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Prey selection in *Octopus rubescens*: possible roles of energy budgeting and prey nutritional composition

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Abstract This study explores the relationship between energy budgeting and prey choice of *Octopus rubescens*. Seventeen male *Octopus rubescens* were collected between June 2006 and August 2007 from Admiralty Bay, Washington. Prey choices made by individuals in the laboratory deviated widely from those expected from a simple optimal foraging model. *O. rubescens* chose the crab *Hemigrapsus nudus* over the clam *Nuttallia obscurata* as prey by a ratio of 3:1, even though prey energy content and handling times suggested that this octopus could obtain 10 times more energy intake per unit time when choosing the latter compared to the former prey species. Octopus energy budgets were similar when consuming either of the prey species except for lipid extraction efficiency that was significantly higher in octopuses consuming *H. nudus*. This suggests that lipid digestibility may play an important role in the prey choice of *O. rubescens*.

Introduction

Shallow water octopuses can be important predators in the habitats they occupy. Their high metabolic rate compared with that of many other benthic predators (Seibel and Drazen 2007) suggests that they likely consume more prey per unit time than do most other predators common in their habitat. They are generalist predators (Ambrose 1984; Anderson 1991; Anderson et al. 1999; Dodge and Scheel 1999) which further have been suggested to be “switching predators” (Vincent et al. 1998) that vary their diets with prey abundance and as a result can stabilize prey populations (Murdoch 1969). Although they have well-developed adaptations for predator avoidance including the production of distracting ink clouds and the ability to rapidly adjust their texture and coloration (Hanlon and Messenger 1996), they are readily consumed by the wide assortment of predators including pinnipeds (Oxman 1995), fishes (Hunt et al. 1999), and seabirds (Ainley et al. 1996).

These roles of octopuses as both generalist predators and widely used prey make it likely that they play an important role in shaping the benthic faunal community structure, an ecological function of octopuses that has gone virtually unassessed. Despite being generalists, octopuses seem to show discrimination in their prey selection (Vincent et al. 1998; Anderson and Mather 2007). A logical first step in elucidating the impact of octopuses on their communities is to determine the rules by which octopuses make this discrimination, such as maximizing energy consumption, maximizing absorption efficiency, or minimizing predation risk.

Energy budgets account for all major inputs and expenditures of energy in an organism and provide a valuable tool for assessing the overall dynamics of metabolic physiology (Lucas 1996). Energy budgets track energetic inputs, primarily consumption (C) in heterotrophic organisms, and outputs, including energy expended in growth (G), aerobic respiration (R), egestion of feces (F), and excretion of urine (E). Absorption efficiency (AE), the portion of energy consumed which is not egested, is another useful metric in determining an organism’s use of energy and can be

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calculated for total energetic intake as well as for energy from individual macronutrients such as protein or lipids. Although energy budgets have been previously established for octopuses (Van Heukelem 1976; Daly and Peck 2000; Rigby and Sakurai 2004; Perez et al. 2006; Petza et al. 2006; Rosas et al. 2007; Farías et al. 2009), the vast majority have been constructed for large species and with special emphasis on evaluating food quality for aquaculture. Only one has been produced in the context of investigating trophic ecology (Mather and O'Dor 1991).

Previous studies have consistently indicated that octopuses have a protein-dominated metabolism, even while on high lipid diets (Boucher-Rodoni and Mangold 1985, 1988; Daly and Peck 2000; Katsanevakis et al. 2005; Petza et al. 2006; Rosas et al. 2007). Carbohydrates are not likely an important nutritional component of *Octopus rubescens*' diet due to the carbohydrate-poor diet of most cephalopods (Lee 1994), including *O. rubescens* (Anderson et al. 1999). The few carbohydrates that are ingested appear to be rapidly catabolized with the remainder stored in the muscle tissue, likely in the form of glycogen. These muscle carbohydrate reserves are used mainly during locomotion rather than as an energy reserve during starvation (O'Dor et al. 1984).

Lipids are found in low amounts in cephalopods except for relatively high concentrations in their digestive gland (Lee 1994) and reproductive structures such as eggs (O'Dor et al. 1984). Due to the lack of evidence that octopuses normally metabolize lipids for energy, it is assumed that their use of lipids is mainly limited to structural purposes such as cellular membranes and as hormone precursors (Lee 1994). Another potential use of lipids is for energy storage. O:N, the atomic ratio between oxygen consumed by an organism and the nitrogenous wastes produced, is used to determine metabolic substrates. Theoretical calculations suggest that O:N values between 3 and 16 indicate pure protein catabolism, while O:N values between 50 and 60 indicate equal amounts of protein and lipid catabolism (Mayzaud and Conover 1988). During starvation, the O:N of *Octopus vulgaris* rises, indicating an increased reliance on non-protein metabolic substrates, which could include lipids from the digestive gland (Boucher-Rodoni and Mangold 1985). One investigation reported that lipid content in the digestive gland dropped from 0.30% of total body mass to 0.06% of body mass within 6 days in fasting *Octopus vulgaris*, suggesting that lipids in the digestive gland may indeed be an alternate metabolic substrate (O'Dor et al. 1984).

