

Prey preference of the common long-armed octopus *Octopus minor* (Cephalopoda: Octopodidae) on three different species of bivalves*

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Abstract *Octopus minor* is widely distributed along the northern coast of China. To date, there is little information on the prey selection process of this species. To understand this process, several experiments were carried out. Three types of bivalves, namely, *Ruditapes philippinarum*, *Macra chinensis*, and *Mytilus galloprovincialis*, were used to observe the prey selection of *O. minor* and to analyze the potential causes of prey selection from three aspects: prey profitability, adductor muscle tension and handling time. Under single-prey conditions, we found that the average (\pm SD) predation rates of *O. minor* on *R. philippinarum*, *M. chinensis*, and *M. galloprovincialis* were 1.73 ± 0.50 , 1.27 ± 0.42 , and $0.8\pm 0.2/d$, respectively. Under different prey combinations, octopods actively selected one type of prey over the other(s), and the order of prey preference was *R. philippinarum*, followed by *M. chinensis* and lastly *M. galloprovincialis*. Furthermore, the shells of the consumed prey showed that *O. minor* only consumed bivalves by pulling them apart since there was no evidence of drill holes on the shells. The prey selection of *O. minor* was related to the prey profitability and handling time; *O. minor* appeared to select preys with a higher profitability and a shorter handling time. However, the difficulty in opening the bivalve was not consistent with the prey preference of the octopods. These results suggest that *O. minor* prefers to consume *R. philippinarum* possibly due to a high profitability and a short handling time that supports the optimum Foraging Theory.

Keyword: *Octopus minor*; bivalve; prey preference; prey selection; prey profitability

1 INTRODUCTION

Predators and prey are important components of ecological communities. There is a series of established relationships between them and predation is one of the most important interactions (Hu et al., 2016). Predators often hunt different prey in their natural surroundings. Under conditions of multiple prey availability, however, predators have many prey preferences (Ambrose, 1984; Wong and Barbeau, 2005). A thorough understanding of prey preferences by predators is essential to understand the ecological significance of predation. A predator's selection of prey is affected by many factors, including detectability, accessibility, ease of capture, prey energy content, prey handling time and the time required for non-predatory behaviors (Hughes and Dunkin, 1984). Therefore, it is necessary to use the

optimal foraging theory in order to model and predict this decision made by animals during foraging (McQuaid, 1994). To date, optimal strategies have been established by which predators select prey to maximize the net rate of energy per unit foraging time (Schoener, 1971; Hughes, 1980). Although cephalopods are common predators, there are limited information on their individual predation strategies (Ambrose, 1984; Iribarne et al., 1991).

Octopuses are important predators in the habitats they occupy. They have a higher metabolic rate than many other benthic predators, suggesting that they

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Table 1 Biological indices of the experimental predator and prey animals

Predator and prey species	Mantle length (mm) (mean±SD)	Shell length (mm) (mean±SD)	Shell height (mm) (mean±SD)	Fresh weight (g) (mean±SD)
<i>O. minor</i> (n=50)	72.40±5.20	-	-	133.72±6.75
<i>R. philippinarum</i> (n=100)	-	33.10±0.90	18.20±0.60	10.30±0.45
<i>M. chinensis</i> (n=100)	-	34.00±0.90	20.70±0.70	12.94±0.87
<i>M. galloprovincialis</i> (n=100)	-	35.94±0.85	19.23±0.86	11.36±0.37

n: the number of experimental animals; -: no data.

may be consuming more prey per unit time than most other predators in their habitat (Seibel and Drazen, 2007; Onthank and Cowles, 2011). They are generalist predators with behavioral and morphologic adaptations that enable them to search, capture and handle different types of prey (Portela et al., 2014); they can also be further named “switching predators” (Vincent et al., 1998) that vary their diets based on the abundance of prey and as a result, can stabilize prey populations (Murdoch, 1969).

