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Respiration of four species of deep-sea demersal fishes measured *in situ* in the eastern North Pacific

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ABSTRACT

The lack of data on the metabolism of deep-sea demersal fishes is a major gap in our ecological knowledge of the deep ocean. Metabolism influences individual rate processes such as resource utilization, growth, and reproduction. It also correlates with an animal's ability to accommodate ocean acidification. Here we describe an autonomous *in situ* respirometry system that is deployed autonomously from a ship to capture fishes attracted to bait, and measure their rate of oxygen consumption. This instrument is multi-chambered and relies on the fish to actuate the capture mechanism and start the experiments. Although capture rates were low, data on five fishes were obtained including *Eptatretus deani*, two *Coryphaenoides acrolepis*, *Antimora microlepis*, and *Pachycara gymninium*. The metabolisms of the latter two species were measured for the first time. The metabolic rates were low (0.09–0.40 μmols O_2 g^{-1} h^{-1} at temperatures of 1.8–4.0 °C) in comparison to shallow water species. After taking temperature differences into account only the metabolic rates of benthopelagic species, *C. acrolepis* and *A. microlepis*, were substantially lower, by an order of magnitude, than shallow water relatives such as cod and pollock. The metabolic rate of the deep-sea fishes varied considerably clearly warranting further experiments to ascertain which factors are likely to explain the differences.

1. Introduction

The deep sea is the largest habitat on earth. It is increasingly under threat from anthropogenic perturbations such as fisheries, mineral resource extraction, and ocean acidification (Glover and Smith, 2003; Robison, 2009), but our knowledge of deep sea ecosystems remains very limited compared to that for the continental shelves. Many studies of deep-sea animals have characterized food habits (Anderson, 2005; Drazen et al., 2001; Gartner et al., 1997; Iken et al., 2001) and documented regional and depth related patterns in biomass, abundance, and community composition (Carney, 2005; Haedrich and Rowe, 1977; Lampitt et al., 1986; Merrett and Haedrich, 1997). However, one important gap in our knowledge of deep-sea benthic communities is information on rate processes. Metabolic rate is one such process that is fundamentally important to ecology. It is the process of energy assimilation, transformation, and allocation that strongly influences individual rate processes such as resource utilization, growth, and reproduction (Brown et al., 2004; McNab, 2002). Through the integration of individuals, the dynamics of populations and communities can be inferred. Metabolic rates can be used to construct models of the flow of energy and materials in an ecosystem (Childress and Thuesen, 1992; Christiansen et al., 2001; Smith, 1992; Smith et al., 2001) providing valuable input for ecosystem based management scenarios.

In the deep-sea, demersal fishes are a diverse group with wide ranging food habits and many large species are the top predators (Buckley et al., 1999; Cailliet et al., 1988; Drazen et al., 2001; Madurell and Cartes, 2005b; Mauchline and Gordon, 1986; Pearcy and Ambler, 1974; Sedberry and Musick, 1978). Demersal fishes can be very abundant (Alton, 1972; Bergstad et al., 2008; Clausen, 2008; Haedrich and Rowe, 1977; Tolimieri and Levin, 2006) and may have considerable influence on prey populations and community structure as has been demonstrated in shallow water systems (Frank et al., 2005; Jennings and Kaiser, 1998). At midslope depths the biomass of demersal fishes can exceed that of other megafauna and studies have suggested that these populations subsist by intercepting vertically migrating pelagic prey (Mauchline and Gordon, 1991; Stefanescu et al., 1993). Pelagic prey and carrion are an important food resource for many slope dwelling and abyssal fishes (Carrasson and Matallanas, 2002; Drazen et al., 2001; Drazen et al., 2008; Madurell and Cartes, 2005b; Pearcy and Ambler, 1974). Their foraging habits may represent a significant form of benthic–pelagic coupling. To assess the importance of these animal's trophodynamics we must have information on the flow of energy, or feeding rates, of their

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populations. Only a few estimates of deep-sea demersal fish feeding rates exist. Of those few estimates, calculations using underlying rate processes extrapolated from shallow water species (Macpherson, 1985; Madurell and Cartes, 2005a; Madurell and Cartes, 2006) give dramatically different results than those that utilize the few *in situ* measurements of metabolic rate available (Drazen, 2002; Koslow, 1996). Clearly, a better understanding of deep-sea fish metabolism using *in situ* measurements is needed to develop food web models for deep-sea systems.

