METABOLIC MEASUREMENTS OF ENERGY FLOW THROUGH *OCTOPUS RUBESCENS*

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ABSTRACT

Cephalopods are active predators which form a unique and important link in the food webs of the oceans. Virtually all convert a high percentage of the food they consume into body mass (gross conversion efficiency, GCE). In turn, their soft bodies without shells or bones make them favored prey items of many higher predators. This suggests that cephalopods, including the octopuses, may play a disproportionately larger role in the energy flow of their food webs than their biomass would indicate. To date little work has been done to explore this ecological role. The first step in evaluating octopus' role in energy flow is to make careful metabolic measurements under controlled conditions. 17 male Octopus rubescens were collected from Admiralty Inlet, Washington and their metabolic rate measured around the clock by respirometry. Stepwise multiple regression was used to determine correlation between metabolic rate and other factors. Octopus mass and time of day were found to have the strongest correlation with metabolic rate while diet and amount of time spent in the respirometer were found to have weaker yet still significant correlation.

INTRODUCTION

Cephalopod metabolic physiology and energetics have long been a neglected area of cephalopod biology (O'Dor R.K. and Wells M.J., 1987). Recently, however, a growing interest in the use of cephalopods in aquaculture has led to an explosion of energetics studies of cephalopods, particularly octopuses (Perez *et al.*, 2006;Petza *et al.*, 2006;Rosas *et al.*, 2007;Semmens *et al.*, 2004). Aspects that make octopuses attractive candidates for aquaculture is a quick growth rate (life cycle generally complete in less than two years) and high gross conversion efficiency (GCE, percentage of mass consumed converted into body mass) (Vaz-Pires, P. and Seixas, P. and Barbosa, A., 2004). The more basic questions concerning how octopuses impact their local food webs have been largely overlooked. Little work on octopus energy budgeting has been focused on assessing octopuses' impact on the shallow water communities in which they live. The same characteristics that make octopuses attractive for aquaculture, along with their abundance, make them likely candidates to exert considerable pressure on lower trophic levels and provide an important pathway for energy flow to higher trophic levels.

The most common octopus in shallow water off the west coast of North America is *Octopus rubescens* (Hochberg, 1997). *O. rubescens* is a small, benthic octopus which reaches an average adult weight of 150-200g (though some weigh as much as 400g). In the Pacific this octopus ranges from as far north as the Gulf of Alaska (Hochberg, 1998) and south to the Gulf of Tehuantepec in southern Mexico (Sánchez, 2003), covering an extremely wide variety of habitats from the intertidal to 300m. Very little work has been published that quantifies *O. rubescens*' prey choice, but what has been done has revealed it to be a voracious predator that consumes a wide variety of taxa including gastropods, bivalves, and decapod crustaceans (Anderson *et al.*, 1999). The pelagic paralarvae are also important predators, forming large schools to feed on euphausids (Norman, 2000). Additionally, *O. rubescens* is a prey species for many species including chinook salmon (*Oncorhynchus twsawychtwsa*) (Hunt *et al.*, 1999), marine birds such as pelagic and Brandt's cormorants (*Phalacrocorax pelagicus* and *P. penicillatus*) (Ainley *et al.*, 1981) and shallow foraging pinnipeds such California sea lions (*Zalophus californianus*) and harbor seals (*Phoca vitulina richardsi*) (Stewart and Yochem, 1999). In some areas *O. rubescens* is the single most common prey item of harbor seals, composing as much as one-third of their total diet (Oxman, 1995).

To better understand *O. rubescens'* ecological niche, this species' metabolic physiology must be studied along with its foraging behavior. Measurements of metabolic rate provide an important first step in determining *O. rubescens*' role in the energy flow and structure of shallow-water marine communities. These measurements can begin to elucidate the magnitude of energy that passes through this species revealing the importance of *O. rubescens* to its food web.

