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Cautious clams? Energetic state modifies risk assessment in giant clams

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Abstract

A fundamental trade-off exists between the essential activities of acquiring energy and avoiding predators, thus animals are expected to make decisions that optimize foraging and avoid predation. These assessments are often state-dependent with hungrier animals taking greater risks when foraging. Previous studies have explored state-dependent risk assessment in a variety of taxa, yet no studies have focused on giant clams, genus *Tridacna*. These organisms provide a unique system to test foraging-risk trade-offs because they have two main energy sources: photosynthesizing symbiotic algae and siphoning nutrients from the water column. These activities can only occur when the clams' shells are open and the mantle is vulnerable to predation. Here, we tested whether risk assessment in giant clams was state-dependent. We designed three experiments of different shading durations (within-day and multiday) to block photosynthesis while allowing limited water flow for siphoning. We measured the latency of the clams to reopen after a simulated predator touch to determine whether different duration of shading modified their antipredator response. Our single-day experiment did not show a change in the hiding times across the three treatments. However, clams increased their hiding time as the treatments increased food deprivation (no restrictions on flow or photosynthesis, restriction on flow, restriction on flow and photosynthesis) when exposed to treatments for multiple days. Overall, we found that clams that were more energy-deprived had a longer hiding time. This contrasts with findings from previous state-dependent risk assessment literature and suggests that clams are more cautious when energy deprived, a result that may be generalizable to other sessile invertebrates.

Introduction

Researchers have long been interested in the trade-off between an animal's decision to forage or flee from predators and the behavioral effects that predators have on prey (e.g., Fraser & Huntingford, 1986; Lima & Dill, 1990; Lima, 1998). Animals must devote time to forage to acquire energy necessary for growth and reproduction (Middlebrooks, Pierce, & Bell, 2011), while evading predators to maximize their fitness (Heithaus *et al*., 2007). We assume that animals' decisions reflect trade-offs between risk of starvation and predation, and thus, their decisions should be influenced by their physiological state (Lima & Dill, 1990; Lima, 1998). This state-dependent behavior is seen when an animal's physiological state (e.g., body condition) impacts its behavior and decisions (Anholt & Werner, 1995). The effects of state-dependent risk assessment can be tested in different ways: habitat selection based on body state (Jones & Boulding, 1999; Alonzo, 2002; Heithaus *et al*., 2007), decisions when to forage during high and low predation risk with low energy reserves (Morgan, 1988; Lima, 1988; Skutelsky, 1996), or amount consumed when hungry or satiated in the presence of a predator (Walker & Rypstra, 2003; Wormington & Juliano, 2014).

Previous studies across many taxa have shown that an animal in a hungrier state will make riskier decisions to eat. For example, hungry bluntnose minnows (*Pimephales notatus*) accept greater risks and return to foraging faster (shorter latency time) after noting the presence of a predator than satiated minnows (longer latency time) (Morgan, 1988). Similarly, starved wolf spiders (*Pardosa milvina*) consume the same amount of prey regardless of predation risk, whereas satiated spiders forego eating and flee in the presence of a predator (Walker & Rypstra, 2003). Energy-deprived dark-eyed juncos (*Junco hyemalis)* initiate feeding earlier in the morning than juncos with higher energy reserves despite increased predation risk when foraging in poor light (Lima, 1988). Finally, upon detecting predator cues, starved mosquito larvae spend more time foraging than well-fed larvae which prioritized vigilance over foraging (Wormington & Juliano, 2014).

However, relatively few of these studies (e.g., Wahle, 1992; Smee & Weissburg, 2006; Middlebrooks *et al*., 2011) have focused on sessile marine invertebrates. Sessile animals may

be constrained in the ways in which they can feed or react to predators, thus making their foraging-risk trade-offs different than mobile organisms. We aim to address this knowledge gap and explore the possible influence of state-dependent risk assessment in giant clams (*Tridacna maxima*). Giant clams are an important organism to study as they are a base of coral reef food webs (Alcazar, 1986; Neo *et al*., 2015) and serve as a major source of primary productivity in dense populations because their net primary productivity per square meter is higher than most other coral reef primary producers (Rees *et al*., 2003; Andréfouët *et al*., 2005; Gilbert *et al*., 2006).