Despite limited use as a metabolic substrate, lipids are nevertheless likely to be an important dietary component for octopuses. Lipids have been suggested to be the limiting nutrient for egg production by female *Octopus vulgaris* on a crab diet (O'Dor et al. 1984). Additionally, lipids have been shown to be important dietary components for octopus paralarvae (Navarro and Villanueva 2003). High lipid diets, however, could possibly be detrimental to growth (Garcia Garcia and Cerezo Valverde 2006) and to digestibility of the food (Petza et al. 2006).

The objectives of this study were to determine how the energy budgeting of *Octopus rubescens*, the most abundant shallow water octopus living in the waters bordering the western coast of North America (Hochberg 1998), is altered with specific variations in diet, and to relate changes in energy budgeting to choices of prey by this species. Cephalopods, including octopuses, are unique among marine predators in their near total reliance on protein as a metabolic substrate, an aspect of their physiology that likely plays a key role in their selection of preferred prey.

Materials and methods

To determine the relationship between energy budgets and prey choice in *Octopus rubescens*, a simplified two-prey model system consisting of the purple shore crab *Hemigrapsus nudus* and the purple varnish clam *Nuttallia obscurata* was chosen. To calculate energy budgets, food and oxygen consumption, ammonia production, and growth were measured for 1 week for each octopus on each diet. To determine prey choice, octopuses were allowed to freely choose between *H. nudus* and *N. obscurata* in captivity. *H. nudus* and *N. obscurata* were chosen because they are locally available, can be obtained in large quantities, and are readily eaten by *O. rubescens*. A diet of the snail *Olivella baetica*, the dominant prey item reported by Anderson et al. (1999) for *O. rubescens* farther south in Puget Sound, was also attempted but that species was not easily collected at our study site. An alternative snail, *Nucella lamellosa*, a prey item commonly consumed by octopuses in the collection area (unpublished data), was not readily consumed by the octopuses during this study, so snails were not used in this experiment.

Octopus collection and maintenance

Seventeen male *Octopus rubescens* ranging in size from 43 to 353 g were collected by SCUBA from Admiralty Bay on Whidbey Island, Washington (48°09′47.81″N 122°38′14.81″W) between June 2006 and August 2007. Only males were collected to minimize the variability in energy allocated to reproduction. Divers inspected discarded glass bottles for the presence of octopus (Anderson et al. 1999). Bottles containing an octopus were placed in sealable plastic bags and transported within the hour to the Rosario Beach Marine Laboratory where they were held in 15 L flow-through tanks of aerated seawater at 11°C and a salinity of 32 ppt, matching the salinity where the octopuses were collected. Octopuses were maintained with natural light/dark (L:D) cycles for the season in which they were collected which were approximately 16 h light:8 h dark.

The octopuses were given a 1-week acclimation period before any experimental trials began. During acclimation, they were fed both *Nuttallia obscurata* and *Hemigrapsus nudus* ad libitum. During the final 2 days of this acclimation period, the octopuses were not fed so that any previously eaten food could clear the digestive system before experiments began (Boucher-Rodoni and Mangold 1977).

Prey preference

Prey preference trials were conducted in a flow-through tank 58 cm × 116 cm × 45 cm deep. For each trial, four *H. nudus* and four *N. obscurata* were massed and marked with a number for identification. One of each prey species was placed in each corner of the tank. The octopus to be tested was then placed in the center of the tank and given 4 h to freely capture and consume its preferred prey. After the trial, the octopus and prey items were removed, and the remains of eaten prey items were identified and massed to determine the mass of each species consumed.

Prey-handling time

The time *O. rubescens* used in handling each of the two prey species was determined by using a time-lapse video camera during feedings. Handling time was measured from the moment the octopus pulled the prey item under its arms until it dropped the last of the remains. Generally, all prey remains (such as all crab pieces) were dropped simultaneously. Prey items were massed before feeding, and the remains were massed after feeding to determine mass consumed.