There are relatively large data sets for the metabolism of deep-sea pelagic taxa (Seibel and Drazen, 2007) but not for demersal fishes. Working with demersal fishes is certainly more difficult because collecting specimens in good health is more complicated (Childress et al., 1990). Trawling in this habitat usually crushes and/or suffocates the fishes in the cod end with rock and sediment. This situation is exacerbated by the often lethal expansion of these species' gas bladders upon recovery to the surface. As a result, only a handful of respiration measurements have been made on deep-living demersal fishes (reviewed in Drazen and Seibel, 2007). Whilst large variation in metabolic rates has been reported from this limited research, it does suggest that, after taking into account temperature and body mass, the mass-specific metabolic rates of some groups of deep-sea species are much lower than shallow water species.

The aim of this research was to develop an *in situ* fish trap respirometer and measure the metabolic rates of deep-sea demersal fishes off the California Coast. This data could then be added to existing data to further improve our understanding of metabolic rate variation in deep-sea species and in relationship to shallow water species. We targeted demersal fishes that are attracted to bait. These are often the top predators in the deep sea (Drazen et al., 2001; Hoff et al., 2000; Madurell and Cartes, 2005a; Pearcy and Ambler, 1974). Many are also the targeted by commercial fisherman using baited longlines and trawls, hastening our need for information (Clausen, 2008; Devine et al., 2006; Haedrich et al., 2001). In addition to these important ecological criteria, species actively attracted to bait can be captured autonomously allowing for *in situ* experimentation (Drazen et al., 2005; Smith and Baldwin, 1997). The *in situ* fish trap respirometer was developed and deployed as a free vehicle from ~100 to 3000 m depth to autonomously capture and measure the metabolic rate of fishes attracted to bait. During the testing and first deployments of this instrument, the respiration rates of four species of demersal fish were measured: *Eptatretus deani* Evermann & Goldsborough 1907, *Coryphaenoides acrolepis* Bean 1884, *Antimora microlepis* Bean 1890, and *Pachycara gymninium* Anderson & Peden, 1988. The respiration rates of the last two species were measured for the first time.

2. Methods

2.1. In situ respirometer

In situ measurements of oxygen consumption of deep sea fish were obtained using a four-chambered free-vehicle respirometer. The mechanisms of the system are similar to those described for a hyperbaric trap by Drazen et al. (2005). The major components of the respirometer included four acrylic respirometry chambers, floatation (twelve 17 in. spheres and two 10 in. spheres), dual acoustic releases, an electronics and battery housing, and 100 kg of ballast (Fig. 1). Each respirometry chamber was 100.2 L in volume (internal diameter=33 cm, length=122 cm, wall thickness=2.5 cm) and closed by 2.5 cm thick acetal endplates. The front end cap was equipped with a sealing door (22 cm diameter). Capture of a fish employed a baited hook attached via a short line

