HUNGRY AND AFRAID:
The effects of starvation on the foraging behavior of *Panopeus herbstii* in the presence of a
higher-order predator

By
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ABSTRACT

This study utilizes an experimentally simulated three-tiered trophic chain between *Menippe mercenaria* (stone crabs), *Panopeus herbstii* (marsh mud crabs), and juvenile *Mercenaria mercenaria* (quahog clams), to analyze the influence of hunger on mesopredator foraging behavior in the presence and absence of a higher-order predator as predicted by principles of the ecology of fear and the optimal foraging theory. A 2x2 factorial design utilizing *P. herbstii* that were subjected to 7-day starvation or fed 30 minutes before the each experiment in combination with or without a stone crab, or a "fear factor," was used to analyze biomass consumption and prey size selection differences influenced by hunger and fear response. The optimal size class of juvenile clams selected was also predicted by generating a curve of net kcal gained during experiments by subtracting kcal expended during crushing from kcal of soft tissue ingested for each size class of clam. Results suggest that 7-day starvation does not significantly increase consumption in the presence of fear ($p=0.485$), but fear does significantly affect prey biomass consumed ($p=0.0175$) and prey size selectivity ($p<0.0001$). Foraging practices deviated from optimal foraging predictions, indicating a wider range of factors outside of energy to crush this prey species—such as search time, ability to manipulate prey of different sizes, etc.—should be taken into consideration when formulating predictions of optimal prey size.

KEYWORDS: ecology of fear, optimal foraging theory, nonconsumptive effects, predator-prey effects, *Panopeus herbstii*, *Mercenaria mercenaria*, *Menippe mercenaria*

INTRODUCTION

Predators are typically treated as consumers of prey in modeling food webs. However, predators can also have indirect, nonconsumptive effects on prey species that can be equally influential in community dynamics (Lima and Dill, 1990; Brown et al, 1999; Werner and Peacor, 2003; Preisser and Bolnick, 2008), a process sometimes termed "the ecology of fear." These effects, collectively referred to as trait-mediated interactions, include alterations in behavior (such as changes in foraging activity levels and locomotion), morphology, and development (Werner and Peacor, 2003; Preisser and Bolnick, 2008). Nonconsumptive effects by top predators on mesopredators or prey species have been observed in terrestrial and aquatic systems. In Yellowstone National Park, Ripple and Beschta (2004) observed profound increases in plant coverage with the resurgence of wolves, largely due to alterations in elk and deer grazing patterns rather than decreases in their populations. Schmitz et al. (1997) demonstrated that spiders rendered harmless by having their mouths glued shut induced the same levels of grasshopper mortality at the population level as unmanipulated spiders, each equally effective in reducing the grasshoppers' consumptive effects on grass. Heithaus et al. (2007, 2008) showed that the nonlethal effects of predation risk on sea turtles by tiger sharks can modify spatio-temporal patterns in turtle aggregations and influence immediate refuge choice based on turtle body condition. Grabowski and Powers (2004) and Grabowski and Kimbro (2005) documented the release of juvenile hard clam populations from mesopredator crab predation through the nonconsumptive effects of oyster toadfish and other higher-order predators.

The magnitude of nonconsumptive effects can be similar to those of consumptive effects or reductions in mesopredator or prey species density (Peacor and Werner, 2000). There are several studies investigating the roles that habitat complexity plays in mitigating the

nonconsumptive effects of predator presence on mesopredators and prey (Grabowski and Powers, 2004; Orrock et al., 2013) as well the effects of prey body size on fear responses (Preisser and Orrock, 2012). Fodrie et al. (2012) found that prolonged hunger in oyster drills weakens their avoidance response to predator present during habitat selection. There are few studies, however, examining the effects of the hunger level of mesopredators in modifying trophic cascades.

