


ORIGINAL RESEARCH

Nutrient enrichment alters risk assessment in Giant clamsB. E. Barbee*, M. K. R. Lin*, I. A. Min*, A. M. Takenami*, C. S. Philson & D. T. Blumstein 

Department of Ecology and Evolutionary Biology, University of California at Los Angeles, Los Angeles, CA, USA

Keywordsrisk assessment; anti-predator behaviour; nutrient enrichment; *Tridacna maxima*.**Correspondence**

Daniel T. Blumstein, Department of Ecology and Evolutionary Biology, University of California at Los Angeles, 621 Young Drive South, Los Angeles, CA 90095-1606, USA.

Email: marmots@ucla.edu

*These authors have equal authorship.

Editor: Gabriele Uhl

Associate Editor: Lauren Des Marteaux

Received 3 March 2022; revised 13 September 2022; accepted 23 September 2022

doi:10.1111/jzo.13030

Abstract

Many species exhibit state-dependent risk assessment. Photosynthetic giant clams (e.g. *Tridacna maxima*) retract their mantles and close their shells as an anti-predator response. Although being open allows clams to photosynthesize or siphon-feed, staying open increases vulnerability to predation. Prior studies indicate that giant clam risk assessment is state-dependent. Hiding time differs based on body condition, shown by the light deprivation of clams for varying amounts of time. Nutrient enrichment has been shown to impact giant clam growth and photophysiology through their symbiotic zooxanthellae (*Symbiodinium* sp.). Although previous work by Hayes et al. (2021) examined risk assessment in light-deprived giant clams, nutrient enrichment and its potential effects on giant clam risk assessment are unstudied. Here, we tested whether nutrient enrichment would alter risk assessment of giant clams by conducting two experiments that quantified hiding time for nutrient-enhanced clams and two control treatments following an experimentally induced mantle closure: one with a singular simulated predator probe per trial and then with repeated simulated predator probes in the same trial. In our single predation probe experiment, nutrient-enriched clams significantly increased their hiding time over multiple days. Nutrient-enrichment did not, however, modify their response to repeated probes. Overall, our results support that nutrient enrichment modulates clam risk assessment. This indicates support for prior state-dependent risk assessment literature, suggesting nutrient enriched clams will take less risks to forage. This is in direct contrast to results found by Hayes et al. (2021) that suggested that energetically depleted clams were taking less risks to forage, warranting additional research into the mechanisms behind clam energetics and behaviour.

Introduction

An individual's energetic state often influences their predation risk assessment (Anholt & Werner, 1995; Fraser & Huntingford, 1986; Lima, 1998). Individuals with different satiation levels, and therefore varying nutritional demands, often alter their foraging decisions when encountering a predatory threat. For example, starved wolf spiders (*Pardosa milvina*) forage more compared to satiated spiders under periods of increased predation risk (Walker & Rypstra, 2003). Alternatively, starved common water frog tadpoles (*Pelophylax kl. esculentus*) forage significantly less than satiated tadpoles in the presence of predatory threats (Gazzola et al., 2018). Regardless of the exact response, such state-dependent anti-predator responses should permit individuals to maximize their fitness under different environmental conditions.

Giant clams, a sessile marine invertebrate, are an ideal species to study risk assessment because they retract their mantle and close their shell under predatory threat. Predators of giant clams include triggerfish (*Pseudobalistes flavimarginatus*), octopi

(*Octopus* spp.) and eagle rays (*Aetobatis narinari*) (Chambers, 2007). Giant clams can detect predators visually by detecting light or shade with several hundred pinhole eyes on their mantle as well as mechanically from bites or grazing from predators (Fankboner, 1981; Soo & Todd, 2014; Wilkens, 1986). Because giant clams must expose their mantles for photosynthesis and siphon-feeding, anti-predator behaviour is costly because it consumes energy stores and directly limits energy acquisition (Hayes et al., 2021; Johnson et al., 2017; Todd et al., 2009). Following a threat, giant clams must determine how long to remain closed in a way that minimizes their predation risk while optimizing foraging times (Doyle et al., 2020).

Photosynthetic animals in oligotrophic reefs, such as giant clams and corals, are affected not only by light availability but also nutrient availability (Middlebrooks et al., 2011; Titlyanov et al., 2000). The majority of giant clam nutrition is supplied through their symbiotic relationship with the photosynthetic dinoflagellate zooxanthellae, which transfer photosynthates that include glucose, oligosaccharides, and other amino acids to their hosts (Lucas, 1994).