Octopus minor is widely distributed on the coast of China, the Korean Peninsula, and the coast of Japan (Yamamoto, 1942; Dong, 1988). In recent years, its capture has decreased rapidly (Kim et al., 2008), and, as a dominant species in aquaculture, many researchers have carried out in-depth studies of its histology (Iwakoshi et al., 2000), physiology (Seol et al., 2007), nutritionology (Qian et al., 2010), embryonic development (Kim and Kim, 2006; Qian et al., 2016), breeding (Zheng et al., 2014) and genetics (Bo et al., 2016; Gao et al., 2016; Xu et al., 2018). However, to date, there is no publication in the literature on its prey selection.

It is well known that octopods prefer to ingest a wide variety of crustaceans and mollusks, and when offered, tend to hold as many crabs as possible (Guerra, 1978; Hartwick et al., 1981; Hanlon and Messenger, 1996). During octopus’s artificial breeding, however, crabs are more difficult to obtain than bivalve mollusks. Therefore, it is of practical value to understand the bivalve prey selection of *O. minor*. In this study, we fed *O. minor* with three species of bivalves, namely, *Ruditapes philippinarum*, *Macra chinensis*, and *Mytilus galloprovincialis* and we observed and analyzed the selection of prey under laboratory conditions.

Here we address the following questions. Of the three prey bivalves provided, which of these species do *O. minor* show a preference for? Do these prey preferences by *O. minor* follow the optimal Foraging Theory and if so, what are the possible driving forces that predicate these choices? The answers to these

questions will ultimately provide additional insights into understanding the prey selection process of *O. minor*.

2 MATERIAL AND METHOD

2.1 Experimental material

This investigation was conducted at the Ocean University of China, Shandong, China, from October to November 2017. All experimental animals (*O. minor*, *R. philippinarum*, *M. chinensis* and *M. galloprovincialis*) were obtained from the local sea. Fifty active, undamaged *O. minor* (mix of gender) were collected from the Moon Lake and separated in two rectangular cement pools (10 m×1 m×0.6 m) containing PVC pipes shelters (diameter, 90 mm; length, 700 mm), with open water circulation (temperature, 17.4–20.5°C; salinity, 29–30) and a water depth of 50 cm to maintain oxygenation. *R. philippinarum*, *M. chinensis* and *M. galloprovincialis* were individually maintained in a similar tank until they were used. During the acclimation period, *O. minor* were fed with fresh Manila clams which were collected from the local sea. Only healthy animals were used for the experiments and the biological indices of the experimental animals was shown in Table 1.

2.2 Experimental design

Predation rates and prey preferences were examined in single-prey (no choice), two-prey (choice) and three-prey (choice) experiments. These experiments were conducted in a white cuboid plastic tank (70 cm×60 cm×60 cm), a water depth of 50 cm, a water temperature of 18.0±1.0°C, a salinity of 29–30 and a photoperiod of 14 h light and 10 h dark. Two days prior to the experiments, a single *O. minor* was randomly selected and transferred to the tank to adapt. On a daily basis with prior cleaning of the sundries, 50% of the water volume was changed at 5:00 pm, with prior cleaning of the sundries. The prey were randomly offered at the bottom of the tank at 5:00 pm

Table 2 Experimental design of predation rate and prey selection

Experiment group	Prey species	Prey quantity	Replicate number	Duration (d)
OP	<i>R. philippinarum</i>	12	3	5
OC	<i>M. chinensis</i>	12	3	5
OG	<i>M. galloprovincialis</i>	12	3	5
OPC	<i>R. philippinarum</i> + <i>M. chinensis</i>	6+6	3	5
OPG	<i>R. philippinarum</i> + <i>M. galloprovincialis</i>	6+6	3	5
OCG	<i>M. chinensis</i> + <i>M. galloprovincialis</i>	6+6	3	5
OPCG	<i>R. philippinarum</i> + <i>M. chinensis</i> + <i>M. galloprovincialis</i>	4+4+4	3	5

In single-prey experiment, *R. philippinarum*, *M. chinensis* and *M. galloprovincialis* are represented by OP, OC and OG, respectively. In two-prey experiment, *R. philippinarum* plus *M. chinensis*, *R. philippinarum* plus *M. galloprovincialis* and *M. chinensis* plus *M. galloprovincialis* are represented by OPC, OPG and OCG, respectively. In the three-prey experiment, *R. philippinarum* plus *M. chinensis* plus *M. galloprovincialis* are represented by OPCG.

on the first day, and the consumed prey was collected and replaced with the same species at 7:00 am and 5:00 pm on the next day.