METHODS

30 male *Octopus rubescens* were collected from Admiralty Beach, on Whidbey Island, Washington near Keystone. Females were excluded because of the high energetic cost of producing eggs and the difficulty of determining which females are gravid. The octopuses ranged from 40g to 350g and were held in 4 gallon holding tanks for one week before use in respirometry trials. Oxygen consumption was measured in a closed respirometry chamber. In this manner oxygen pressure was kept between 100% and 70% saturation. Respirometry trials lasted twenty-four hours with alternating hours of oxygen consumption measurements and re-aeration of the chamber. Oxygen consumption was recorded around the clock with an oxygen electrode and data logging computer. Octopuses were fed approximately three hours after entering the respirometer. The food was either *Nuttallia obscurata* (Mollusca:Bivalvia) or *Hemigrapsus nudus* (Crustacea:Brachyura) solely for one week, and then the other dietary item for the following week.

RESULTS

Stepwise multiple linear regression

The relationship between *O. rubescens'* routine aerobic metabolic rate and other factors was determined by stepwise multiple linear regression. In this regression the most significant relationship was found between metabolic rate and the $\log_{10}$ transformation of octopus mass, which were negatively correlated, and the metabolic rate and time since last feeding, which also were negatively correlated. Weaker, yet still significant correlations were also found between metabolic rate and time in the respirometer, oxygen saturation of the seawater, time of day and diet. Together these factors accounted for 33% of the variation in the metabolic rate observed.

Mass and scaling effects

Total metabolism is tightly correlated to mass by an exponential curve (Figure 1). Metabolism increases to the 0.83 power, slightly, but not significantly higher than predicted by the Kleiber equation for metabolic scaling would predict of 0.75 (Kleiber, 1947). As expected, mass-specific respiration rates decrease exponentially with increasing size. The average mass specific routine metabolic rate for a 150g, second year octopus was 2.58 $\text{umolO}_2 \cdot g^{-1} \cdot hr^{-1}$. The slope of the log-log relationship was -0.1742.

Octopus rubescens has a comparable or higher metabolic rate relative to other invertebrate predators, ans shown in Figure 2, but is still substantially lower than their vertebrate competitors such as rockfish (*Sebastes*). Figure 3 shows that *Octopus rubescens* has a very high metabolic rate when compared with other temperate octopuses, while having a comparable metabolic rate to larger tropical octopuses.

Feeding effects

O. rubescens' specific dynamic action appears to be about 14 hours in duration on average and take three to four hours to reach its peak of about 50% above routine metabolism (Figure 4). This is a longer SDA than found for O. vulgaris, which lasts only about 10 hours and reaches its pinnacle in the first hour (Katsanevakis *et al.*, 2005). This is expected considering the O. vulgaris being observed were being kept at 20C and 28C, as opposed to 11C for this species.

Critical oxygen pressure.

Despite a weak correlation between oxygen pressure and metabolic rate in the stepwise multiple linear regression *Octopus rubescens* seems to be an oxyregulator (Figure 5). This is agreement with previous work that has found shallow water octopuses to largely regulate their oxygen uptake.

