatic pressure on oxygen consumption in the mesopelagic *Melanostigma pammelas*. Mar Biol 50:275–281

Brey T (2010) An empirical model for estimating aquatic invertebrate respiration. Methods Ecol Evol 1:92–101. doi:10.1111/j.2041-210X.2009.00008.x

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85:1771–1789

Chave EH, Malahoff A (1994) In deeper waters: photographic studies of Hawaiian deep-sea habitats and life-forms. University of Hawaii Press, Honolulu

Childress JJ (1975) The respiratory rates of midwater crustaceans as a function of depth of occurrence and relation to the oxygen minimum layer off southern California. Comp Biochem Physiol 50A:787–799

Childress JJ (1977) Effects of pressure, temperature and oxygen on the oxygen-consumption rate of the midwater copepod *Gaussia princeps*. Mar Biol 39:19–24

Childress JJ (1985) Capture and live recovery of deep-sea crustaceans. Natl Geogr Soc Res Rep 21:67–69

Childress JJ (1995) Are there physiological and biochemical adaptations of metabolism in deep-sea animals? Trends Ecol Evol 10:30–36

Childress JJ, Thuesen EV (1993) Effects of hydrostatic pressure on metabolic rates of six species of deep-sea gelatinous zooplankton. Limnol Oceanogr 38:665–670

Childress JJ, Cowles DL, Favuzzi JA, Mickel TJ (1990) Metabolic rates of benthic deep-sea decapod crustaceans decline with increasing depth primarily due to the decline in temperature. Deep Sea Res 37:929–949

Childress JJ, Seibel BA, Thuesen EV (2008) N-specific metabolic data are not relevant to the 'visual interactions' hypothesis concerning the depth-related declines in metabolic rates: comment on Ikeda et al. (2006). Mar Ecol Prog Ser 373:187–191

Clarke TA (1972) Collections and submarine observations of deep benthic fishes and decapod Crustacea in Hawaii. Pac Sci 26:310–317

Collins MA, Priede IG, Bagley PM (1999) In situ comparison of activity in two deep-sea scavenging fishes occupying different depth zones. Proc R Soc Lond B 266:2011–2016

Company JB, Sarda F (1998) Metabolic rates and energy content of deep-sea benthic decapod crustaceans in the western Mediterranean Sea. Deep-Sea Res I 45:1861–1880

Cowles DL, Childress JJ, Wells ME (1991) Metabolic rates of midwater crustaceans as a function of depth of occurrence off the Hawaiian Islands: food availability as a selective factor? Mar Biol 110:75–83

Dalhoff EP (2004) Biochemical indicators of stress and metabolism: applications for marine ecological studies. Annu Rev Physiol 66:183–207

Donnelly J, Torres JJ (1988) Oxygen consumption of midwater fishes and crustaceans from the eastern Gulf of Mexico. Mar Biol 97:483–494

Drazen JC, Seibel BA (2007) Depth-related trends in metabolism of benthic and benthopelagic deep-sea fishes. Limnol Oceanogr 52:2306–2316

Drazen JC, 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 JC, Reisenbichler KR, Robison BH (2007) A comparison of assimilation efficiencies between four species of shallow and deep living fishes. Mar Biol 151:1551–1558

Drazen JC, Yeh J, Friedman JR, Condon N (2011) Metabolism and enzyme activities of hagfish from shallow and deep water of the Pacific Ocean. Comp Biochem Physiol A 159:182–187

Erdman RB, Blake NJ, Torres JJ (1991) Oxygen consumption of the deep-sea crabs *Chaceon fenneri* and *C. quinquedens* (Brachyura: Geryonidae). Comp Biochem Physiol A 99A:383–385

Gooding RM (1984) Trapping surveys for the deepwater caridean shrimps, *Heterocarpus laevigatus* and *H. ensifer*, in the northwestern Hawaiian Islands. Mar Fish Rev 46:18–26

Gooding RM, Polovina JJ, Dailey MD (1988) Observations of deepwater shrimp, *Heterocarpus ensifer*, from a submersible off the Island of Hawaii. Mar Fish Rev 50:32–38

Hughes SJM, Ruhl HA, Hawkins LE, Hauton C, Boorman B, Billett DSM (2011) Deep-sea echinoderm oxygen consumption rates and an interclass comparison of metabolic rates in Asteroidea, Crinoidea, Echinoidea, Holothuroidea and Ophiuroidea. J Exp Biol 214:2512–2521. doi:10.1242/jeb.055954

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

Karl DM, Lukas R (1996) The Hawaii Ocean Time-series (HOT) program: background, rationale and field implementation. Deep-Sea Res II 43:129–156

Longhurst AR (1998) Ecological geography of the sea. Academic Press, New York

Mickel TJ, Childress JJ (1982) Effects of pressure and pressure acclimation on activity and oxygen consumption in the bathypelagic mysid *Gnathophausia ingens*. Deep Sea Res 29:1293–1301

Moffitt RB, Parrish FA (1992) An assessment of the exploitable biomass of *Heterocarpus laevigatus* in the main Hawaiian Islands. Part 2: observations from a submersible. Fish Bull 90:476–482

Raymond EH, Widder EA (2007) Behavioral responses of two deep-sea fish species to red, far-red, and white light. Mar Ecol Prog Ser 350:291–298

Ruhl H (2008) Community change in the variable resource habitat of the abyssal northeast Pacific. Ecology 89:991–1000

Seibel BA, Drazen JC (2007) The rate of metabolism in marine animals: environmental constraints, ecological demands and energetic opportunities. Philos Trans R Soc Lond B 362:2061–2078

Seibel BA, Thuesen EV, Childress JJ, Gorodezky LA (1997) Decline in pelagic cephalopod metabolism with habitat depth reflects differences in locomotory efficiency. Bio Bull 192:262–278

Smith KL Jr (1983) Metabolism of two dominant epibenthic echinoderms measured at bathyal depths in the Santa Catalina Basin. Mar Biol 72:249–256

Smith KL Jr, Kaufmann RS, Wakefield WW (1993) Mobile megafaunal activity monitored with a time-lapse camera in the abyssal North Pacific. Deep Sea Res 40:2307–2324

Steffensen JF (1989) Some errors in respirometry of aquatic breathers: how to avoid and correct them. Fish Physiol BioChem 6:49–59

Vetter EW, Smith CR, De Leo FC (2010) Hawaiian hotspots: enhanced megafaunal abundance and diversity in submarine canyons on the oceanic islands of Hawaii. Mar Ecol:1–17. doi:10.1111/j.1439-0485.2009.00351.x

Warrant EJ, Locket NA (2004) Vision in the deep-sea. Biol Rev 79:671–712

Webster SK (1975) Oxygen consumption in echinoderms from several geographical locations, with particular reference to the Echinoidea. Bio Bull 148:157–164

Widdicombe S, Spicer JI (2008) Predicting the impact of ocean acidification on benthic biodiversity: what can animal physiology tell us? J Exp Mar Biol Ecol 366:187–197. doi:10.1016/j.jembe.2008.07.024