Determination of metabolic rate

Closed respirometry chambers were used to determine oxygen consumption. The chambers were glass cylinders with acrylic lids, with an inside diameter of 22 cm and height of 14 cm. Chamber volume was approximately 6 L. A magnetic stir bar in a cage on the chamber floor kept the water well mixed. An external water jacket maintained the chamber water at 11°C. Water was pumped out an excurrent port from the chamber by peristaltic pump at a rate of 1.3 L min^{-1}. This water passed into a smaller chamber 0.17 L in volume containing either a Nester 8500A® or Hach Sension 8® Clark-type polarographic oxygen electrode, with both a sensitivity of 0.1% air saturation and a stir bar. Oxygen concentration was recorded from this chamber by computer every 30 s. After exiting the electrode chamber, the water passed through an aeration column, then back into the respirometry chamber. A shunt periodically bypassed the aeration column and closed the respirometry system during actual respirometry runs. Automated pinch valves placed before and after the aeration column controlled water flow into either the aeration column or the shunt as needed. Respirometers were filled with artificial seawater prepared with distilled water and Instant Ocean to match the holding tank water in temperature, salinity, and pH. Periodically, respirometers were cleaned with hydrogen peroxide to eliminate any microbial growth. Blank respirometry cycles without organisms were performed using a chamber and water from the end of a test trial to assess the potential background respiratory rate; however, none was observed.

After the 1-week acclimation period, respirometry trials began on each octopus. These trials were performed while the octopus was on a week-long diet of daily feedings of either *H. nudus* or *N. obscurata*, chosen randomly. After a week of eating one prey item, the octopus diets were switched to the alternate prey for the following week. During each week, before week days 1, 3, and 5, octopuses were removed from their holding tanks and placed into the respirometry chambers filled with clean artificial seawater at approximately 2100 h. The chambers were sealed, and aerobic respiration was measured for 1 h, followed by an hour of flow-through with aerated water, and this cycle was repeated for 24 h. During measurement periods, oxygen levels in the chambers varied between 70 and 100% saturation, which is well above the octopus' critical oxygen pressure (P_C) (38% saturation or below, Onthank unpublished data). Feeding during days in which the octopus was in the respirometer took place during the re-aeration periods that started at either 2300 or 0700 hours. Prey remains were removed from the respirometer as soon as possible after the octopus dropped them.

Octopuses were massed before the first and after the last respirometry trial of each week. This was accomplished by putting the octopus in a cup and pouring out the excess water. Octopuses reliably expelled the water in their mantle cavity within a few moments after being exposed to air. Excess water in the cup was then blotted with a paper towel. After the octopus was massed, it was allowed to crawl out of the cup into the respirometer, and then the cup was tared. The whole massing process generally lasted <90 s.

Ammonia production

Water samples were taken for ammonium analysis during several aeration periods near the end of each respirometry day, but never when prey remains were in the respirometer. Total ammonia nitrogen (TAN) was determined colorimetrically using the reagents found in the Aquarium Pharmaceuticals® aquarium ammonia test kit (product # LR8600), which uses the indophenol/salicylate method of Grasshoff and Kremling (1999), and compared to standards prepared with ammonium chloride in artificial seawater. Samples were centrifuged for 2 min to settle any cloudiness before reading absorbance. Absorbance was read at 640 nm using a Beckman DU-530 spectrophotometer. Precision of this assay was routinely within 0.25 µg/L TAN when measuring known solutions.

Feeding and feces collection

All food items were massed before they were presented to the octopus. After the octopus had eaten the items, any uneaten portions were collected, massed, and the mass subtracted to determine the mass consumed.

All feces were collected using a small transfer pipette throughout each week-long diet and were frozen at −20°C until nutrient analysis could be performed. Before analysis, the feces were dried to constant mass in a room temperature desiccator and massed. Salt content was estimated by calculating water lost during desiccation and multiplying by 32 ppt, the approximate salt content by mass of seawater in Rosario Bay and in the experiment.

Nutrient analysis

Lipid, crude protein, gross energy, and ash content were determined by the Washington State University Wildlife Nutrition Laboratory, Pullman, WA. Lipid content was determined by ether extraction; gross energy content was determined by bomb calorimetry and crude protein using the total nitrogen ×6.25 method. Samples analyzed were a combined homogenate of the soft tissues of five *N. obscurata*, a combined homogenate of soft tissue from inside the carapace and chelipeds of approximately 45 *H. nudus* (except the gills, which are not usually consumed by *O. rubescens*), a combined homogenate of all the feces produced by the octopuses while on a *N. obscurata* diet, and a combined homogenate of all the feces produced while on a *H. nudus* diet. Each analysis was performed once for each combine homogenate due to the amount of material needed for each analysis.

Energy budget calculation

All data for energy budgets were collected between June and August 2007. O:N was calculated from respirometry and ammonia production data and were used to estimate the ratios of protein versus other metabolic substrates catabolized.

Statistical analysis

Energy budgets between the two diets were compared by MANOVA. Energetic efficiencies and O:N were compared by Student's *t* test. Prey handling times were compared by a Mann–Whitney *U* test. The choices of one prey type were not independent from choices for the alternate prey type in this experimental setup. Therefore, in lieu of a Student's *t* test, the Quade's test, a non-parametric analysis of ranks (Roa 1992), was employed to compare octopus preferences. All statistical analyses were performed with *R* (R Development Core Team 2008) and Gnumeric, an open source spreadsheet program similar to Microsoft Excel but with superior accuracy in statistical computations (McCullouch 2004).