Giant clams are an ideal organism to study how state influences risk assessment and antipredator trade-offs because it is easy to determine when the clams are feeding (shell open) versus exhibiting their antipredator response (shell closed) (Dehaudt *et al*., 2019; Soo and Todd, 2014). Within the genus *Tridacna*, *T. maxima* is the most common and widely distributed species (Rosewater, 1965). Clams are unique in that they are facultative planktotrophs and autotrophs and sequester energy through two methods: mutualistic photosynthesis and siphonic filter feeding (Kawaguti, 1950; Gwyther & Munro, 1981). For both energy-acquisition methods, the clams' mantle must be exposed to the environment. This species of Indo-Pacific clam thrives in oligotrophic euphotic zones where abundant sunlight allows the symbiont zooxanthellae (*Symbiodinium* sp.) to efficiently and effectively photosynthesize (bin Othman, Goh, & Todd, 2010; Yonge, 1975). The zooxanthellae fix carbon and provide energy to the clam (Ishikura, Adachi, & Maruyama, 1999). Studies on *T. maxima* illustrate that their symbionts contribute between 62% and 84% of the clam's total carbon requirements (Trench, Wethey, & Porter, 1981). This mutualistic relationship has enabled clams to rely on autotrophic energy sources from their endosymbionts, and without this relationship, the clams would be energy-deficient (Sutton & Hoegh-Guldberg, 1990).

Clams are sessile, and their antipredator behavior is restricted to retracting their mantle and closing their shells to protect them from predators such as triggerfish (*Pseudobalistes flavimarginatus*), octopuses (*Octopus* spp.), puffer fish (*Tetradon stellatus*), and eagle rays (*Aetobatis narinari*) (Chambers, 2007). Giant clams can detect predator stimuli through at least two mechanisms: visual (Fankboner, 1981; Wilkens, 1986) and mechanical (bites or grazes from predators) (McMichael, 1974; Morton, 1978; Soo and Todd, 2014). Clams possess several hundred pinhole eyes on their mantle that are capable of detecting light or shade (Fankboner, 1981). When the clam detects a shadow over the mantle, the mantles are withdrawn and the shells close (Land, 2003; Soo and Todd, 2014). Clam antipredator behavior becomes more costly as the duration of shell closure increases because they are not able to filter feed or photosynthesize.

Here, we conducted an experiment that used a gradient of food deprivation to determine whether giant clams' antipredator behavior is state-dependent. We deprived clams of energy by applying one of three treatments: covering clams with blackout container (blocked photosynthesis and reduced water flow), covering clams with a transparent container (reduced water flow), and a no-container control to permit normal light and flow. After the clams were subjected to the treatments for a predetermined duration of time, we rubbed the clams' mantle to simulate a predatory threat and timed the latency they took to reopen their shells. We hypothesized that after clams were subjected to a light-blocking treatment, their physiological state would be reduced, and they would have a shorter hiding time.

Materials and methods

We tested the antipredator response of giant clams on Gump Reef, a marine protected area in Moorea, French Polynesia (17°29025.0″S, 149°49033.1″W). This location was chosen due to the abundance and accessibility of giant clams.

We conducted a total of three experiments of different durations to determine whether the length of energy deprivation affected clams' hiding times. For each experiment, we covered clams with one of three treatments: black cover (no light and low water flow), transparent cover (full light but low water flow), and no cover control (regular light and flow) (Fig. S1). These clam covers were made out of 9.4 x 30.5 x 22.4 cm large rectangle Ziploc containers (Racine, WI, USA). Black covers were spray painted black with RUST-OLEUM High Heat Ultra Spray Paint (Vernon Hills, IL, USA). All covers had a ½ inch hole drilled into each of the four sides of the containers to permit water flow (to prevent hypoxia and total starvation). The covers additionally had a ¼ inch hole drilled into the four corners of each container for a cable tie to loop through the hole (for securing the treatment over the clam).

To estimate the amount of light blocked by the black and transparent covers, we used a PAR LI-COR LI-190R Quantum Sensor (Lincoln, NE, USA). We tested the treatments outside where ambient light was approximately 179 PAR. There was a 14.5% decrease from ambient light for the transparent treatment, and a 99.9% decrease in light from ambient for the black treatment. Additionally, there was a 99.9% decrease in light from the transparent treatment to the black treatment.