The optimal foraging theory is another concept important to understanding predator behaviors. This theory states that a forager should select a food item (or items) that will provide the most energetic reward per unit energy spent during the broadly defined consumption process (Schoener, 1971). Components of energy expenditure include search costs (energy used to find and catch prey) and handling costs - the energy used in manipulating the acquired prey, chewing/swallowing, etc. (Schoener, 1971). Factors contributing to energy gain include type, size, and nutritional value of the selected food source (Schoener, 1971). Brown and Kolter (2004) extend optimal foraging considerations to include foraging time allotted to one location over another based on variability in food availability and predation risk, the value of alternate fitness-enhancing activities, and the risk an organism is willing to accept when foraging for prey. Though a useful tool for predicting feeding behavior of a particular species in the presence of a particular range of food sources, the optimal foraging theory does not explicitly account for the possible effects hunger may have on prey selection. The parameters considered in the optimal foraging theory include effects on predator avoidance behavior, food acquisition, and reproduction (Mangel and Clark, 1986). Studying the interactions between the ecology of fear and the optimal foraging theory is important for making predictions of food web dynamics and for designing future studies investigating which factors most influence food web interactions (Brown et al., 1999).

According to local knowledge, Florida stone crabs (*Menippe mercenaria*) have become abundant in Morehead City, NC within only the past ten years or so, possibly due northward range increases with increasing ocean temperatures and expansion of rock revetment, jetty, groin, and breakwater structures on shore to protect against storm damage. Their relatively recent population enhancement in NC waters provides an interesting opportunity to observe the potential effects of range expansions induced by climate change on existing trophic dynamics, especially on processes affecting commercially important species, such as *Mercenaria mercenaria.* One of the most prominent consumers of juvenile *Mercenaria* clams is the mesopredator *Panopeus herbstii,* commonly known as a mud crab. While the fear response of *P. herbstii* is well documented through its interactions with oyster toadfish (Grabowski and Kimbro 2005, Grabowski et al. 2008), the potential role of hunger in their foraging and fear response has yet to be investigated. Additionally, McNamara (1990) begins to combine the ideas of hunger into selectivity within the framework of the optimal foraging theory, but he does not delve into the implications of applying elements of selectivity to trophic interactions as part of the ecology of fear. Using the trophic interactions between stone crabs, *P. herbstii*, and *Mercenaria* clams, this study provides insight as to how the vastly unexplored effects of prolonged hunger in mesopredators modifies foraging predictions arising from the ecology of fear and from the optimal foraging theory in the presence and absence of a higher-order predator.

MATERIALS AND METHODS

Arena Design

Experiments took place in two 0.75 x 0.75 x 0.5 m wooden fiberglass mesocosm tanks on separate flow-through water tables. Separate water tables were used to avoid the possible influence of predator-derived chemical signals in the control treatments void of apex predators. The tanks were filled with filtered seawater from Bogue Sound. Water was allowed to flow through the tanks during the day until one hour before the mud crabs were introduced into the environment, at which point flow was shut off and the water level kept constant at 10 cm measuring from the bottom of the tanks. There was an approximately 3 mm thick layer of soft sandy sediment on the bottom of each tank, washed through a 2 mm mesh screen sieve before running the initial experimental trial since the sediment would be sieved before each experimental set thereafter. Each tank was oxygenated with a single hose bubbling oxygen into the water. The average water temperature of each tank was 24.4° C throughout each trial and did not vary between tanks. Each tank was divided in half diagonally by a plastic partition that allowed water flow but no crab or clam passage between the two halves. There were two empty mussel shells and one reclining flower pot 5 cm in diameter with the bottom end cut off in each half tank offered as hiding places for the mud crabs. In the non-divided corner of each tank, there were cages made from plastic baskets with strong, 2 cm plastic mesh zip-tied down over the top. Each cage took up a 25 cm by 16 cm area of the bottom of the tank. In one tank, there was a stone crab present in each cage. In the other tank, the cages were empty as controls for the cage itself.

Animal Collection and Maintenance

Apex predators (stone crabs), used as the 'fear factor' in this study, were captured near shore in the Bogue Sound in Morehead City, NC using crabs pots baited with dead baitfish, such as pinfish and juvenile pigfish. Only male stone crabs were used to avoid possibly confounding experimental results with differences between males and females. Stone crabs used were approximately the same size across the carapace (83.5 and 89.1 mm), and the same 2 individuals were used throughout the experimental trials. Mesopredators (*P. herbstii*) were collected from the Hoop Pole Creek area of Bogue Sound in Atlantic Beach, NC. Males and females were used, and they ranged between 28.2-33.4 mm across the widest part of the carapace and from 9.3-11.4 mm in major chelae length. When the mesopredators were not being starved, they were fed ribbed mussel flesh ad libitum.