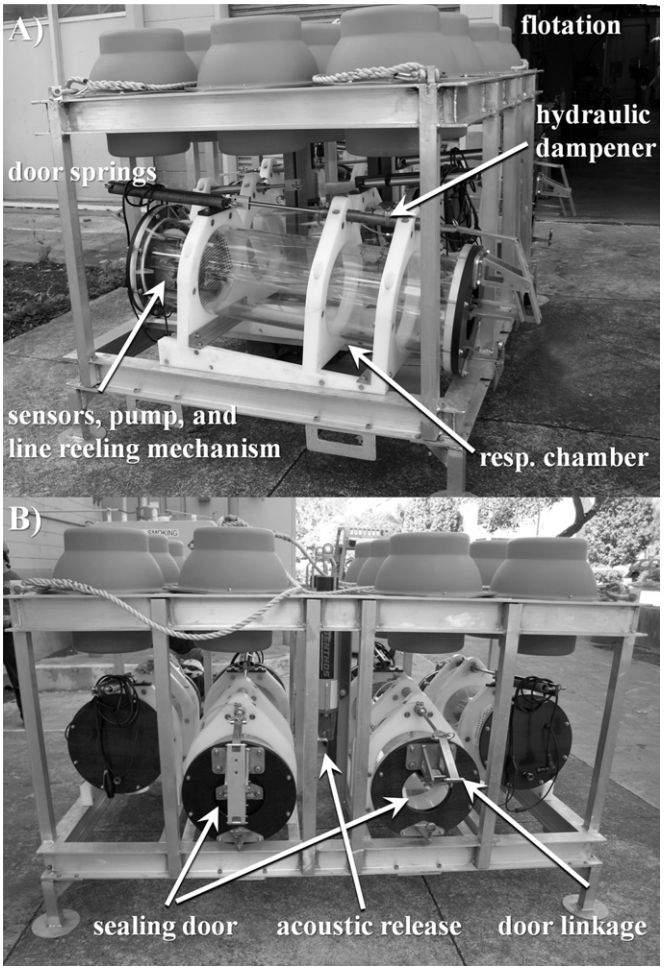

Fig. 1. (A) Side and (B) front views of the *in situ* fish trap respirometer showing the main components. Each of the four respirometry chambers has a door, shown open and closed in (B), that moves on a linkage mechanism and is connected to actuating springs through a hydraulic dampener. At the back of each chamber behind a protective screen is a line reeling mechanism, oxygen and temperature sensor, and water circulation pump.

to a spring loaded reel. The mechanism was actuated by the fish pulling on the hook, which opened a quick release shackle clamped around a metal pin at the mouth of the trap. Later deployments utilized a timed release to actuate the shackle release. A high torque but low speed reel retracted the fish into the chamber. The line connected to the reel passed through a secondary trigger located adjacent to the reel at the rear of the trap. The quick release shackle (now opened) at the end of the line then hit the trigger, which released the door. The door was pulled closed, from the inside against the annular end cap with an O-ring seal, via the force of large coiled springs (73 kg of force), which were speed dampened by a hydraulic piston for a consistent and moderated closure. Once at the back of the trap the short line to the hook and fish was cut, freeing the animal to swim about the chamber. The retraction mechanism was placed behind 1 cm square plastic mesh to protect the fish. Also at the rear of each chamber an oxygen optode (Aandera 4330) measured oxygen concentration and temperature. A water pump (Seabird 5T) was plumbed with plastic tubing so that water circulated from one end of the chamber to the other and passed water over the oxygen optode. Mixing was determined to be adequate based on dye experiments in the laboratory. Data from each oxygen optode were recorded onto data loggers housed in a central electronics pressure resistant housing.

2.2. Field experiments

The entire system was deployed as a free vehicle during two cruises in April and October of 2009 in Monterey Bay. All doors were in the open position upon deployment, each with a squid baited hook secured to the outside of the chamber. During each deployment one chamber was designated as a control experiment to measure background respiration. This chamber was set with a timed release that closed the chamber door approximately 4 h following deployment. The contents of this chamber were available for inspection upon return to the surface to confirm the absence of animals. On a few occasions several very small amphipods were found in the chamber but no detectable change in oxygen consumption was noted probably because their combined mass ($\ll$ 1 g) was so low in relation to the large volume of the chamber. Data for all chambers were downloaded after each experiment. Each fish was identified to species using a variety of keys aboard ship. Fish length was measured aboard ship the specimen was frozen and its mass and sex was determined in the laboratory.