To determine the predation rates, single-prey experiments were implemented. In the single-prey experiment, 12 individuals of each prey species (*R. philippinarum*, *M. chinensis* or *M. galloprovincialis*) were offered to one octopus. The predator-prey grouping are designated as OP, OC and OG, respectively. Three octopuses were selected to repeat this treatment and lasted for 5 days (Table 2). To examine prey selection, experiments with two and three different prey were designed. In the two-prey experiment, prey were provided in three treatment combinations as follows: six *R. philippinarum* plus six *M. chinensis*, six *R. philippinarum* plus six *M. galloprovincialis*, and six *M. chinensis* plus six *M. galloprovincialis*, represented by OPC, OPG, and OCG, respectively. Three octopuses were selected to repeat this treatment and lasted for 5 days (Table 2). In the three-prey experiment, one octopus was provided with four *R. philippinarum*, four *M. chinensis*, and four *M. galloprovincialis*, represented by OPCG and this experiment was repeated three times and lasted 5 days (Table 2).

2.3 Data collection and analysis

2.3.1 Predation and selectivity data

In the single-prey experiment, the number of prey consumed per day by *O. minor* was calculated by the predation rate of each replicate. In the two- or three-prey experiments, the selection index was calculated by:

$$\alpha_i = \frac{r_i/n_i}{\sum_{j=1}^q r_j/n_j}, \quad (1)$$

where α was the selection index, i and j were the prey types, r was the number of prey consumed by the predator, n was the total number of prey in the tank, and q was the total number of prey types in the experiment (Chesson, 1978).

In the two-prey experiment (choice), the number of each prey type consumed was treated as the observed frequency. In the single-prey experiment (no choice), the number of prey consumed was treated as the expected frequency. To analyze the selection of prey, we examined the active selection by comparing the observed frequencies with the expected frequencies using the χ^2 test with Yate's correction for continuity (Liszka and Underwood, 1990; Zar, 1996). The expected frequencies were calculated by the following equations:

$$E_i = R \left(\frac{S_i}{S_i + S_m} \right), \quad (2)$$

$$E_m = R \left(\frac{S_m}{S_i + S_m} \right), \quad (3)$$

where E_i and E_m were the expected number of prey type i and prey type m consumed, respectively, R was the number of prey type i plus the number of prey type m consumed when presented together, and S_i and S_m were the number of prey type i and prey type m consumed under single-prey conditions (Liszka and Underwood, 1990).

2.3.2 Characteristics data of the prey

To further understand the prey selection of the predators, we evaluated the characteristics of the prey by including the prey energy content, handling time, prey profitability and prey adductor muscle tension. To measure the energy content per prey, *R. philippinarum*, *M. chinensis* and *M.*

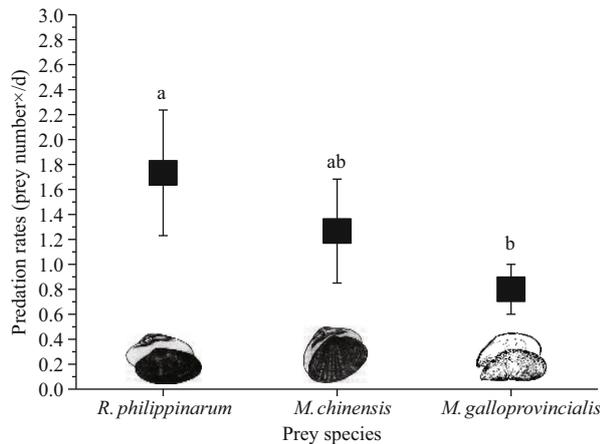


Fig.1 The average (\pm SD) predation rates of *O. minor* on *R. philippinarum*, *M. chinensis* and *M. galloprovincialis*. Different letters indicate significant differences (Tukey, $P<0.05$)