To observe and quantify effects of hunger on *P. herbstii* foraging behavior in the presence of a higher-order predator, a 2x2 factorial design between starvation level and apex predator presence was used for this experiment. The two starvation levels were created by starving one set of *P. herbstii* for 1 week and feeding exposed ribbed mussel flesh to another set of *P. herbstii* every other day and 30 minutes before the start of each trial. *P. herbstii* subjected to the latter condition were observed eating the flesh offered before each replicate. In total, there were 4 treatments incorporating the following parameters: starved mesopredator placed in the presence of a fear factor, satiated mesopredator placed in the presence of a fear factor, starved mesopredator without a fear factor, and satiated mesopredator without a fear factor. Eight replicates of each treatment were completed during the month of July in 2015. At the beginning

of each experimental trial, *P. herbstii* were measured across the carapace to the nearest tenth of a mm and placed in small metal mesh cages within their respective arenas for one hour, starting at 8 PM each night of an experimental set to acclimate to the experimental conditions. After the acclimation period, the *P. herbstii* were released from their cages near the center of the dividing wall.

Consumption of Mercenaria prey of varying sizes

Juvenile *Mercenaria* clams used during the experiment ranged from 4.0 to 9.9 mm in length across the widest part of the shell parallel to the axis around which the valve pivots when opening and closing. This size range was selected because preliminary observations showed that similar methods were used to open clams 10.0 mm and smaller in length (i.e., by crushing through the center of the shell rather than chipping around the edges). Clam lengths were measured with calipers and categorized into 6 size classes: 4.0-4.9 mm, 5.0-5.9 mm, 6.0-6.9mm, 7.0-7.9 mm, 8.0-8.9 mm, and 9.0-9.9 mm. Five clams of each size class were used in each tank subdivision, giving a total of 30 clams in each treatment. The clams were oriented and buried in living position (valve axis perpendicular to the bottom of the tank). To reduce the effects that clam proximity could have on consumption, clams were placed in the unobstructed areas of the arenas using a 6x12-lined grid. These grid dimensions were selected because they generated 30 intersecting points at which the clams could be placed, unobstructed by the stone crab cages. The size class of the clam placed at each point on the grid was randomized for each experimental set using random number sampling tables (Hald, 1952). Twelve hours after the initiation of the experimental set, the trial was ended and all crabs removed. The sediment in each half of the tanks was sieved through a 2-mm mesh screen sieve to remove clam remains. The number of clams consumed in each length class was recorded and later converted into units of biomass based on measurements described below to compute rewards of consumption.

Energetic Intake

To estimate the energy ingested from consuming clams of each size class, the average biomass of soft tissue for each size class was measured. Clams were opened carefully with a small scalpel, and all the soft tissue from inside the shell was extracted and placed on an aluminum foil tray. Soft tissue was dried for 5 days to constant weight in a drying oven at 60° C, and then weighed for dry biomass. Dry biomass was averaged for 3 clams for each size class. Average biomass of each size class was converted to kcal using a caloric content value of 5.014 kcal•g^{-1} (Hibbert 1977).

Energetic Costs of Clam Consumption

To estimate consumption costs for a clam of each length class, it was assumed that the energy required for the *P. herbstii* chelae to crush the clam was the overwhelmingly dominant energy expenditure, rendering travel costs of search, excavation costs, and handling costs (chewing/swallowing and manipulation not involving actual crushing) trivial. To estimate the energetic costs of crushing live clams of different shell lengths, a crushing device was constructed (**Figure 1**) based on a similar device used by Weiss (*unpublished master's degree thesis* 2001). The device utilized a wooden arm attached to a pivot point that came to rest on a