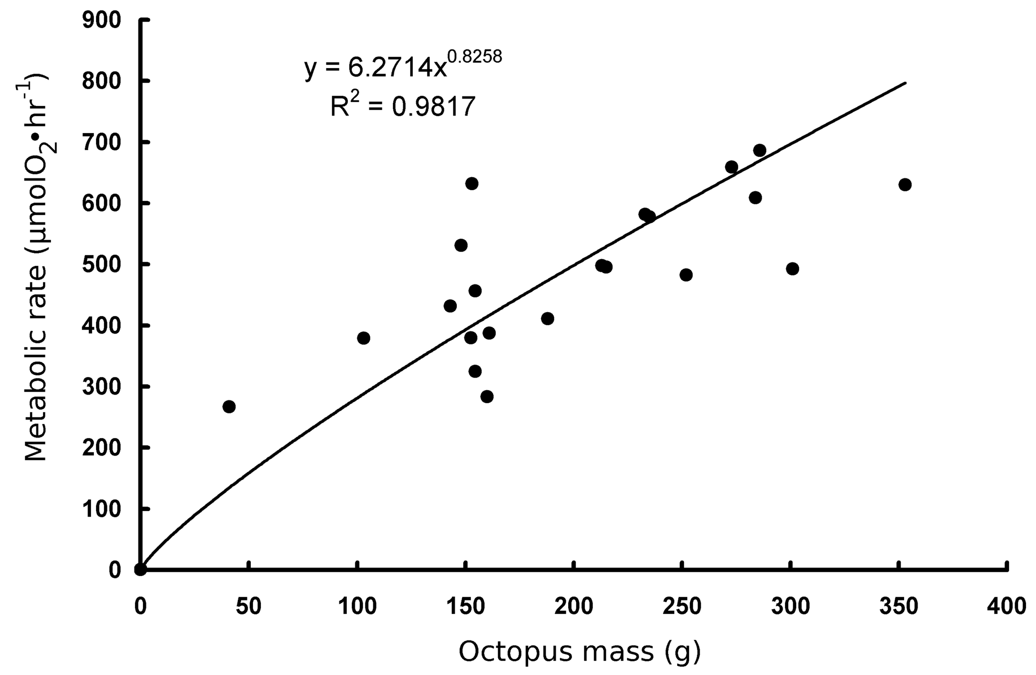

Figure 1: Aerobic metabolic rate plotted against octopus mass. Metabolic data is taken from octopuses that have been fasting for at least 14 hours to avoid effect of SDA.

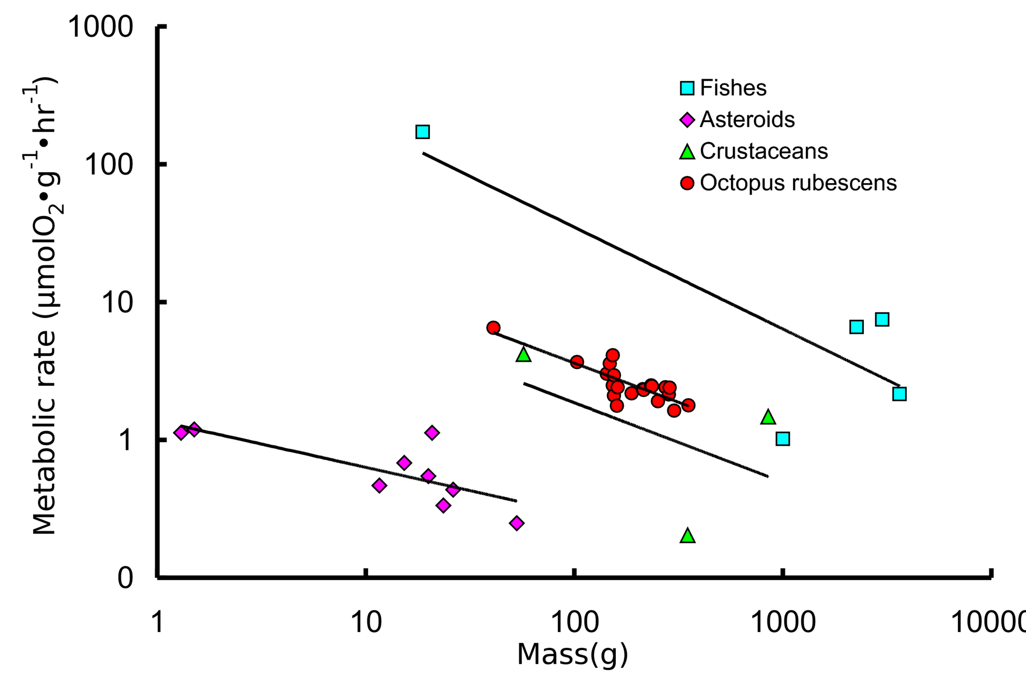

Figure 2. Routine metabolic rate plotted against mass of *Octopus rubescens* and three other classes of benthic marine predators: Fishes (Farrell and Daxboeck, 1981; Lee et al., 2003; Yoon et al., 2003), Crustaceans (Bradford and Taylor, 1982; McMahon et al., 1979; Cowles, 2002), and Asteroids (Webster, 1975)