galloprovincialis ($n=10$ each) soft tissues were dried for 48 h at 80°C. The average dry weight per prey specimen was equal to the total dry weight divided by the number of prey specimens. The average energy per unit dry weight was measured using an oxygen bomb calorimeter (Parr 6400). The energy content per prey specimen was equal to the average dry tissue weight multiplied by the mean energy content per unit dry weight. The handling time was calculated as the total time spent by the predator to capture and consume a single prey, from the encounter to the end of consumption. During the single-prey experiment, the handling time of prey was recorded by videos during the daytime with a camera (Brinno TLC-200), which was placed at a height of 1.5 m above the water surface. The prey profitability was equal to the average energy content divided by the average handling time per prey (Stephens and Krebs, 1986). The entry techniques used by *O. minor* to consume bivalves which had been eaten were judged by the integrity of the shells. The pulling force, which was used to separate the bivalve shells, was measured with a “clam rack” (Anderson and Mather, 2007) that employed rubber suction cups to adhere to the center of each shell after washing and drying. One rubber suction cup was fixed to the scale, and the other one to the clam rack platform. The tension was increased until a gape (approximately 1 mm) was visible at the ventral margin of the valves and the resulting pull tension data was recorded.

2.4 Statistical analysis

Statistical analysis of data was performed using IBM SPSS Statistics Software. An independent

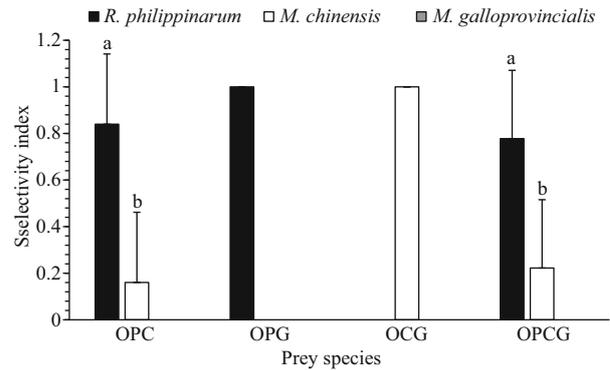


Fig.2 The prey selectivity index of *O. minor* (O) in the presence of different *R. philippinarum* (P), *M. chinensis* (C), and *M. galloprovincialis* (G) prey species combinations

Values in the same group with different letters indicate significant differences ($P<0.05$).

sample *t*-test was used to analyze the selection index. Other predation and selectivity data, as well as the prey characteristics data, were analyzed using one way analysis of variance (ANOVA). Levene’s test was used to test the assumption of homogeneity of variances. When this assumption was violated, Square root transformation was performed to obtain homogeneity of variance. For multiple comparisons, Tukey’s test was used to compare the means. All means were presented \pm standard deviation, and statistical significance was defined as $P<0.05$.

3 RESULT

3.1 Predation and selectivity data

3.1.1 Predation rate

In single-prey experiments, the predation rates (Fig.1) of *O. minor* on *R. philippinarum*, *M. chinensis* and *M. galloprovincialis* were 1.73 ± 0.50 , 1.27 ± 0.42 and 0.8 ± 0.2 per day, respectively. There was a significant difference (ANOVA, $F=8.65$, $P=0.02$) among *R. philippinarum*, *M. chinensis* and *M. galloprovincialis* consumed by *O. minor*. The predation rate on *R. philippinarum* was significantly higher (Tukey, $P=0.01$) than that on *M. galloprovincialis*, but there was no significant difference (Tukey, $P>0.05$) in the predation rates between *M. chinensis* and *R. philippinarum* or *M. galloprovincialis*.