stationary wooden arm that rested on the tabletop. A small metal plate was built into the stationary arm at the point where the pivot-arm came to rest. This is where a series of individual, live clams were placed. At the end of the pivot-arm, the blunted point of a small screw was incorporated to simulate the morphology of *P. herbstii* chelae, which have a small, rounded protrusion near the hinge on the major chelae where the organisms place clams to be crushed during the feeding process. A bucket was hung on the end of the pivot-arm, and water was gradually added to the bucket until the shell of the clam cracked. The entire bucket of water was then weighed and added to the weight of the pivot arm at rest. This process was repeated three times for each size class. The mass required to crush each size class was computed by averaging crushing weight required for that size class. It was assumed average joules of force required for crushing was also the average energy expended by *P. herbstii* to crush a clam of that size. After converting joules of energy expended to kcal, kcal required for crushing were compared to kcal of soft tissue energy ingested to compute a net product of energy gained from ingestion minus energy expended when crushing each size class of clams. By examining the actual size-specific patterns of clam predation during the foraging trials to the estimated average size-specific reward (intake benefits - crushing costs) of consumption (Pyke et al. 1977), I assessed whether the fed *P. herbstii* differed from the starved *P. herbstii* in prey size selection and whether either pattern was consistent with optimal foraging predictions of maximizing rewards of foraging.

RESULTS

Consumption

For the treatments in which the fear factor was excluded, consumption occurred in each of the 8 trials. For the treatment in which the mud crabs were starved and exposed to a fear factor, clams were consumed in 6 out of 8 replicates, and in the treatment in which satiated mud crabs were exposed to a fear factor, clams were consumed in 4 out of 8 replicates. As seen in **Figure 2**, total kcal consumed, average kcal consumed across all 8 trials, and average kcal consumed over actual consumption events for each treatment all demonstrate that treatments that used starved *P. herbstii* and no fear factor induced the greatest amounts of consumption, while treatments that used satiated *P. herbstii* with a fear factor present induced the lowest amounts of consumption. Using JMP 10 statistical software, a 2-way ANOVA was used to investigate the influences of starvation level and fear factor presence on total kcal consumption. The effects tests of this function show that starvation did not significantly influence total kcal consumption (p=0.485), while there was a significant effect produced by the presence or absence of the fear factor (p=0.0175). There was not a significant interaction between the combined influenced of starvation and fear factor presence (p=0.406). These results suggest that even after weeklong starvation, a strong fear response repressing foraging activity is invoked in this mesopredator by the presence of a higher-order predator.

Size Selection

Figure 3 shows the projected net energetic gain of each size class. Solely based on kcal of energy used to crush the clams subtracted from kcal of dry biomass for each size class and excluding any negative consequences of energy expended in search costs or potential chelae wear, it would appear that the largest size class presented is the most optimal for consumption. This suggests that, if size selection decisions were being made solely on these two parameters,

mud crabs should consume clams in in the 9.0-9.9 mm size class until there are none to be found and then move to clams in the 8.0-8.9 size class, and so on until satiation. Upon analysis of the actual number of clams of each size class consumed, however, the most frequently consumed size class summed across all treatments and replicates was the 7.0-7.9 mm size class, followed by the 6.0-6.9 mm size class (see **Figure 4**). The trend produced by actual actions rather than mathematical predictions suggests that optimal foraging is occurring that incorporates inputs not directly measured in this experiment.

Again using JPM 10, a log-linear analysis was conducted through a Generalized Linear Model fit with a Poisson distribution to contrast the effects of treatment type on size selection. The effects tests reveal that there is a significant influence on size selection by treatment type (p<0.0001). Considering significance of predator presence on consumption and the frequency of size class consumption within each treatment across all trials, I inferred that apex predator presence or absence is the driving factor in selectivity. By comparing the differences in standard deviations of clam sizes consumed across each treatment as indicators of selectivity (see **Table 1**), there is indeed a trend of differing clam size selectivity between treatments incorporating and excluding the fear factor. These standard deviations also suggest more profound size selectivity in the two treatments that have a fear factor present than those devoid of a fear factor.