2.3. Data analysis

Oxygen concentration ($\mu mol\, l^{-1}$) data were plotted against time and the rate of change from captured fish was determined. This rate ($\mu mol\, l^{-1}\, h^{-1}$) was converted to oxygen consumption ($\mu mol\, g^{-1}\, h^{-1}$) by multiplying by the chamber volume (l: minus the fish's volume) and dividing by the mass (g) of the fish. The time of fish capture was evident from a transition from a constant oxygen concentration to a declining trend (Fig. 2) and the period from 1 to 3 h following capture was omitted from the calculations. Background respiration was determined from control experiments and oxygen consumption rates were adjusted accordingly, though the background rates were negligible. Temperature rapidly declined upon descent and took from 1 to 2 h to reach a steady state on the seafloor. All fish were captured after this time period. Each oxygen optode was calibrated before each cruise. Optodes have slower response times ($\sim$25 s) than electrodes (Glazer et al., 2004) but are very stable in terms of their oxygen response over periods of weeks to months (Glud et al., 2001; Stokes and Somero, 1999). The temperature response of optodes is also very predictable and is corrected internal to the sensor.

To place the results into a broader context, the rates of oxygen consumption for each fish were standardized to 5 °C, using a Q_{10} of 2.3 (Clarke and Johnston, 1999). This is mean value from a large meta-analysis of within species Q_{10} relationships. The data were plotted as a function of body mass along with data compiled for all other deep-sea fishes. Representative shallow water and phylogenetically related species were also selected for comparison. This data is presented in the review by Drazen and Seibel (2007) and was augmented by laboratory measurements of deep and shallow living hagfish (Drazen et al., 2011) and zoarcid fishes (Montgomery and Wells, 1993; Moser et al., 1996; Van Dijk et al., 1999; von Dorrien, 1993) for comparison to the *in situ* measurements of this study.

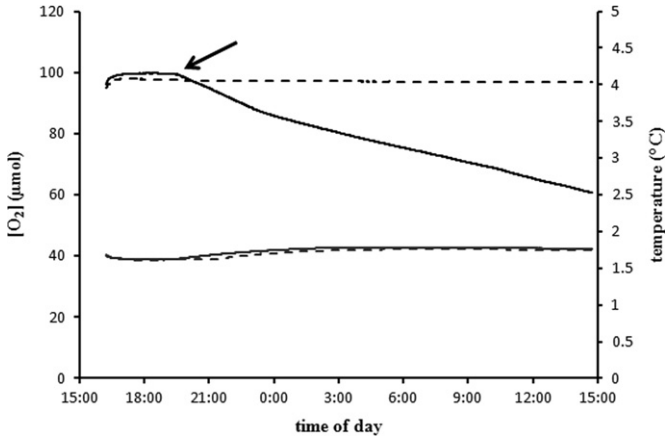

Fig. 2. Oxygen consumption and temperature recorded for *Pachycara gymninium* (solid lines) at 3034 m in conjunction with a control chamber (dashed lines). Lower lines represent the temperature profiles. The point at which the capture of the fish is evident is indicated by the arrow.

3. Results

The respirometer was deployed five times at depths between 100 and 500 m but no fish were captured. The chambers were retrieved with hooks still outside of the trap but without bait. Concurrent baited camera deployments at these depths revealed few fishes and thousands of lysiannasid amphipods, which rapidly consumed bait (Yeh and Drazen, 2011). It is likely that amphipods out-competed fish for the bait at these depths.

Twelve deployments were carried out between $\sim$1000 and 3000 m. Twelve fishes were captured and five for which respiration data was successfully recorded (Table 1). During some of the first deployments, two Pacific rattails (*Coryphaenoides acrolepis)* and one small sablefish (*Anoplopoma fimbria)* failed to trigger the retraction mechanism and in two instances, with black hagfish (*Eptatretus deani)*, the door failed to close properly. In one instance, a Pacific rattail was captured but a considerable amount of noise in the oxygen data, likely due to a clogged pump, prevented the intrepretation of reliable oxygen consumption data. For later deployments the tension required to actuate the trigger was reduced and ultimately a timed release was used to actuate the door, eight hours after deployment.

In the cases of successful fish captures there was a steady decline in oxygen consumption sometimes with a steeper depletion of oxygen occurring for the first 1–3 h, as would be expected immediately after capture (Fig. 2). Oxygen consumption was measured for periods from 4.0 to 14.6 h (Table 1). Oxygen concentrations in the chamber did not fall below 25 μM except during the measurement on the black hagfish where the oxygen fell to 15 μM, still above this species critical partial pressure (Drazen et al., 2011).