3.1.2 Prey selectivity

In experiments performed with different prey combinations, the selectivity index was estimated

Table 3 Results of χ^2 tests comparing the observed frequencies with the expected frequencies

Group	Species of prey	Observed frequency	Expected frequency	Value	P
OPC	<i>R. philippinarum</i>	25	16.76	4.229	0.040
	<i>M. chinensis</i>	4	12.24		
OPG	<i>R. philippinarum</i>	22	15.05	6.116	0.013
	<i>M. galloprovincialis</i>	0	6.95		
OCG	<i>M. chinensis</i>	18	11.03	6.384	0.012
	<i>M. galloprovincialis</i>	0	6.97		

All probabilities were calculated using the Yate's correction for continuity.

(Fig.2). In the OPC combination group, the selectivity index for *R. philippinarum* (0.84 ± 0.30) was significantly higher (*t*-test, $F=33.048$, $P<0.0001$) than that for *M. chinensis* (0.16 ± 0.30). In the OPG and OCG combination group, *O. minor* only consumed *R. philippinarum* or *M. chinensis*, respectively. In the OPCG combination group, where three different prey were provided at the same time, *O. minor* did not consume *M. galloprovincialis*, and the selectivity index for *R. philippinarum* (0.78 ± 0.29) was significantly higher (ANOVA, $F=26.923$, $P<0.001$) than that for *M. chinensis* (0.22 ± 0.29). Consequently, *O. minor* preferred *R. philippinarum* as their first choice of prey, followed by *M. chinensis* and *M. galloprovincialis*, a distant third.

3.1.3 Observed and expected frequency

In the two-prey experiments, the number of consumed prey differed significantly than the expected number calculated from the single-prey experiment (Table 3). The octopuses preferred one type of prey when provided with a choice. In the OPC and OPG combination groups, *O. minor* preferentially selected *R. philippinarum* over the other two bivalves. In the OCG combination group, *O. minor* actively selected *M. chinensis* than *M. galloprovincialis*. When *R. philippinarum* were provided together with *M. chinensis* or *M. galloprovincialis*, *O. minor* actively selected *R. philippinarum*. In the presence of *M. chinensis* and *M. galloprovincialis*, *O. minor* actively selected *M. chinensis*.

3.2 Prey characteristics data

3.2.1 Handling time

Regarding the handling time (Fig.3), there was a significant difference (ANOVA, $F=8.976$, $P=0.001$) among *R. philippinarum*, *M. chinensis* and *M.*

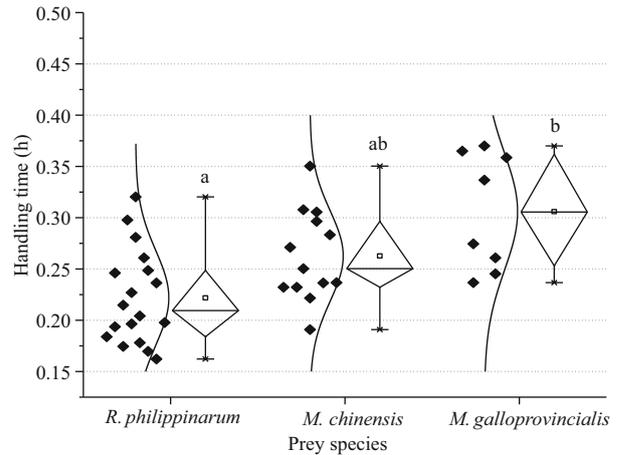


Fig.3 Handling time of *O. minor* on *R. philippinarum*, *M. chinensis* and *M. galloprovincialis*

Different letters indicate significant differences ($P<0.05$). Box-plot presenting average, median, 25 and 75 percentiles, minimum and maximum time taken to handle the three types of prey by octopuses, black diamonds indicate an individual prey item.