DISCUSSION

The results of this study are consistent with the principles of the ecology of fear. It is clear that the most extensive consumption of clams by *P. herbstii* occurred in the treatments that combined starvation without a fear factor produced the apex predator, a trend that follows intuitive expectations. What does not follow initial intuition, however, is the difference in consumption of clams between *P. herbstii* starved and satiated in the presence of a fear factor, especially in average kcal consumed across replicates in which consumption actually took place. It was expected that increased hunger would increase consumption whether an apex predator was present or not, but in actuality the satiated mesopredators consumed more kcal of clam than starved mesopredators when an apex predator was present. This could be due to several factors that could not be accounted for, such as the presence of an unknown, suboptimal food source that was used by the starved mesopredators as emergency sustenance in place of increased risk-taking. Alternatively, it could be simply that, after week-long (or less) food deprivation, the risk of mortality by predation exceeds that of starvation in *P. herbstii*.

Complications affecting consumption differences between treatments with and without a fear factor could have arisen from the clams' response to predator presence. Although the sediment layer did not allow for complete burial to avoid predation, Smee and Weissburg (2006) suggest that alterations in clam feeding behavior can emerge in response to olfactory cues given off by predators. This response may have been stronger in the treatments in which the both the mesopredator and the apex predator were present than in treatments that only had the mesopredator. Given that *P. herbstii* sense this prey species based on olfactory cues produced when their siphons are exposed (Grabowski and Kimbro 2005), alterations in clam feeding behavior may have reduced the perceived presence of prey and therefore further reduced the capability of mesopredators to acquire food in addition to reductions in foraging activity.

There were clear deviations from the predicted optimal size class upon analysis of actual size preference, indicating that foraging costs outside of energy expended in handling are important considerations for optimal foraging. Hughes and Seed (1995) discuss four competing models for consideration within the optimal foraging theory: (1) chelae wear, (2) prey-evaluation, (3) relative-stimulus, and (4) mechanical selection. The most relevant to this study are the chelae wear, prey-evaluation, and mechanical selection models. The chelae wear model suggests that smaller prey sizes are optimal to crustaceans because they can be consumed with lower risk of chelae damage. This model is directly contradicted by the mechanical selection model, which proposes that smaller prey are too difficult to manipulate to be optimal (as are prey that are too large), and ties in with the prey-evaluation model's prediction that preference is given to prey of intermediate sizes. In this study, there is a stronger demonstration of selectivity for intermediate sizes over the predicted optimal size as suggested by these latter two models. Jubb et al. (1983) observed similar selective preference in shore crabs towards prey of intermediate sizes, especially as foraging time lengthened. Their hypotheses for this pattern in selectivity, however, assume that selectivity increases as hunger decreases. The results of this study provide little to support this assumption. While starved mesopredators showed less selectivity in clam size than satiated mesopredators when there was no fear factor present (based on standard deviations in size selections in **Table 1**), starved mesopredators exposed to a fear factor stimulant were shown to be more selective than their satiated counterparts. Interestingly, selectivity is more prominent in treatments in which the fear factor was present than in those in which it was absent. For this study, fear increased the expression of optimal foraging on prey of intermediate sizes.

This study provides an investigation into unexplored linkages between the ecology of fear and the optimal foraging theory and the effects that the universal sensation of hunger has on the outcomes of these two theories. Future investigations should be cognizant of the combined influences of competing foraging models (based on assuming different selective advantages) when conducting optimal foraging predictions, as well the consequences of responses of live prey to predator cues. As these results contradict hypotheses of selective behaviors as a function of hunger level, it will also be important to consider possible deviations from optimal foraging induced by elements of fear on a species-specific basis when studying tri-layer trophic interactions.

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FIGURES AND TABLES

Figure 1: Clam Crushing Device (Based of design from Weiss 2001)

Fig 1. Live juvenile clams were placed in the small divot in metal plate on the bottom arm. The top arm was placed gently on the clam with the blunted end of a screw—serving as a mimic for the round protrusion of mud crab chelae—resting on the center of the shell (perpendicular to the valve axis). A bucket was suspended from the top arm and slowly filled with water with a hose resting at the bottom of the bucket until the shell cracked.