We quantified how the treatments influenced flow by filling a 1-mL syringe with red food dye and releasing the dye beneath the center of a clear cover, timing how long it took for the dye to completely dissipate. To eliminate observer bias, only one observer practiced with timing how long the dye took to dissipate. This was practiced away from the clams in our study but within the same area. Once the practice timings were precise, the observer timed how long the dye took to dissipate from under each treatment. They repeated this procedure for the no cover treatment and timed how long it took the same amount of dye to dissipate from where it was released in the water. They repeated this twice for each treatment. There was a 57% decrease in flow rate from no cover to covered treatment.

Because of the clams' siphonic feeding, we acknowledge that flow regime may be an important factor for giant clam settlement. However, all of our clams were spaced such that they did not cover a large area and we assumed that significant differences in flow were minor. Additionally, our analysis compared the differences in time per treatment per clam so this way, the differences in flow could be accounted for.

We located clams on dead coral mounds (hereafter referred to as a bommie). Four nails were nailed into the bommie so that a cable tie could be looped around the nail and attached to the inverted container over the clam. We identified each clam with a visible tag nailed into the bommie and ensured that the tag was far enough away from the clam to avoid triggering an antipredatory response. All clam depths were between 0.36 and 0.95 m.

We simulated a predator encounter by running a pencil's eraser side along the length of the clam's mantle and shell both forwards and backwards. Before Experiment 1 began, we observed the responses of non-experimental clams to standardize the pressure of our touches and standardized our measures of their hiding times. For Experiments 2 and 3, we only had one observer to avoid an observer effect. We defined hiding time as the time it took the clam to recover to their initial state, where the mantle was exposed to the extent that it was immediately prior to being touched. Each clam's initial state varied so we ensured to acknowledge the extent to which each clam exposed its mantle.

For Experiment 2 (multiday experiment), the clams received a new treatment in the afternoon and were stimulated the following experimental morning. Because we were testing the clams at the same times per experiment (all in the morning or all in the afternoon), the light levels may have differed between experiments, but this is insignificant as we were comparing the differences in time between each treatment per experiment.

The test began when the clam's treatment cover was removed. The jostling of the cover removal oftentimes caused the clam to close so we waited a full minute for the clam to reset and open. The observer began to time the latency as soon as the pencil left the clam's surface and timing continued until the clam returned to its initial state. As part of our initial observations, we noted that the presence of the observer had a negligible effect on the clam when over a meter away, and thus, after applying the stimuli, the observer backed up at least one meter. For Experiment 1, we had three observers and tested for observer effects; for Experiments 2 and 3, we only had one observer to avoid any possible observer effects. All data and code are in Hayes *et al.* (2020).

Experiment 1: Within-day food deprivation

We initially had a sample size of thirty clams that were given the treatments for ca. 6 h ($X \pm SD$: 6.63 ± 0.44 h, $N = 86$). However, four covers (2 black and 2 transparent) became detached, and thus, we excluded these observations from further analysis. We recorded the clam's size and depth as well as the number of conspecifics in a m^2 radius around the clam. To reduce variation, we only studied clams with a shell length between 6 and 13 cm (9.81 ± 2.05 cm).

The clams received the treatments in the morning and in the afternoon (about 6 h later) is when the covers were taken off, and we stimulated the clam. To eliminate any influence from varying factors such as depth, day in which the clam received a treatment, different flow regimes based off the settlement of the clam we used a Latin square design where clams systematically received one of the three treatments on consecutive experimental days (total of 3); each experimental day was separated by a non-experimental day. All clams, except for the individuals where a cover prematurely became detached, received all three treatments. There were three observers, and each observer tested a block of 10 different clams each experimental day. After removing the cover (or after the arrival of the observer for the control treatment), the clam was exposed to the environment. In many, but not all cases, the removal of the cover stimulated the clam, and therefore, after the removal of the treatment, we gave the clam 1 min to recover before we stimulated shell closure and measured hiding time. For Experiment 1, hiding times ranged from 6 sec to 145 sec.