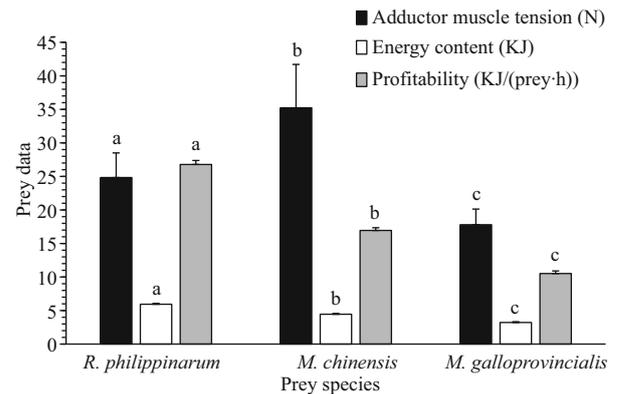


Fig.4 The average (\pm SD) of adductor muscle tension, energy content and profitability of *R. philippinarum*, *M. chinensis* and *M. galloprovincialis*

Values in the same group with a different letter indicate significant differences (Tukey, $P<0.05$).

galloprovincialis. *O. minor* spent 0.22 ± 0.05 h to handle *R. philippinarum*, which was significantly lower (Tukey, $P<0.0001$) than that of *M. galloprovincialis* (0.31 ± 0.06 h). *O. minor* spent 0.26 ± 0.04 h to handle *M. chinensis*, which was not significantly different (Tukey, $P>0.05$) from *R. philippinarum* or *M. galloprovincialis*. The order of the handling time for the three different preys was as follows: *M. galloprovincialis* > *M. chinensis* > *R. philippinarum*.

3.2.2 Prey adductor muscle tension, energy content and profitability

For all bivalve prey species, *O. minor* consumed them by pulling apart the shells. The pulling force

used by *O. minor* to separate *R. philippinarum*, *M. chinensis* and *M. galloprovincialis* was 24.84 ± 3.67 , 35.22 ± 6.48 and 17.80 ± 2.33 N, respectively (Fig.4). There were significant differences (ANOVA, $F=30.26$, $P<0.0001$) in the strength used by *O. minor* to open the three different prey. According to the rankings (Fig.4), the bivalves are more easily opened from *M. galloprovincialis* to *R. philippinarum* to *M. chinensis*. The energy contents (Fig.4) were significantly different (ANOVA, $F=1313.2$, $P<0.0001$) among the three different preys. The energy content of *R. philippinarum* (5.94 ± 0.13 KJ) was significantly higher (Tukey, $P<0.0001$) than that of *M. chinensis* (4.45 ± 0.11 KJ), which, in turn was significantly higher (Tukey, $P<0.0001$) than that of *M. galloprovincialis* (3.22 ± 0.12 KJ). As for the profitability, there were significant differences (ANOVA, $F=3030.7$, $P<0.0001$) among the three different preys. The profitability of *R. philippinarum* (26.78 ± 0.60 KJ/(prey·h)) was significantly higher than that of *M. chinensis* (16.95 ± 0.40 KJ/(prey·h)) and *M. galloprovincialis* (10.52 ± 0.39 KJ/(prey·h)). In summary, both the energy content and profitability of *R. philippinarum* were the highest relative to the other two prey species.

4 DISCUSSION

A predator's diet consists of many prey species, but each predator has a preference for a specific prey. For instance, *O. bimaculatus* consume more than 55 prey species and Ambrose (1984) through laboratory experiments, found that octopuses prefer to consume crabs the most. In contrast, *Rapana venosa* (a gastropod) prefers *Anadara (Scapharca) inaequalis* when *M. galloprovincialis*, *R. philippinarum* and *A. inaequalis* were provided at the same time (Savini and Occhipinti-Ambrogi, 2006). In this study, *O. minor* consumed different prey, although they had an apparent preference for *R. philippinarum*. Carlsson et al. (2009) and Robinson et al. (2015) suggests that predators may avoid consuming new species of prey due to unfamiliarity. In this research, we found that *R. philippinarum* is abundant in the moon lake where experimental octopuses were collected, but *M. chinensis* and *M. galloprovincialis* could not be found. We speculated that *O. minor*'s high preference for *R. philippinarum* is related to its familiarity with feeding on this prey. This phenomenon is consistent with a high preference for native mussels *Semimytilus algosus*, when *Jasus lalandii* (a lobster) and *Marthasterias africana* (a starfish) are offered with

familiar native mussels *S. algosus* and unfamiliar invading mussels *M. galloprovincialis* as prey (Skein et al., 2018).