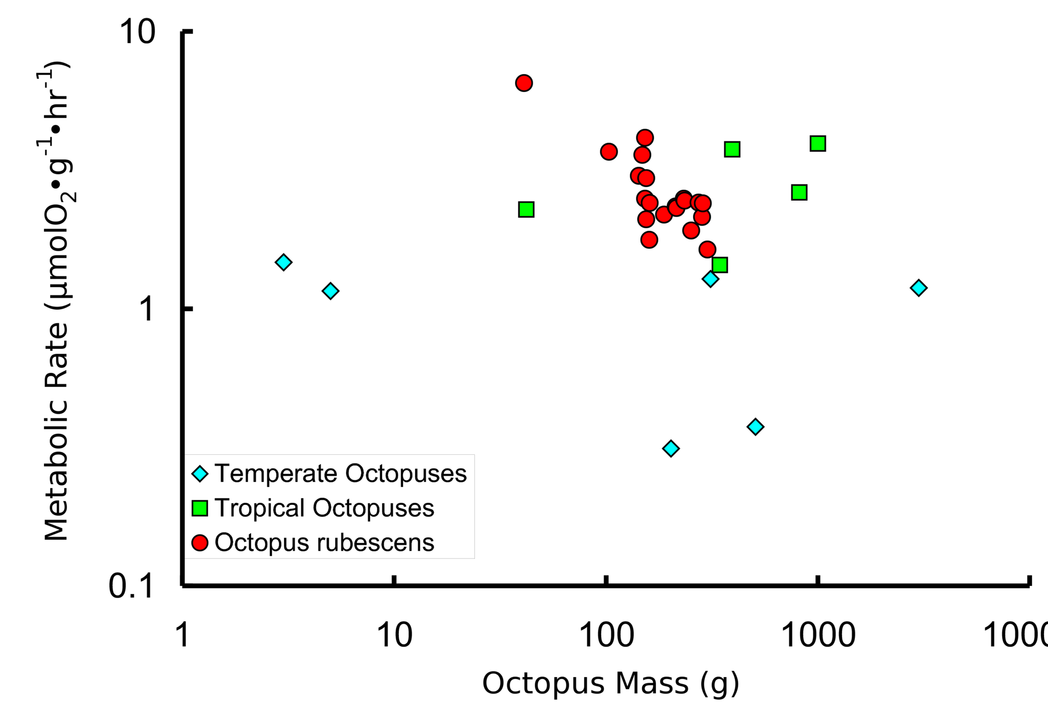

Figure 3: Respiration rate of *O. rubescens* compared to literature respiration rates for both temperate and tropical species by mass. (Daly and Peck, 2000; Rigby and Sakurai, 2004; Seibel and Childress, 2000; Petza et al., 2006; Van Heukelem, 1976; Wells and Wells, 1983; Wells and Wells, 1995)