We fitted a linear mixed-effects model of the $\log_{10}$ transformation of the hiding time (in sec) using the lmerTest package in R (Kuznetsova, Brockhoff, & Christensen, 2017). Fixed effects included clam size (in cm), which day/order the treatments were received for each individual clam, observer, and treatment type. While we assessed both clam depth and conspecific density, neither factor was significant, and thus, we excluded them from the model. Because we were testing the clams at the same hour per experiment (all in the morning or all in the afternoon), the light levels may have differed between experiments, but this is insignificant as we were comparing the differences in hiding time between each treatment per experiment. We included clam identity as a random effect to account for repeated observations on individuals. The no cover control was the reference level for treatment. We then ran the same model with the black cover as the reference level to test for differences between the transparent and black cover treatments. We calculated a pseudo-R^2 for linear mixed-effects models using the MuMIn package to estimate the proportion of variance explained by the random effect of individual clam (Barton, 2019). We calculated linear contrasts to compare treatments (Tukey's method) and calculated Cohen's d using the emmeans package (Lenth, 2020). We tested the assumptions of our linear mixed model by plotting the residuals (they were approximately normal), Q-Q plots (they were straight), and fitted values versus residuals (there was no pattern). All figures were generated using the plotly package in R (Sievert, 2018) and exported with the orca package (Hocevar & Demsar, 2016).

Experiment 2: Multiday food deprivation

We sampled 30 new clams for Experiment 2 (size: 8.05 ± 1.25 cm). For the first two days of Experiment 2, thirty clams were covered for 42–46 h (44.5 ± 1.94 h, $N = 59$; one clam was excluded after its transparent cover became detached). Similar to the first experiment, we used a Latin square design where clams systematically received one of the three treatments on consecutive experimental days. However, in this experiment and unlike Experiment 1, we deployed a new treatment immediately after measuring hiding time, and therefore, the clams received a new treatment in the afternoon and were stimulated the following experimental

morning. This was done for the first and second experimental day. This change in experimental design had potential to influence the results and was accounted for in our models by including experimental day. However, a large storm struck on the third experimental day, creating a large plume of terrestrial runoff that made the water opaque and therefore impossible to locate or study the clams. We had to wait for three additional days to re-test clams which meant that this third block of treatments was more than twice as long as the first two (104.45 ± 0.147 h, $N = 27$; three clams were excluded from the analysis after their covers detached (two black and one transparent)). Due to this disturbance, we elected to analyze our data in two parts: with and without the third block. For Experiment 2, hiding times ranged from 3 sec to 205 sec.

Analysis was identical to that in Experiment 1, and here too, we found that histograms of the residuals were approximately normal, Q-Q plots were straight, and there were no patterns between fitted values versus residuals. Because we only had one observer, we did not include the observer in our analysis.

Experiment 3: Longer-term food deprivation

We designed Experiment 3 to test the hiding times after a longer-term deprivation. To reduce potentially harmful effects on the clams, we chose to only use 11 clams (7.82 ± 1.23 cm) and restricted the experiment to one round. We deployed the treatments for 134 h (134.0 ± 0.07 h, $N = 11$) before measuring clam hiding time. For Experiment 3, hiding times ranged from 8 sec to 92 sec.

We fitted a linear model of the $\log_{10}$ transformation of the hiding time after the treatment was removed with fixed effects including clam size (in cm), and treatment type using the lmtest package in R (Zeileis & Hothorn, 2002). To test for assumptions, we analyzed the histogram of the residuals (approximately normal), ensured the Q-Q plot was straight, and acknowledged that there were no patterns between fitted values versus residuals.

Results

Experiment 1: Within-day food deprivation

There was no significant difference between the $\log_{10}$ of clam hiding time (ok looking a) as a function of treatment (Table 1; Fig. 1). Observer 2 was significantly different from observers 1 and 3 (Table 1). The random effect of clam identity explained roughly 17.5% of variance.

Experiment 2: Multiday food deprivation

There was no significant difference between the $\log_{10}$ of hiding times (in sec) between the control and the transparent cover treatment for the first two experimental days (Table 2a). However, the black cover treatment was significantly different from both the transparent treatment and the control (Fig. 2a). Hiding times increased in an approximately stepwise manner (Fig. 2a).