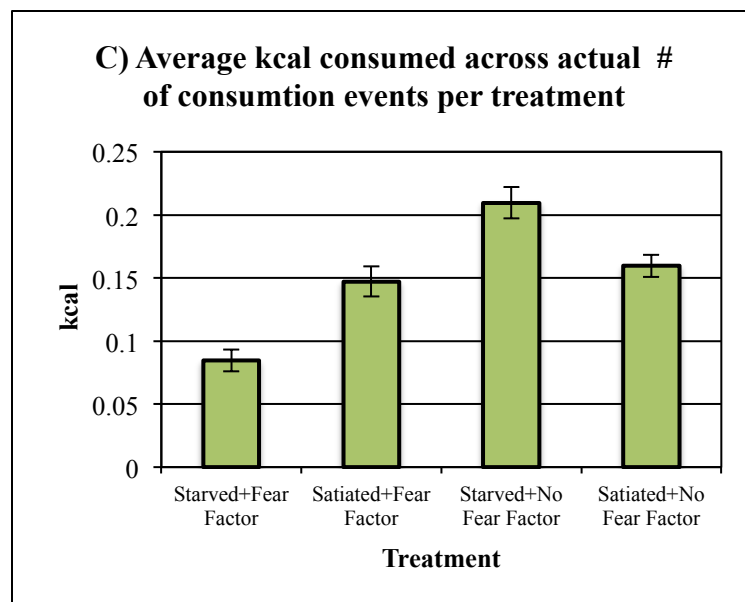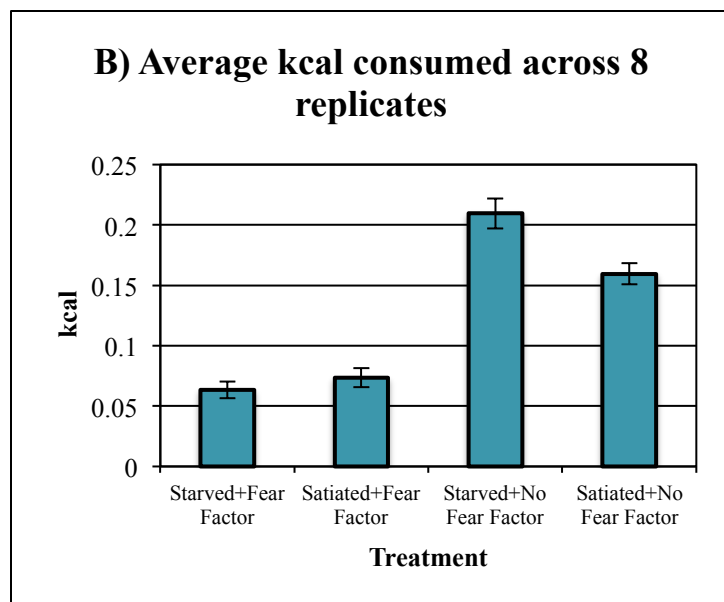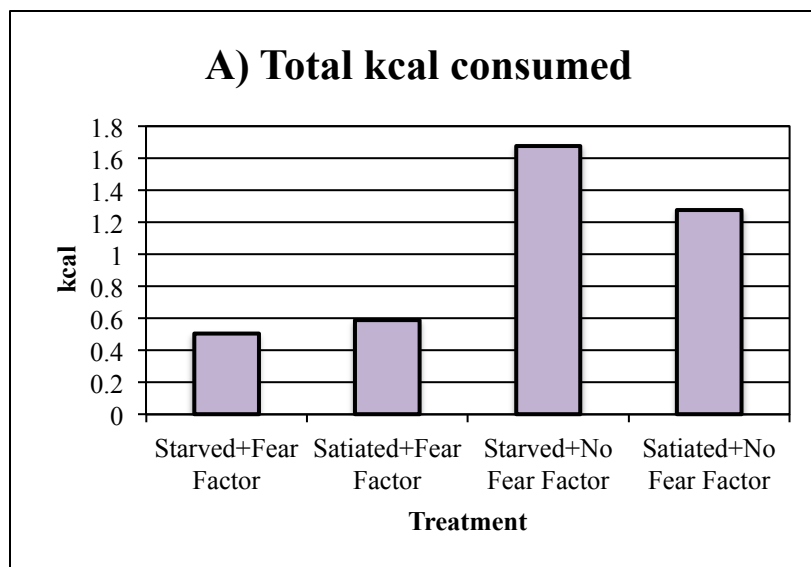# Figure 2: Mesopredators' kcal of clam consumption in each treatment