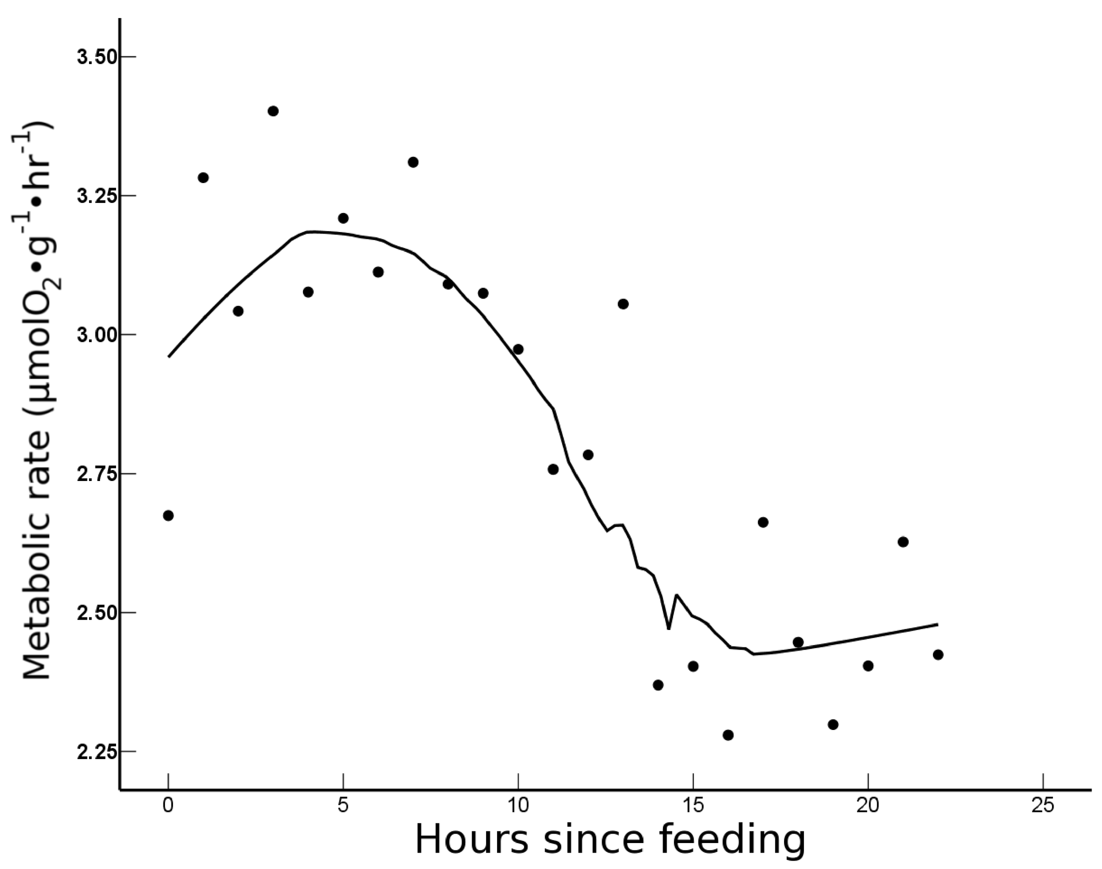

Figure 4: Specific dynamic action (SDA) of *Octopus rubescens* shown as metabolic rate against times since last feeding. Triweighted LOWESS regression shown.

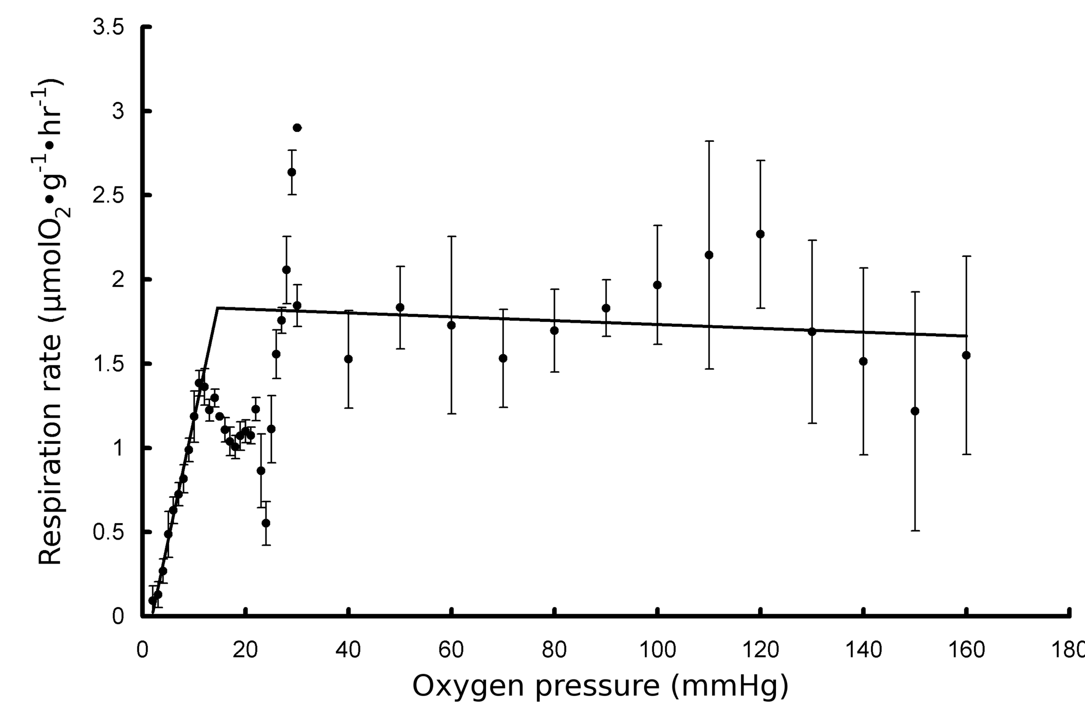

Figure 5: Respiration rate plotted by oxygen pressure for a 113g *Octopus rubescens*. Critical oxygen pressure is 14.6 mmHg.