Results

Prey preference

Nineteen prey choice trials were conducted, during which the octopuses chose a total of 47 prey items. Typically, octopuses displayed a "hoarding" behavior by initially capturing multiple prey items of each type and carrying all captured prey items to a corner of the tank. The octopuses would then only consume a subset of the prey items captured. Unconsumed crabs were always killed. Drill holes were never observed in any shells of either prey species. Numerically, octopuses chose the crab *H. nudus* three times more often compared with the clam *N. obscurata* (Fig. 1). However, the prey mass consumed by octopuses was virtually identical between the two prey species (the clams had more consumable tissue) (Fig. 1). Octopuses appeared to have individual preferences, consuming both clams and crabs in five trials, only clams in four trials and only crabs in ten trials.

Prey handling time

Prey handling times were recorded during nine crab feedings and six clam feedings using six octopuses (four octopuses used for each prey type and two octopuses were used for both prey types). Each octopus was fed 1–4 prey items; however, multiple prey items were not fed to the same octopus within 24 h. *Octopus rubescens*' prey handling time was significantly longer when consuming *H. nudus* (averaging more than 2.0 h) than when consuming *N. obscurata* (slightly longer than 0.5 h) (Mann–Whitney *U* test, $U = 120$, $N_1 = 9$, $N_2 = 6$, $P < 0.001$) (Table 1). Furthermore, the mass of the tissue consumed from each *N. obscurata* was more than double that consumed from each *H. nudus* (Table 1). When

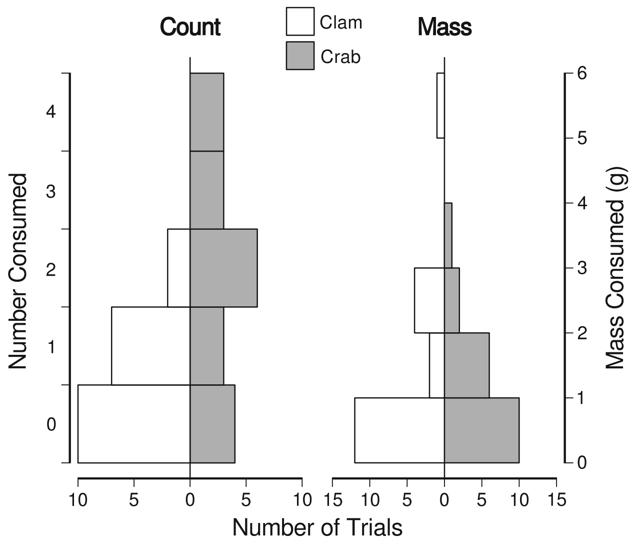

Fig. 1 Back-to-back histograms of crabs (*Hemigrapsus nudus)* and clams *(Nuttallia obscurata)* eaten by individual *Octopus rubescens* during prey choice trials by count and by mass. The numbers of prey items eaten are significantly different (Quade's test, $n = 19$, Quade $F = 12.1513$, $P = 0.003$). Since clams weigh more than crabs, the mass of clams and crabs eaten was not significantly different (Quade's test, $n = 19$, Quade $F = 0.1118$, $P = 0.742$)

Table 1 Prey-handling time and mass consumed per prey item for crab prey ($n = 9$) and clam prey ($n = 6$) by *Octopus rubescens* (mean ± SD)

Measure of feeding efficiency	*H. nudus* (crab)	*N. obscurata* (clam)	*P* value
Handling time (min)	123.9 ± 88.3	36.8 ± 18.1	0.002
Mass prey item^{-1} (g)	1.9 ± 0.9	5.1 ± 2.1	0.0008
Mass consumed min^{-1} (g)	0.02 ± 0.01	0.15 ± 0.04	0.0004
Energy obtained min^{-1} (kJ)	3.042 ± 1.185	27.99 ± 8.72	0.0004

Energy consumed per minute was calculated from mass consumed min^{-1} multiplied by the energetic values found in Table 2. Treatments were compared by Mann–Whitney test with *P* values shown

considered together, the amount of food energy *O. rubescens* obtained per minute handling time of *N. obscurata* was nearly an order of magnitude greater than that obtained from consuming *H. nudus* (Table 1).

Nutritional composition

Nutritional compositions of prey items and octopus feces are shown in Table 2. The energy content per unit tissue was about 10% higher in *N. obscurata* than in the crab *H. nudus*. The crude fat content was nearly 10% of the dry mass in *H. nudus* compared to less than 5% of the dry mass in *N. obscurata*.