All of the metabolic rates were quite low. The two Pacific rattails had similar size and metabolic rate. The flat-nosed codling (*Antimora microlepis*) was similar in size to these two fish but had a metabolic rate 2.5–3 times higher. The zoarcid *Pachycara gymninium* had the highest metabolic rate, which is partially explained by its smaller size (Table 1).

The rates are best evaluated in the context of data for other deep-sea species and related shallow living ones. Fig. 3 presents the metabolic rate data as a function of body mass with all measurements standardized to a common temperature (5 °C). There is a wide variation in the metabolic rates of the fishes. The metabolic rate of the hagfish, *E. deani*, measured *in situ* was similar to laboratory measurements of this species (Drazen et al., 2011). In comparison to shallow dwelling species, black hagfish has an intermediate metabolic rate. Amongst the gadiform fishes the Pacific rattail had a metabolic rate similar to the deeper living abyssal rattail (*C. armatus*) and an order of magnitude lower than shallow living gadiformes and the eurybathic sablefish. As mentioned before, the flat-nosed codling had a considerably higher metabolic rate compared to the rattails but this rate was still substantially lower than the shallow gadiform fishes or sablefish. The pudgy cusk-eel (*Spectrunculus grandis)*, a benthopelagic ophidiiform fish, had a metabolic rate similar to that of the flat-nosed codling considering the differences in size. *P. gymninium's* metabolic rate is similar to shallow zoarcids and scorpaenids and higher than deep living scorpaenids and hagfishes.

Table 1
Measurements of oxygen consumption in demersal fish captured in the *in situ* respirometer in Monterey Bay, California. In one instance, specific depth was not available so it was estimated based on deployment location and multibeam bathymetry. Trigger is the trap acutuation mechanism either self triggered by the fish or a timed trigger (see text). Type is the type of length measurement (PAFL—pre-anal fin length, FL—forklength, TL—total length). Time is the duration over which oxygen consumption was measured excluding the period directly after capture. Oxygen consumption data adjusted to a common temperature of 5 °C is given (see text).

Species	Depth	Trigger	Length (cm)	Type	Mass (g)	Sex	Time (h)	Temp (°C)	O_2 consumption (μmols g^{-1} h^{-1})	
									In situ	5 °C
Eptatretus deani	1010	Timed	37	TL	92.3		7.5	4.0	0.351	0.382
Coryphaenoides acrolepis	1398	Self	25.5	PAFL	1306.3	M	11.7	2.9	0.091	0.108
Coryphaenoides acrolepis	~1500	Timed	23	PAFL	1215	F	14.2	2.8	0.113	0.136
Antimora microlepis	2063	Self	52.7	FL	993.9	M	4.0	2.2	0.270	0.340
Pachycara gymninium	3034	Timed	44.1	TL	414.2	F	14.6	1.8	0.403	0.529

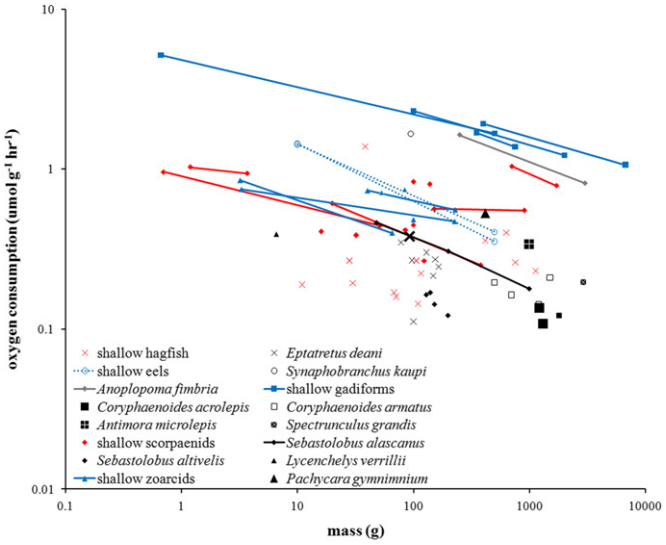

Fig. 3. Oxygen consumption as a function of mass for the captured fish (large black symbols), all other deep-sea measurements (smaller black symbols), and several shallow water related species (colored symbols). *x*'s indicate hagfish (family Mxyinidae), circles are eels (order Anguillformes), squares are cods and their relatives (order Gadiformes), diamonds are scorpionfish (family: Scorpaenidae, except for *A. fimbria*, which is in the sister family Anoplomatidae), triangles are eelpouts (family: Zoardicae). Points connected by lines indicate the mass scaling relationship for many data points for a species.