Table 1 Results from linear mixed-effects model explaining the difference in the $\log_{10}$ duration of clam hiding time (in sec) following treatment for Experiment 1

Fixed Effects	Estimate ± SE	*t*	*P*
Intercept	1.178 ± 0.202	5.835	<0.001
Observer: 2	0.153 ± 0.062	2.468	0.017
Observer: 3	−0.109 ± 0.064	−1.702	0.095
Size	0.015 ± 0.018	0.851	0.402
Day	−0.028 ± 0.031	−0.878	0.384
Treatment: Transparent	0.039 ± 0.063	0.615	0.541
Treatment: Black	−0.017 ± 0.063	−0.270	0.788

Random Effect	Variance	SD
Individual Clam	0.016	0.126

No cover control is the reference level for treatment. Observer 1 is the reference level for observer. $N = 86$.

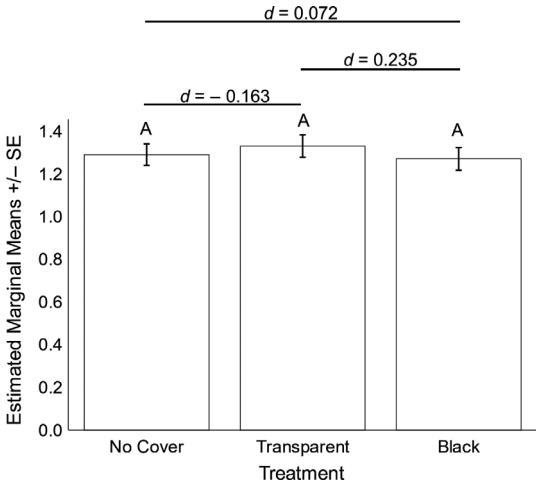

Figure 1 Estimated marginal means (±1 SE) of the $\log_{10}$ of clam hiding time (in sec) from Experiment 1. Letters above each bar signify statistically indistinguishable differences in the log10 of hiding times between treatments by *P*-value. Cohen's *d* values indicate the effect size between treatments.

The random effect of clam identity explained roughly 5.4% of the variance for the two-treatment block. Including the third treatment block revealed a significant difference in the $\log_{10}$ of hiding times between the control, transparent, and black treatments (Table 2b) and hiding times progressing upward in a stepwise manner (Fig. 2b). Approximately 13.5% of the variance for all three blocks was explained by the random effect of clam identity.

Experiment 3: Long-Term Deprivation

There was no significant difference in the $\log_{10}$ of clam hiding time as a function of treatment (Table 3; Fig. 3). However, treatments retained an approximately stepwise increase in hiding time (Fig. 3).

Table 2 Results from linear mixed-effects model explaining the difference in the $\log_{10}$ duration of clam hiding time (in sec) following treatment for (a) Experiment 2.1 and (b) Experiment 2.2

Fixed Effects	Estimate ± SE	*t*	*P*
a			
Intercept	0.553 ± 0.312	1.772	0.084
Size	0.065 ± 0.035	1.858	0.073
Day	0.012 ± 0.079	0.150	0.881
Treatment: Transparent	0.189 ± 0.099	1.910	0.063
Treatment: Black	0.491 ± 0.097	5.040	<0.001
Random Effect	Variance		SD
Individual Clam	0.008		0.089
b			
Intercept	0.412 ± 0.287	1.435	0.160
Size	0.077 ± 0.034	2.288	0.030
Day	0.065 ± 0.039	1.673	0.100
Treatment: Transparent	0.171 ± 0.077	2.211	0.031
Treatment: Black	0.427 ± 0.076	5.596	<0.001
Random Effect	Variance		SD
Individual Clam	0.020		0.141

No cover control is the reference level for treatment.
$N = 59$ for Exp. 2.1 and $N = 86$ for Exp. 2.2.

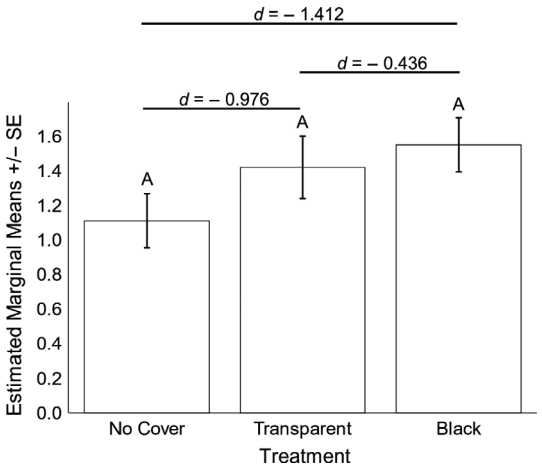

Figure 3 Estimated marginal means (± 1 SE) of the $\log_{10}$ of clam hiding time (in sec) from Experiment 3. Letters above each bar signify statistically indistinguishable differences in the $\log_{10}$ of hiding times between treatments by *P*-value. Cohen's *d* values indicate the effect size between treatments.