Energy budgeting and growth

Energy budgets were determined for eight *O. rubescens* individuals while on a diet of *N. obscurata* and for nine individuals while on a diet of *H. nudus*. Energy budgets associated with each diet did not differ significantly (MANOVA, Wilks' $\Lambda = 0.401$, $F_{5,10} = 2.99$, $P = 0.07$). Values for each component of the energy budgets were quite variable among individuals (Fig. 2). For example, several octopuses had negative growth rates during week-long trials while others displayed positive growth rates. When fed *N. obscurata*, one of eight octopuses lost mass whereas four of nine octopuses on a *H. nudus* diet lost mass.

Absorption efficiencies were very high both in terms of energy and mass and were very similar between diets (Table 3). Total absorption efficiency in terms of energy was 94.4 ± 2.7% on the *N. obscurata* diet and 95.8 ± 3.2% on the *H. nudus* diet. Similarly, protein absorption efficiencies were also very high averaging 96.7 ± 1.6% on the *N. obscurata* diet and 95.4 ± 3.6% on the *H. nudus* diet. On the other hand, lipid absorption efficiency was quite different between *N. obscurata* diets (74.6 ± 12.4%) and *H. nudus* diets (94.9 ± 4.0%), a highly significant difference (Welch two sample *t* test, $t_{11.669} = -5.3718$, $P < 0.0002$).

The values of O:N calculated from energy budgets were well within the range consistent with pure amino acid metabolism (below 15), with a single outlier of 60.4 obtained for one octopus that lost 3% of its body mass during a week-long trial on a crab diet, suggestive of equal portions of lipid and protein metabolism (Table 3). Despite this outlier, there was insufficient evidence to reject the hypothesis that O:N varied between diets, with *N. obscurata*

Table 2 Nutrient values for soft body tissues of *Octopus rubescens* prey items and for *O. rubescens* feces excreted while on each diet

Material	% Dry matter	% Ash	% Crude fat	% Crude protein	Gross energy content (kJ g^{-1})
Nuttallia obscurata (clam)	20.14	9.34	4.09	51.78	18.63
Hemigrapsus nudus (crab)	19.88	24.64	9.53	45.36	17.15
Feces from *N. obscurata* diet	–	59.15	7.62	12.53	7.60
Feces from *H. nudus* diet	–	70.24	2.76	11.54	4.04

Other than % dry matter, all values are reported as a function of dry matter

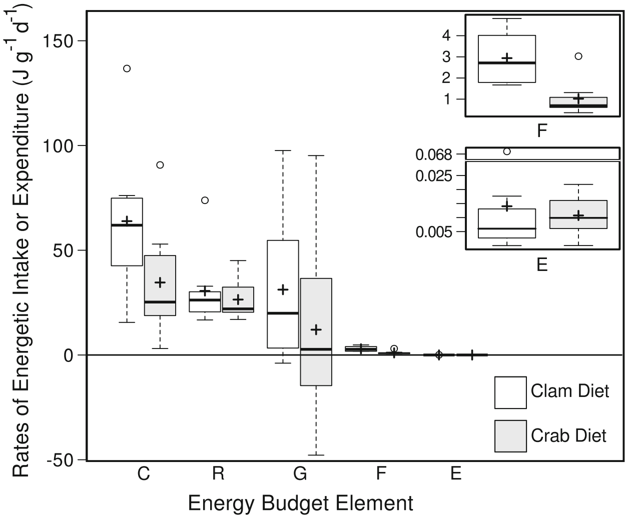

Fig. 2 *Box plots* of the energy budgets of nine *Octopus rubescens* by energy budget element and diet type. Means are indicated by *plus signs* (+). All energy budget components are reported in J g(wet wt)$^{-1}$ d^{-1} and are parameters of the equation $C = R + G + E + F$ (see Table 4 legend). The terms E_F and E_U are rates of energy loss from urine excretion and the egestion of feces, respectively, and are shown on a magnified scale in the *inset*. Energy budgets were not significantly different between the two diets (MANOVA, Wilks' Λ = 0.401, $P = 0.07$)

fed octopuses averaging 5.70 ± 5.48 and *H. nudus* fed octopuses averaging 13.55 ± 19.17 (6.85 ± 3.25 without the aforementioned outlier) (Mann–Whitney *U* test, $U = 17$, $N_1 = 7$, $N_2 = 8$, $P = 0.2319$).

Discussion

Prey preference and handling time

Octopus rubescens' numerical preference for *Hemigrapsus nudus* despite a considerable energetic advantage that could be gained by consuming *Nuttalli obscurata* suggests that there is more included in the octopus' prey choice than a simple optimal foraging model would imply. In these experiments, the prey choices made by *O. rubescens* deviated from those expected from a simple model of maximizing energetic intake per unit time. *O. rubescens* obtained nearly an order of magnitude more energy per unit time when consuming the clam *N. obscurata* rather than the crab *H. nudus* (Table 1), but nevertheless chose *H. nudus* over *N. obscurata* as prey by a ratio of 3:1 (Fig. 1; Table 1). Interestingly, even with this disparity in choices between *H. nudus* and *N. obscurata*, the octopus consumed nearly equal mass of each prey item over the course of the experiment since there is much more edible mass in *N. obscurata*. Octopuses in part respond to movement in prey items (Hanlon and Messenger 1996), and it is conceivable that there was a selection bias in favor of the octopuses consuming crabs due to the greater movement displayed by this prey item. This seems unlikely, however, in these trials due to the hoarding behavior of the octopuses during which both prey items were collected but only a few consumed.