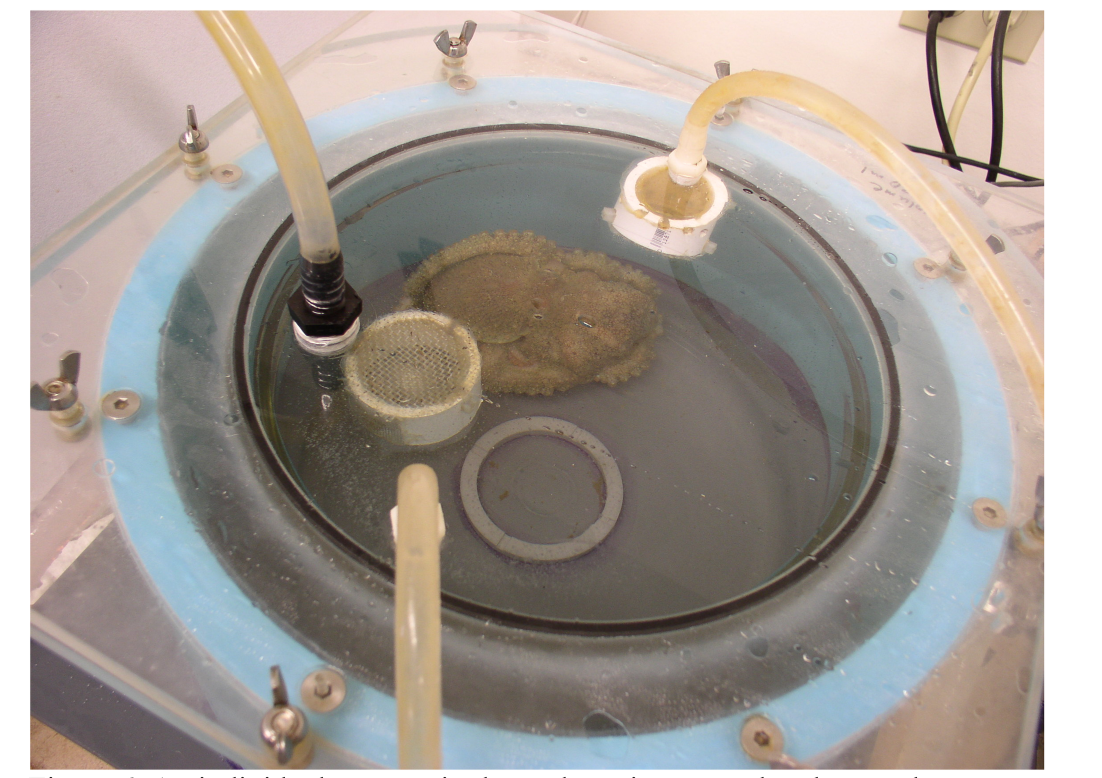

Figure 6. An individual octopus in the seal respirometer chamber used to measure *Octopus rubescens*' metabolic rate.