Discussion

As predicted, we found that reducing the clams' ability to acquire energy modified their antipredator behavior and this effect was dependent on both treatment type and experiment length. However, the effect of treatment type was opposite to our predictions; shaded clams had longer average hiding times than those with transparent covers, which had longer average hiding times than those with no cover. Interestingly, this stepwise pattern was only observable when clams were subjected to long periods of energy deprivation—over six hours. Prior work has shown that giant clams can survive being closed for at least 72 h (Fankboner, 1971).

We analyzed our disturbed Experiment 2 in two ways, with and without the third block, and learned two things. First, when we analyzed without the third block, there were significant differences between the hiding times of clams with transparent and black treatments as well as no cover and black treatments. However, hiding times of clams with transparent and no cover treatments were not significantly different. This shows that photosynthesis deprivation (black cover) impacted clam energetics on the 44-h timescale, but flow (the main difference between transparent and no cover) was not as important on this timescale. When including the third block where the deprivation time was greatest, all treatments were significantly different from each other. This shows that as light deprivation is prolonged, flow becomes a more important factor in energy acquisition. Interestingly, there was no significant treatment effect in Experiment 3 (134-h treatment). However, this is likely due to the experiment being conducted on a small sample of clams, as the effect size was similar to Experiment 2. To explain these findings, we believe there are at least two proximate and one ultimate explanation for our results: (1)

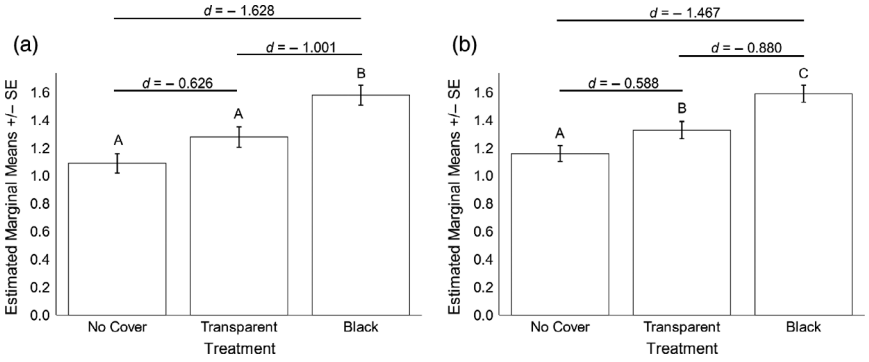

Figure 2 Estimated marginal means (±1 SE) of the $\log_{10}$ of clam hiding time (in sec) from Experiment 2.1 (a) and Experiment 2.2 (b). Letters above each bar signify statistically indistinguishable differences in the $\log_{10}$ of hiding times between treatments by *P*-value. Cohen's *d* values indicate the effect size between treatments.

Table 3 Results from linear model explaining the difference in the $\log_{10}$ duration of clam hiding time (in sec) following treatment for Experiment 3

Fixed Effects	Estimate ± SE	*t*	*P*
Intercept	2.000 ± 0.653	3.063	0.018
Size	−0.114 ± 0.080	−1.415	0.200
Treatment: Transparent	0.305 ± 0.239	1.277	0.242
Treatment: Black	−0.442 ± 0.222	1.995	0.086

No cover control is the reference level for treatment. $N = 11$.

circadian rhythm changes due to the cover being perceived as night, (2) reduced energy reserves from food deprivation, and (3) error management theory.

Giant clams have a distinct circadian rhythm and are often inactive and lethargic at night (Soo & Todd, 2014). We hypothesize that the clams responded to the dark treatment as 'night' and the no cover and transparent treatments as 'day'. Because day length at this latitude is ~12 h, this may explain the results from the six-hour treatment as not sufficiently long to induce circadian changes. However, in Experiments 2 and 3 when the covers were deployed for over 12 h, the clams' behavior changed. While this circadian hypothesis is possible, because it could not explain the difference between the transparent and no cover treatments (flow), we think it is unlikely and rather we think an energetic mechanism is more likely.