4. Discussion

4.1. Metabolism of deep-sea fishes

Our data confirm earlier measurements of rattail and hagfish metabolism as being very low (Fig. 3). Previous estimates of the metabolic rates of abyssal rattails (Smith, 1978) and Pacific rattails (Smith and Hessler, 1974) are very similar to those we measured in Pacific rattails. Amongst the benthopelagic fishes, those that live in association with but swim above the seafloor most of the time, the rattails have the lowest metabolic rates. Both flat-nosed codling and pudgy cusk-eel, a benthopelagic ophidiiform fish with a similar body form as that of the rattails (Uiblein et al., 2008), have higher metabolisms. The *in situ* measurement for the black hagfish *Eptatretus deani* is similar to laboratory measurements for this species done by Drazen et al. (2011). The metabolic rate of this species is lower than for most shallower-living species with the exception of *Eptatretus stoutii* and very low in comparison with most teleost fishes (Drazen and Seibel, 2007).

The metabolic rate of the flat-nosed codling, *A. microlepis*, was measured for the first time. The relative activity of a closely related codling, *A. rostrata*, and the rattail *C. armatus*, attracted to baited cameras, has been conducted in the North Atlantic (Collins et al., 1999), which provides an interesting study for comparison to our direct estimates of metabolic rate for the congener *A. microlepis* and the rattails. Principally *C. armatus* lives deeper than *A. rostrata* but both co-occur at ~2500 m depth. *A. rostrata* had a much higher swimming speed and tail beat frequency than the abyssal rattail, *C. armatus* (Collins et al., 1999) and comparable to shallow living fishes at similar cold temperatures (Bailey et al., 2003). Unlike the behavioral studies, the metabolic rate of *A. microlepis* is substantially lower than related shallow living species at similar temperatures. It is possible that the presence of bait skewed the observations of locomotory behavior in *A. rostrata* towards higher activities. On comparing the two deep-sea fishes, Collins et al. (1999) suggested that the greater locomotory ability and activity of *A. rostrata* in relation to *C. armatus* evolved in response to food supply. *C. armatus*, living mostly deeper than *A. rostrata*, had a much lower metabolic rate to cope with a poor food environment. Our direct estimates of respiration suggest that the congeneric codling, *A. microlepis*, has a higher metabolic rate than the rattails in support of the behavioral work. The higher locomotory and metabolic rates in *Antimora* spp. may also be due to greater competition for food resources at shallow depths where fish densities are higher. More data are needed to evaluate the variation in deep-sea fish metabolic rate and clarify the factors driving the differences.

Pachycara gymninium's metabolic rate was measured for the first time and was surprisingly high compared to other benthic species (Fig. 3). Zoarcids are principally benthic, actually resting on the seafloor and other studies have found them to be very inactive with low metabolic rates (Holeton, 1974). *P. gymninium* and several other species in the genus are attracted to baited cameras (Barry and Drazen, 2007; Yeh and Drazen, 2011) and may be more active and therefore have higher metabolic rates than some members of the family. An alternative is that the high metabolic rate measured is an artifact of the experiment. Some amphipods have elevated respiration rates, after they sense the odor of carrion, which return to a lower "resting" state in about eight hours (Smith and Baldwin, 1982). It was hypothesized that these animals have a strategy of reducing metabolic costs between sporadic bouts of actively searching for and feeding on carrion. It is possible that this is the case for *Pachycara* but the respiration rate measured was steady for over 14 h (Fig. 2) a much longer period of time than was recorded for the amphipods elevated respiration rates. Zoarcids can be amongst the most abundant fishes on the continental slope in the eastern North Pacific (Cailliet et al., 1999; Pearcy et al., 1982; Tolimieri and Levin, 2006). If their energetic demands are high as suggested by our preliminary data then they could exert significant predation pressures on their prey populations.