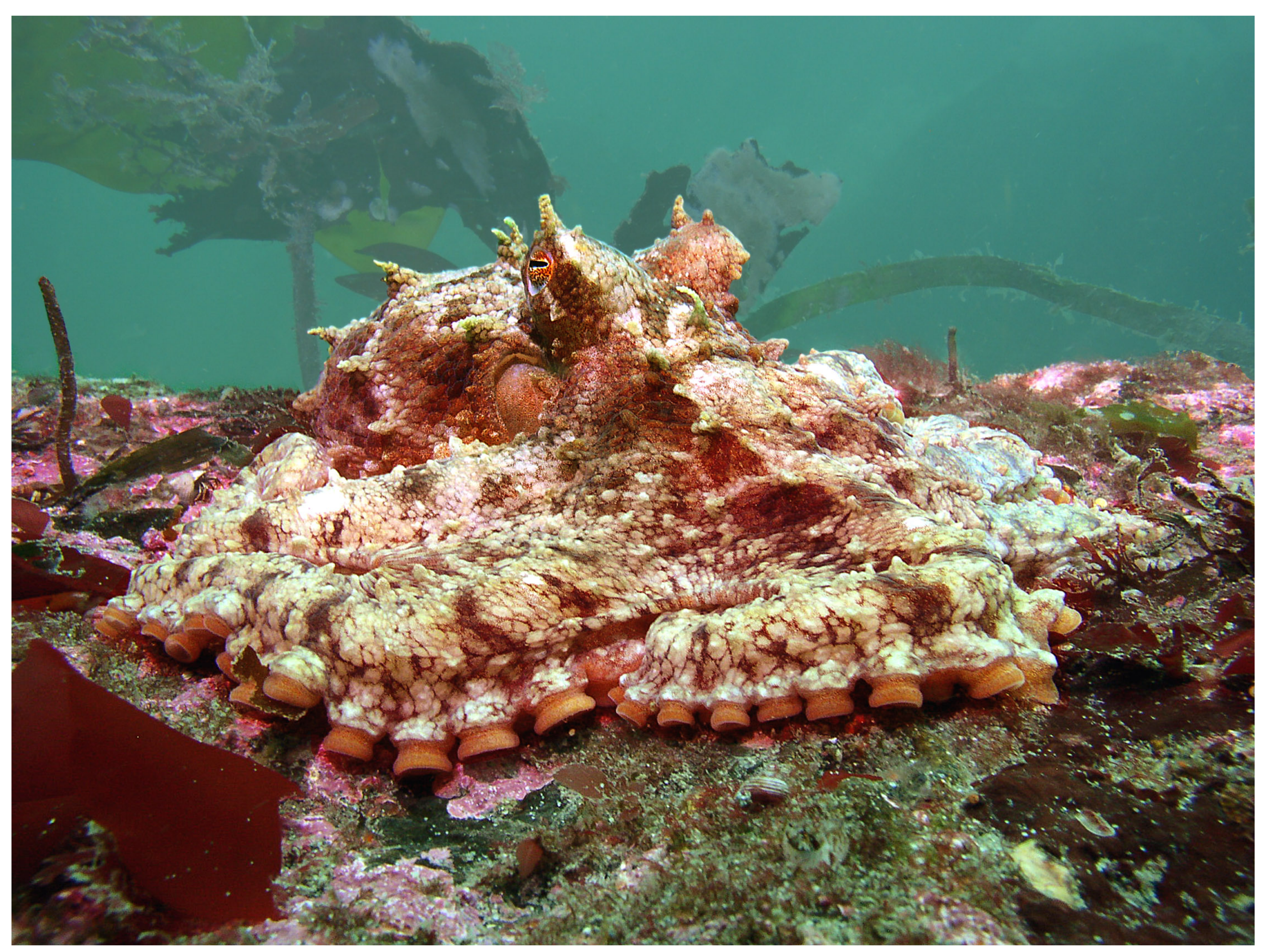

Figure 7. *Octopus rubescens* in its native habitat near Keystone ferry terminal on Whidbey Island, WA

DISCUSSION

Only a modest amount of the variation in *Octopus rubescen's* metabolic rate can be accounted for by the factors that have been included in this study by stepwise regression. This is likely due to the incredible variation in the individual octopuses,both behaviorally and physiologically (Mather and Anderson, 1993) Nevertheless those factors that were found to correlate with metabolic rate were highly significant and therefore likely play an important role in shaping the octopuses' metbolism.

Octopus rubescens has a high metabolic rate for a benthic invertebrate predator. This combined with its abundance in Pacific Northwest waters makes it likely that *O. rubescens* plays a substantial role in shaping benthic community structure in this area.

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