Increased handling time for the comparatively smaller crab prey could be a result of several factors. Crabs have a complex exoskeleton when compared with the external shell of a clam, which likely requires the octopus to take more time to extract edible tissues especially from the legs and chelae of the crab. Increased handling time could also be a function of prey preference, with octopuses investing more time to consume their preferred prey more thoroughly.

Alternatively, *O. rubescens*' selection of *H. nudus* as prey may be a result of instinct or a learned behavioral search image for crabs in general that do not accurately reflect any sort of preference for *H. nudus* specifically (Curio 1976). This, however, seems unlikely due to the flexibility of diet observed in octopuses (Ambrose 1984; Anderson 1991; Anderson et al. 1999; Dodge and Scheel 1999). It is also conceivable that *H. nudus* simply "tastes" better to octopuses, or that they are less distasteful than *N. obscurata*. This also seems unlikely because several octopuses ate primarily *N. obscurata* in prey preference trials.

In the wild, *O. rubescens* could attempt to minimize the risk of predation rather than maximizing the rate of energetic intake while foraging (though these two hypotheses may not be mutually exclusive). *O. vulgaris* juveniles have been found to minimize time spent at risk of predation by

Table 3 Absorption efficiencies (AE, mean ± SD) for *Octopus rubescens* on a diet of the clam *Nuttallia obscurata* or the crab *Hemigrapsus nudus*

Species	Total AE[a]	Protein AE[a]	Lipid AE[a,b]	O:N
N. obscurata	94.4 ± 2.7%	96.7 ± 1.6%	74.6 ± 12.4%	5.7 ± 5.5
H. nudus	95.8 ± 3.2%	95.4 ± 3.6%	94.9 ± 4.0%	13.5 ± 19.7
P values	0.260	0.431	0.0002	0.2319

P values for two-tailed *t* tests shown in table ($df = 15$). O:N for each diet are also included and compared by Mann–Whitney *U* test due to non-normality of the data (mean ± SD, $U = 17$, $df = 14$)

[a] *T* test performed on arcsine transformation of percentages

[b] Welch's *t* test peformed due to heteroscedastic data

Table 4 Comparisons of average energy budgets and total absorption efficiencies (AE_T%) for octopuses

Species	Temp °(C)	C	R	G	F	E	X	AE_T%
Pareledone charcoti[a]	0.0	10.50	7.04	3.13	0.41	0.00	–	96
Octopus vulgaris[b]	20.0	67.92	38.57	17.38	9.06	0.01	–	87
O. cyanea[c]	20.0	83.96	40.47	40.80	3.69	–	1.26	96
O. maya[c]	20.0	76.64	27.95	45.61	3.08	–	–	96
O. maya[d]	?	279.57	63.00	190.57	6.00	20.00	–	98
O. maya[e]	28.0	522.00	9.07	365.00	146.00	2.05	–	72
Enteroctopus dofleini[f]	9.5	80.96	21.48	31.63	4.57	–	–	94
E. megalocyathus (crab)[g]	17.0	147.72	39.94	6.07	1.18	1.28	–	99
E. megalocyathus (mussel)[g]	17.0	2.08	37.82	−1.99	2.97	1.43	–	−43
E. megalocyathus[e]	10.0	358.00	37.60	249.00	64.00	7.18	–	82
O. rubescens (*clam*)[h]	11.0	70.80	32.55	33.46	3.12	0.02	1.65	94
O. rubescens (*crab*)[h]	11.0	34.61	26.46	12.08	1.02	0.01	−4.96	96

All energy budget components are in J $(g\ wet\ wt)^{-1}\ d^{-1}$ and are elements of the equation $C = R + G + E + F + X$, in which C is the energy in the food ingested, R is the energy expended in aerobic respiration, G is the energy used for growth, E and F are energy lost in urine and feces, respectively, and X is the energy used in other processes. Values for *E. megalocyathus* were calculated by using a 16% wet weight to dry weight conversion and an energetic content of flesh of 4,144 J/g dry wt, both of which are published values for *E. dofleini* (USDA 2008)

[a] Daly and Peck (2000), [b] Petza et al. (2006), [c] Van Heukelem (1976), [d] Rosas et al. (2007), [e] Farías et al. (2009), [f] Rigby and Sakurai (2004), [g] Perez et al. (2006), [h] (This study, averages of energy budgets)

reducing foraging time (Mather and O'Dor 1991). It is possible that octopuses can spend less time foraging for crabs away from the safety of shelter than they can for clams. However, octopuses have been shown to readily switch to preferred prey items when constraints on consumption have been lifted, such as opening the shells of otherwise difficult to open clams (Anderson and Mather 2007). Location and collection time for crabs and clams in our trials would be essentially equal, therefore is unlikely that a possible bias for reduced foraging time, and therefore predation risk, in the wild would be reflected in these trials.