These observations are broadly in accordance with the visual interactions hypothesis (VIH; Childress, 1995; Seibel and Drazen,

2007). This hypothesis has been used to explain the decline in metabolic rate with depth in pelagic and demersal fishes (Drazen and Seibel, 2007). It suggests that the declines are the result of reduced light levels, which reduce distance over which visual predators and prey interact with each other. Shorter reactive distances reduce the selective pressure for robust burst swimming performance which, in turn, reduces the maintenance costs/metabolism associated with a powerful locomotory engine. However, it is hypothesized that the reductions in metabolism will only occur in pelagic or benthopelagic taxa where active evasions and chases are the ways in which predators and prey interact. In the benthic environment, where a substrate affords the possibility of camouflage and/or burrowing, sluggish species with low metabolic rates are likely to be at all depths so no depth related declines would be seen in the group as a whole. The benthic species examined in this study, the zoarcid *P. gymninium* and black hagfish, have metabolic rates broadly within the range of shallow water relatives. Whereas, the benthopelagic species, *A. microlepis*, *Coryphaenoides* spp., and *S. grandis,* while having a 2–3 fold range in metabolic rates, all have rates considerably lower than comparable shallow water species as would be predicted by the VIH.

4.2. *In situ fish trap respirometer*

The *in situ* fish trap respirometer provided some of the only metabolic rate measurements of deep-sea fishes. However, capture of the animals proved problematic. The capture mechanism required that the fish actuate the respirometer by pulling on and opening a quick release shackle. This mechanism worked but not as often as desired probably because deep-sea fishes are rather sluggish. A more sensitive mechanism could be engineered but would require some sort of delay prior to arming to prevent pre-tripping during deployment in rough seas. The advantage of the technique was that a single fish was captured in all deployments. A drop chamber design has worked but in most cases captures multiple animals making interpretation of the oxygen consumption data difficult (Bailey et al., 2005; Bailey et al., 2002).

Another problem with a system using bait to attract fishes is that only a subset of the fauna is available for capture. A great diversity of fishes is attracted to bait, demonstrated by a growing body of literature (Bailey et al., 2007). However, there are certain species that arrive first and appear to dominate the scavenging fauna. At depths of 1000–2000 m, Pacific rattails and black hagfish are the dominant scavengers in Monterey Canyon (Yeh and Drazen, 2011) so it is not surprising that these are the species most frequently captured. Smith and Hessler's (1974) remote underwater manipulator (RUM) operated and baited respirometer in the San Diego Trough at similar depths also captured these species. At shallower depths in our study, the fishes were apparently outcompeted by lysianassid amphipods. While this situation may be an impediment to increasing the diversity of fishes studied, it has its benefits too. If the trigger mechanism was refined the use of the *in situ* respirometer in a baited mode would generate a robust set of measurements on common species to evaluate the effects of body size, oxygen concentration, temperature, and other factors on metabolism. The other alternative is to use ROV or submarine assisted experiments. For instance, Smith and Brown's (1983) slurp gun respirometer captured and measured the metabolic rate of the scorpaenid, *Sebastolobus altivelis,* and experiments manipulated in real time were used to collect rattail metabolism data (Smith, 1978; Smith and Hessler, 1974). Of course the use of such assets would greatly increase costs over free vehicle systems.

While only a few measurements of metabolism are reported here, they are a significant contribution to a very sparse yet ecologically important data set. Important differences between the deep-sea species were found, some of which can be explained by differences in morphology and behavior. With additional experiments and improvements in the capture mechanism, much more data could be acquired. The use of ROV operated systems will also broaden the diversity of fishes studied. As more data on the bioenergetics of deep-sea fishes are acquired, we will be able to more accurately model food webs to better understand and manage these deep sea ecosystems.

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