When bivalve preys were presented to octopods, there were two entry methods to open the prey: "drilling" or "pulling" (Anderson and Mather, 2007). In general, the octopods first try to use a quick method requiring enormous energy, that is, pulling the prey apart by the suckers on its arms (Fiorito and Gherardi, 1999). If this method is not successful, the octopuses drill holes into the shell with the help of salivary papilla, which involves little energy but is time consuming (Nixon, 1980; Casey, 1999). In this experiment, we collected the shells of bivalves consumed by *O. minor* and found that all the shells were intact without any evidence of drill holes, suggesting that *O. minor* only used the former method. These results are different from those of *O. dierythraeus* and *Enteroctopus dofleini* that consume bivalves using these two entry methods (Steer and Semmens, 2003; Anderson and Mather, 2007). McQuaid (1994) found that when *O. vulgaris* consume different sizes of brown mussel, *Perna perna*, they adopt different entry methods, that is, they adopt the pulling entry method to consume small sizes of mussels and they utilize the drilling entry method to consume large mussels (McQuaid, 1994). We speculate that in this experiment, *O. minor* is much larger than the bivalves, and it has enough strength to pull the bivalves open. However, further experimental research on larger bivalves is required to determine whether *O. minor* can use other entry methods.

Active prey selection was studied because *O. minor* always selected *R. philippinarum* when offered a choice of prey species (Table 3). There are many factors that influence the prey selection of the predator, but the most important index to affect prey selection is the energy intake rate (Pyke et al., 1977; Pyke, 1984). This means that the predator will consume the higher profitability prey and ignore the lower profitability prey (Wong and Barbeau, 2005). In this study, we collected and analyzed the profitability for *O. minor* of three species of bivalves (Fig.4). We found that the order of profitability, from highest to lowest, was *R. philippinarum*, *M. chinensis* and *M. galloprovincialis*. These results were consistent with the prey selection of octopuses, and the prey selection of *O. minor* is consistent with the optimal foraging theory. In marine invertebrates, "time minimization" has been clearly demonstrated to be an

efficient predation strategy (Hughes and Seed, 1981; Leite et al., 2009), which can optimize foraging and reduce handling time, thereby decreasing its exposure to other predators and risks (Mascaró and Seed, 2001). Handling time was measured in this study (Fig.3) and the relationship between handling time and prey preference was determined; high preference prey had a short handling time and low preference prey had a long handling time and these results are consistent with the “time minimization” strategy. However, these results were different from Hu et al. (2016) who studied *R. venosa* (a gastropod). In this case, high prey preference had long handling time and low prey preference had the shorter handling time such that, there was no obvious relationship between the prey preference and the handling time. This study, we also analyzed the relationship between prey selection and adductor muscle tension, and found that these results were not consistent with prey preference; *M. galloprovincialis* were most easily opened, but *O. minor* had the lowest preference for it. This suggests that the difficulty of consumption was not the main reason for the prey preference of *O. minor* in this study. In contrast to these results, the *Cancer* crab species refused clams (*Protothaca staminea*) because of predation failure (Boulding, 1984). We concluded that the pulling force required to open the three different bivalves was significantly different, but *O. minor* can provide enough pulling force to open them all. Therefore, the adductor muscle tension of bivalves did not affect the prey selection of *O. minor*.

5 CONCLUSION

In this study, we provided *O. minor* with three different bivalves. We observed and analyzed the prey preferences and found that *O. minor* preferred *R. philippinarum*, followed by *M. chinensis* and *M. galloprovincialis*. Moreover, the prey preference was consistent with the prey's profitability and handling time, regardless of the adductor muscle tension. Several studies (Nixon, 1980; Casey, 1999; Fiorito and Gherardi, 1999; Anderson and Mather, 2007) have reported that octopods use two different methods (drilling and pulling) to open bivalves; however, we found that *O. minor* only used the pulling entry method.

6 DATA AVAILABILITY STATEMENT

All data included in this research are available from the corresponding author on reasonable request.

7 ACKNOWLEDGMENT

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