Previous studies showed that nutrient availability affects zooxanthellae development (Ambariyanto & Hoegh-Guldberg, 1996; Belda *et al.*, 1993; Fitt *et al.*, 1993; Klumpp & Lucas, 1994). When nutrient-enriched, giant clam zooxanthellae density increases significantly, while individual zooxanthellae cell volume shrinks (Ambariyanto & Hoegh-Guldberg, 1996; Fitt *et al.*, 1993). Nitrogen is the primary driver of increased zooxanthellae growth with phosphorus having an additive effect only when used in conjunction with nitrogen Belda *et al.*, 1993. This zooxanthellae growth enhances photosynthetic activity, and should therefore result in an increased clam energetic state.

We conducted an experiment to directly test whether nutrient addition modified giant clam risk assessment. We enriched giant clams with nutrients to manipulate their energetic state, and compared them to control treatments to investigate state-dependent risk assessment. It was difficult to make an *a priori* prediction about their response to enrichment because previous energetic state manipulations in marine invertebrates contradict traditional models of state-dependent risk assessment where starved animals take more risks while foraging. Hayes *et al.* (2021) observed that light-deprived clams, which they inferred had reduced energy reserves, increased their hiding time in response to a simulated predatory threat. Similarly, Dill and Fraser (1997) observed that tube-dwelling polychaetes increased hiding times when starved and decreased hiding times when provided with more food. Given that nutrient enrichment increases zooxanthellae density and presumably giant clam energetic state, we expected that nutrient enriched clams would decrease their hiding times. However, an alternate hypothesis based on traditional models of state-dependent risk assessment would suggest that enriched, and therefore presumably energetically replete clams, would increase their hiding time to avoid the additional predation risk from remaining open (McNamara & Houston, 1986).

To investigate these opposing hypotheses, we asked whether nutrient enrichment increases giant clam energetic state by conducting a second experiment. Nutrient enrichment has been shown to increase zooxanthellae density, but it is unclear how much an increase in zooxanthellae density affects clam energetic state. Robson *et al.* (2012) estimates that scallops (*Pecten maximus*), an active marine bivalve that rapidly opens and closes their shell to move, consume 20–40 per cent of their daily energy reserves moving. For giant clams, mantle retractions are likely energetically costly and repeated retractions should rapidly consume energy reserves, though the exact energy required for a mantle retraction is unknown. At low enough energy levels, clams should delay reopening because they do not have the energy required to retract again. To investigate this relationship, we repeatedly induced clam mantle retractions to induce exhaustion and quantified hiding times. If nutrient enrichment increases giant clam energetic state, then nutrient-enriched clams should take longer to reach an exhaustion threshold, or not reach exhaustion at all. Therefore, the hiding times of nutrient-enriched clams should increase more slowly than that of non-enriched clams or not change over successive probes.

Materials and methods

Data collection

We studied giant clam risk assessment on Gump Reef, Cooks Bay, a marine protected area in Moorea, French Polynesia (17°29'02.5" S, 149°49'03.1" W). The location was chosen due to its abundant and accessible giant clams. We tested 60 clams between 21 and 31 January 2022. Starting from 21 January 2022 as day 0, experiments were carried out once every other day for an additional 5 experimental days. Clams were found on outcrops of dead coral reef (hereafter “bommies”) along the fringing reef and occurred at 0.18–1.03 m deep and had a shell diameter range between 4.5 and 15.5 cm. To avoid spillover effects between clams, subjects were ≥ 2 m apart (e.g. Fong *et al.*, 2018). Clams were marked with a flagged nail in the bommie that was placed far enough away from the clam such that it would not trigger an anti-predator response. Clam size and depth from the water surface were recorded initially. On each experimental day, wind was scored using the Beaufort scale. Clams were identified by numbers which were randomly assigned to either our one treatment or two control groups. Nutrient enrichment (hereafter +N) was administered by adding 93 g (weighed out on an Ohaus Compass CX621 scale) of Osmocote slow-release fertilizer (N-P-K Ratio: 15-9-12), poured into a nylon sock, and zip tied to a nail next to (ca. 10 cm) the clam. The clams were given a 2 days acclimation period prior to experimental probing. Possible effects of physical disturbance from a novel object near the clams were accounted for with an experimental control, where nylon socks were filled with gravel rocks; this is referred to as +R. Gravel was rinsed with fresh water and placed into the nylon socks until the socks were approximately the same size as +N socks. Our control group (C) received no sock and was only flagged for subject identification.

Experiment 1: single predation probe

Prior to the first experiment, we conducted a pilot survey of non-experimental clams and observed responses to simulated predation tests to standardize the probing procedure. Before starting an experiment, we waited until the clam was relaxed which we defined as the shell being open and the mantle extended. Following previous studies (Doyle *et al.*, 2020; Hayes *et al.*, 2021; Johnson *et al.*, 2017), we ran the eraser end of a No. 2 pencil along the full length of the clam’s mantle and shell which prompted the clam to retract its mantle into its shell. Following this, the observer moved ≥ 1 m away from the subject to avoid presenting any on-going predatory threat. We recorded the clam’s hiding time, which began immediately after the pencil left the clam’s surface and ended when the clam returned to its initial state of opening. Clams were selected and numbered along a transect parallel to the shore, where probing would begin on either end of the transect, alternating on each experimental day. We initially had a sample size of 60 clams, however, between experimental days 4 and 5, one clam was naturally preyed upon. We conducted

predation probes once every other day from 07:30 h to 12:00 h for a total of 6 experimental days. To avoid observer effects, the same observer conducted all probes.