Energy budgeting

Octopus rubescens' energy consumption was somewhat low when compared with the energy budgets found for other octopuses (Table 4), except for that of the Antarctic octopus *Pareledone charcoti* and for *E. megalocyathus* fed a diet exclusively of mussels. Perhaps this could be accounted for by the fact that *O. rubescens* is a colder-water species than many of the other species and was tested at lower temperature or by differences between monotypic (single component) and mixed diets (*O. rubescens* vs. *E. dofleini*) found in most of the other energy budgets.

There was also variation in the ratio of energy used for metabolism versus growth between diets in *O. rubescens*, and among *O. rubescens* and other species (Table 4). On a diet of *Nuttallia obscurata, O. rubescens* allocated nearly equal energy to respiration and growth, while on a diet of *Hemigrapsus nudus, O. rubescens* allocated less than half the energy for growth that it did for respiration. *O. rubescens* also consumed approximately half as many calories per unit mass of octopus on a diet of *H. nudus*, likely accounting for by the decreased energy allocated for growth. *O. vulgaris* and *P. charcoti* allocated over twice as much energy toward aerobic respiration than toward growth while *O. cyanea* allocated nearly equal amounts of energy to each (Table 4). In contrast, *E. dofleini* and *O. maya* allocated more energy to growth than to respiration. These differences do not seem to be correlated to relative size and may simply be a variation among species or with experimental conditions such as diet. Perez et al. (2006) demonstrated that diet can have a large influence on consumption rate and growth while having relatively little influence on how much energy is allocated to respiration, which is similar to our findings with *O. rubescens*. This suggests that diet is a principal driving factor in relative partitioning of energy. Another possible explanation for the disparity in energy use for growth versus respiration in the different octopus species (Table 4) could be the use of different aged octopuses in the different studies since growth rates slow as the octopus ages (Semmens et al. 2004).

Energy budgeting was variable among individuals, and most components were not significantly different between diets. Growth, for example, was poor and inconsistent on both diets and was slightly but not significantly lower on a *H. nudus* diet. A factor contributing to poor growth could be the use of monotypic diets. *E. dofleini* has been shown to exhibit less growth on monotypic diets than on mixed diets (Rigby and Sakurai 2004). *Octopus vulgaris* has been found to have more robust growth on a diet of equal portions crab and fish than on monotypic diets of either or on a diet of unequal portions (Garcia Garcia and Cerezo

Valverde 2006). Additionally, *E. megalocyathus* fed a monotypic diet of mussels showed very low consumption and a consistent loss of mass (Perez et al. 2006). It has been suggested that when fed prepared diets, cephalopod growth may be limited because ingestion ceases when adequate energy is consumed but a proper amino acid balance has not yet been achieved (Lee 1994). This suggests that octopuses have complex nutritional needs that may not be fully met by a monotypic diet. It is plausible that the diverse diet of *O. rubescens* and other octopuses in the field could be indicative of nutrient-specific foraging to achieve a proper dietary balance of amino acids and lipids. Such behavior has been observed in other invertebrate predators such as spiders and beetles (Mayntz et al. 2005).