Fig 2. (A) The total quantity of kcal of clam flesh consumed in each treatment across 8 replicate trial, (B) the average number of kcal of clam flesh consumed in each treatment across all 8 replicates with standard error, and (C) the average number of kcal clam flesh consumed for each treatment's actual number of consumption events (6 events for Starved+Fear Factor, 4 events for Satiated+Fear Factor, 8 events each for Starved+ No Fear Factor and Satiated+No Fear Factor) with standard error. The treatment for Starved+No Fear Factor provides the largest consumptive outputs for each data set while Starved+Fear Factor provides the least.
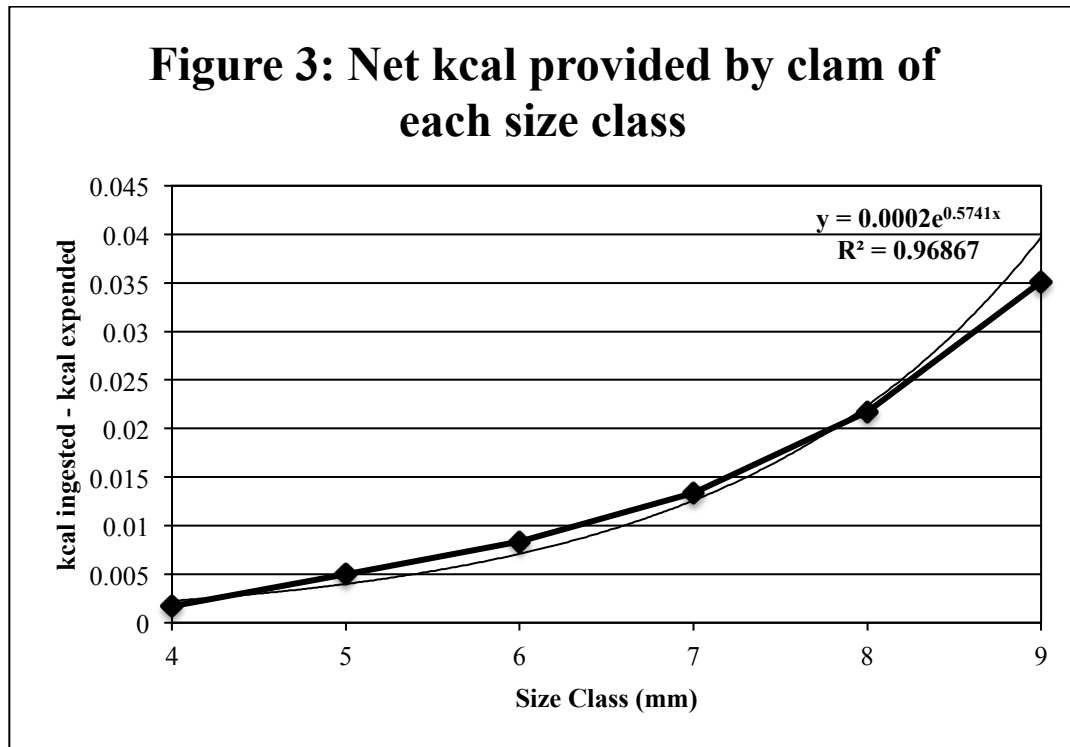
Figure 3: Net kcal provided by clam of each size class

$y = 0.0002e^{0.5741x}$
$R^2 = 0.96867$

kcal ingested - kcal expended

Size Class (mm)

Fig 3. Net kcal gain curve produced from the subtraction of the average kcal expended during crushing efforts from the average kcal of clam flesh for each size class. Suggests that 9.0-9.9 mm is the most optimal size class with optimality descending with size class.