The clams may have alternatively been energy-deprived with longer hiding times being attributable to having fewer energy reserves compared with the control clams. In a past study on scallops (*Pecten maximus*), individuals moved for less than two minutes a day, but this accounted for approximately 29.3% of their daily energy expenditure (Robson *et al.*, 2012). For these bivalves, small movements may be extremely costly. While little literature is available on clam energetics, movement (mantle retraction and shell closing) may be relatively energetically costly. When the mantle is exposed, the clams aerobically respire but if the shells are closed for longer than a couple minutes, they must switch to anaerobic respiration (Ortmann & Grieshaber, 2003). Anaerobic respiration provides clams with 80% less energy when compared to aerobic respiration, and thus, when the clamshells are closed, their energy may become compromised (Ortmann & Grieshaber, 2003). Additionally and importantly, giant clams receive up to 84% of their energy stores from their photosynthetic symbionts (Trench *et al.*, 1981). When these symbionts cannot photosynthesize (compounded with the clams experiencing a decrease in filter feeding from restricted water flow), the clams become energy-deficient. This information is important because it explains why hiding times are higher for the black treatment than the transparent treatment, because the black cover blocked both photosynthesis and flow, while transparent containers only blocked flow. This stepwise exclusion of energy explains the stepwise increase in hiding time seen in Experiments 2 and 3, while the lack of significance from Experiment 1 is because the clams were not deprived long enough.

To be clear, the clams initially responded to us when we approached them, and in all cases (control, clear, black), we were at the same distances from the clams. However, it is possible that the act of removing the covers caused a greater disturbance. In all cases, we waited the same amount of time (1 min) before experimentally touching the clam. If there was a carryover effect, it might drive a difference between the two treatments and the control. However, this would not explain any difference between the clear and black covers. Given that we saw a significant difference between the clear and black treatments in Experiment 2 and the same trend in Experiment 3, we can assume that our food deprivation treatments had a larger effect than the clams closing when we approached them or what was caused by removing the cover in two of the treatments.

Revisiting our initial hypothesis of state-dependent risk assessment, we acknowledge that while energy influenced clam decisions, our specific results differed from both our initial prediction and past literature. At a functional level, energy-deprived clams may have spent more time hiding because of the risks to reemerge. Thus, we may be able to explain their response using error management theory (Haselton & Buss, 2000).

Error management theory explains how decisions are made while in a state of uncertainty and how the costs of false-positive and false-negative outcomes are weighed (Johnson *et al.*, 2013). Error management theory acknowledges that there is a bias toward making the least costly choice (Johnson *et al.*, 2013). Clams can make one of two errors: false positives (remaining closed when there is not a predator) or false negatives (opening when there is a predator). Giant clams may bias their risk assessments toward false positives because animals who overestimate the risk of a predator may have a lower risk of mortality or injury rate (Bouskila & Blumstein, 1992; Johnson *et al.*, 2013). The clams in our experiments may have attempted to minimize false-negative outcomes by waiting longer to reemerge even if the predator is gone. An energy-compromised clam may avoid wasting energy opening and reclosing if a predator is still present by remaining closed longer. On the other hand, clams can deplete their reserves and may not have enough energy to afford so many false positives. Clams may reach a tipping point where the trade-off for food becomes more important than safety. The positive trend we saw for Experiments 2 and 3 would eventually hit a ceiling and begin decreasing, and clams would open faster. This could explain the lack of significance in Experiment 3, and we could have been in this potential tipping point area.

In many animals, antipredator behavior involves having the option to flee and choose a different place to hide, but sessile clams only have two options: shooting a stream of water at predators from their siphon (Stasek, 1965) or retracting their mantle and closing their shell (Morton, 1967). Despite having few antipredator tactics, we conclude that giant clams risk assessment changes according to their physiological state, and they are more cautious opening when energy deprived. This is contrary to a common finding that hungrier animals take greater risks for food. This may be attributed to the fact that clams and other sessile organisms do not have the ability to flee from predators, which may explain our findings that seemingly contradict what has been reported in other species.

Further study of sessile invertebrates may reveal that this to be a common strategy.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Left: no-cover control treatment; middle: transparent cover treatment; right: black cover treatment.