Perhaps the most interesting difference in dietary energy budgeting between the two prey species was the difference in lipid absorption efficiency (Table 3). Absorption efficiencies for individual macronutrients are rare in the published literature although lipid absorption efficiencies for *O. vulgaris* ranging from 46% (Lee 1994) to 77% (O'Dor and Wells 1987) have been reported. In our investigation, the lipid absorption efficiency of *O. rubescens* feeding on *H. nudus* tissue was very high (94.9%) and significantly greater than when feeding on *N. obscurata* (74.6%). Even though the lipid content in *H. nudus* is more than twice that in *N. obscurata*, the octopus egested less than half as much lipid as percent of feces while on a *H. nudus* diet than when on a *N. obscurata* diet. Consequently, *O. rubescens* appears to retain nearly three times as much total lipid from crab tissue than it does from clam tissue. This may explain why *O. rubescens* persists in consuming a higher number of *H. nudus* in preference trials despite gaining much less energy per unit time while feeding on this species. One octopus on a *H. nudus* diet exhibited both mass loss and a high O:N (60.4), indicating under-nutrition and catabolism of lipids along with protein such as Boucher-Rodoni and Mangold (1985) observed in starving octopus. Despite this outlier, values of O:N were low and not substantially different for both diets, suggesting that the increase in lipid absorption efficiency in *H. nudus* diets was not likely connected to an increase in lipid catabolism for energy. The ultimate fate of these lipids is unknown, but it can be assumed that they are being retained (for at least some period of time) in the digestive gland as has been shown for other octopus species (O'Dor et al. 1984). While adult *Octopus maya* and *O. vulgaris* have demonstrated poor growth on high lipid diets (Petza et al. 2006; Rosas et al. 2007), polyunsaturated fatty acid (PUFA) content of dietary items, particularly the ratio of docosahexaenoic acid (DHA) to eicosapentaenoic acid (EPA), has been tied to growth and mortality rates in *O. vulgaris* paralarvae (Navarro and Villanueva 2003). While adult octopuses have a markedly lower lipid composition than do paralarvae, the requirements of specific fatty acid profiles within dietary items could persist into adulthood, especially in regard to lipid-limited physiological processes such as egg production (O'Dor et al. 1984). As discussed earlier, this suggests that *O. rubescens* may choose prey to address specific nutritional needs rather than simply maximizing energy intake over time.

Ecological implications

Generalist octopuses have been suggested to be "switching predators" (Vincent et al. 1998). Optimal foraging theory predicts that once a prey item falls below a threshold density, an optimally foraging predator will switch to alternative prey items (Curio 1976; van Baalen et al. 2001). Switching predators are thought to stabilize prey populations by feeding preferentially on the most abundant species (Murdoch 1969). *Octopus rubescens*, however, does not seem to forage optimally in terms of energetic intake, but rather in a nutrient-specific manner. It nevertheless has a generalist diet. Some work has connected optimal foraging theory with nutrient uptake by modeling nutrient uptake in a fitness (generally defined by growth rate) landscape and showing that some organisms, especially herbivores, will regulate intake to coincide with local maxima in the fitness landscape (Simpson et al. 2004). Invertebrate predators have also been shown to regulate nutrient uptake in this way and will choose prey that rectify nutritional deficiencies (Mayntz et al. 2005). Perhaps this mechanism could drive "switching" in octopuses, but if switching is not density-dependent as with an optimally foraging predator, it is unclear what effect this would have on the population dynamics of prey species.

There have been mixed results concerning optimal foraging behavior in other octopus species. In *E. dofleini*, for example, Vincent et al. (1998) predicted that the crab *Telmessus cheiragonus* would be a preferred prey in an optimal foraging framework because of its large size and short handling time as evidenced by the lack of drill holes in midden remains. However, no such preference was evident from midden analysis. In another, contrasting study, Anderson and Mather (2007) found that *E. dofleini* preferred the clam *Protothaca staminea* over the mussel *Mytilus trossulus* when both were opened and presented to the octopus. However, when these prey shells were closed, preference switched to *M. trossulus*, which has a thinner shell and required less handling time than *P. staminea*, a clear reflection of an optimal foraging strategy. Scheel et al. (2007) studying *E. dofleini* in Alaska found that octopuses were selective of prey species and size in a manner consistent with a rate-maximizing optimal forager, while the unrelatedness of octopus and prey population trends was consistent with a risk-minimizing forager. They hypothesized that octopuses may rate-maximize while foraging and act as a risk-minimizing forager by decreasing movement between foraging patches.

The notion that *O. rubescens* may forage to meet specific nutritional targets would also have implications for its status as a generalist. It has been suggested that *Octopus vulgaris* in the Caribbean is a "specializing generalist"; the generalist feeding is exhibited by the population as a whole, but individuals may be specialists on certain prey taxa (Anderson et al. 2008). If we extend the continuum proposed by Shipley et al. (2009) to predators, *O. rubescens* could be considered an obligatory specialist. *O. rubescens*' apparent requirement for a specific lipid constitution from prey items would represent a narrow fundamental niche that could be met either by few prey taxa with nutritional compositions very similar to the octopus' nutritional needs or by diverse taxa that in combination meet nutritional needs. This narrow fundamental niche is the primary defining characteristic of an obligatory specialist in Shipley's (2009) taxonomy.

Conclusions

In these experiments, the prey choices made by *O. rubescens* deviated widely from those expected from a simple model of maximizing energetic intake per unit time. *O. rubescens* chose *H. nudus* over *N. obscurata* as prey by a ratio of 3:1, even though the octopus could obtain nearly 10 times more energy per unit time from *N. obscurata* than from *H. nudus* when consumable tissue mass and handling time are considered. Octopus energy budgeting was similar when consuming either of the prey species except that lipid extraction efficiency was significantly higher in octopuses consuming *H. nudus*. These data suggest that lipid digestibility may play an important role in the prey choice of *O. rubescens*.

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