Figure 4: Frequency of mesopredators' clam size selection in each treatment across 8 trials
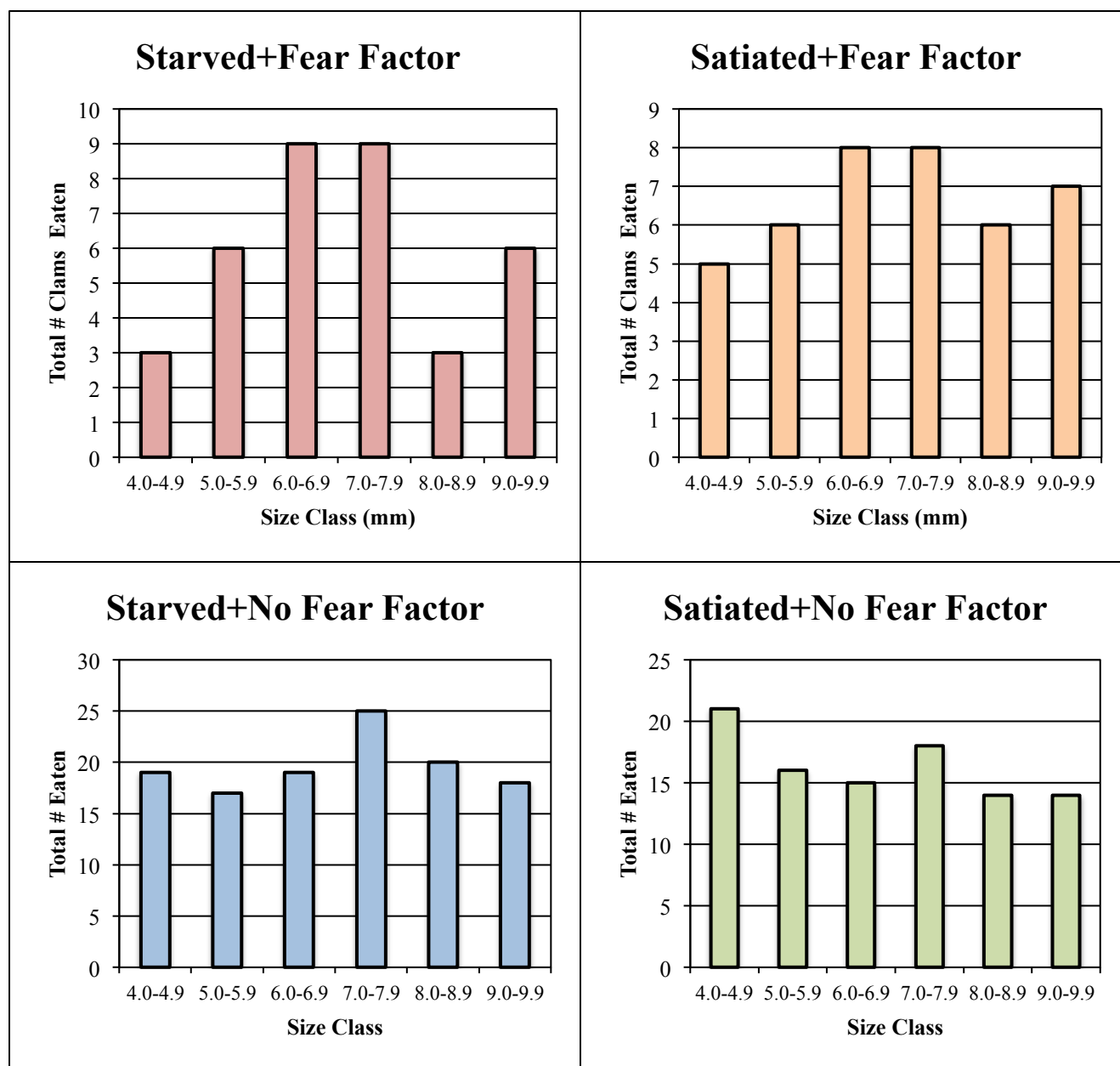

Fig 4. The total number of clams of each size class consumed within each treatment across all 8 replicates. Clams in the 7.0-7.9 mm size class were most frequently selected, followed by those in the 6.0-6.9 mm size class, suggesting the intermediate sizes offered in this study were optimal in a way not predicted by the previous reward/expenditure curve.

Table 1: Standard Deviation of Size Selection by Treatment

Treatment	s (mm)
Starved + Fear Factor	1.518928194
Satiated + Fear Factor	1.55430789
Starved + No Fear Factor	1.769898212
Satiated + No Fear Factor	1.629831036

Table 1. Standard deviation of size selection data by treatment. The higher values for treatments in which no fear factor was present suggest less importance was given to selection of clam size for both starved and satiated *P. herbstii* in low-perceived risk situations.