We fitted a Gaussian linear mixed effects model with a \log_{10} transformation on our dependent variable, hiding time in seconds, using lme4 (Bates *et al.*, 2015) and the lmerTest package in R (Kuznetsova *et al.*, 2017). The fixed effects included in the model were: treatment, scaled clam size (cm), scaled clam depth (cm), the number of days into the experiment, the interaction of treatment with size and the interaction of treatment with the number of days into the experiment. Scaling was conducted to standardize data to a normal distribution by centring and dividing the data by one standard deviation. We included clam identity as a random effect to account for expected individual differences in hiding times. We compared a null model (without clam identity as a random effect), using an ANOVA, to this random intercept model and found that the random intercept model was significantly different than the null model ($P = 0.048$) with a substantially lower Akaike information criterion (AIC). We attempted to fit a random slope model to test for individual differences in the response to treatments in hiding time over the experimental days but were unable to do so because of a singular fit error (Bates *et al.*, 2015; Matuschek *et al.*, 2017). Therefore, we used the random intercept only model for simplicity and interpreted the interaction between experimental day and treatment to test for the average slope. To test the fit of our Gaussian model, we attempted to fit and compare a model with a Poisson distribution. Observing overdispersion in the Poisson model, we proceeded to use a Negative Binomial model. We compared the fit of residuals using a QQ plot and AIC values between our Gaussian and Negative Binomial models. Noting that the fit was better and that the AIC was lower in our Gaussian model, we only used the original Gaussian model with a random intercept in our analysis.

We set our alpha to 0.05 and, using the partR2 package (Stoffel *et al.*, 2021), report marginal and conditional partial R^2 values for our model, and estimated P -values for variables in the model using the car package (Fox & Weisberg, 2019). Because we had a significant interaction between treatment and experimental day, we compared the pairwise estimated marginal means of linear trends (with a Tukey's adjustment) using the emmeans package (Lenth, 2022).

Experiment 2: repeated predation probes

Following the first experiment, on 31 January 2022, we conducted a second study where we repeatedly probed individuals to examine whether the nutrient addition treatment, after 10 days of exposure, influenced giant clam stamina. Due to the potential physiological stress of repeated probing on the clams, we reduced our sample size to 45 clams for this experiment and limited the trial to a single round. Three observers conducted four consecutive probes to each subject. To minimize inter-observer variability from obscuring treatment effects, each observer probed 15 clams each with the same ratio of treatments (5 +N, 5 +R, 5 C). Hiding time was recorded for

the initial probe and each successive probe. After clams reopened to their initial state, observers waited 30 s before initiating another probe.

Similar to the first experiment, we explained variation in \log_{10} hiding time with a Gaussian linear mixed effects model with a random intercept. Similar fixed effects were included, where continuous variables were scaled and experimental day was replaced by probe number (because here we were looking for changes in hiding time over successive probes). Since this experiment contained multiple observers, we tested for observer differences; we found significant differences in average hiding time across observers (ANOVA $P = 0.005$). Therefore, we included observer identity as an additional fixed effect in our model to account for this variation. As with the first experiment, and for the same singularity reasons, we were unable to fit a random slope and thus only report the random intercept results. Since the variance and mean in our data were not similar, we expected overdispersion in a Poisson model similar to the first experiment and opted to test the fit of the Gaussian model against a Negative Binomial model by fitting residuals and comparing AICs. With lower AICs and a better fit of residuals, we opted to also use a Gaussian model for the analysis in this experiment. R^2 values were reported using the partR2 package (Stoffel *et al.*, 2021). The P -values on the fixed effects of the model was estimated using the car package (Fox & Weisberg, 2019).

Results

Experiment 1: single predation probe

The fixed and random effects together accounted for 38% of the variation in clam hiding time. We found significant effects of size, experimental day, and the interaction between treatment and experimental day on \log_{10} hiding times of clams (Table 1). Clam size was positively associated with hiding time (estimate = 0.051 ± 0.012 SE, $P < 0.001$). We found that the +N treatment by experimental day interaction was positively associated with hiding time (estimate = 0.036 ± 0.007 SE, $P < 0.001$). This was because the hiding time of the +N treatment was significantly greater than the control groups (+R, C) by the last experimental day but we found no significant difference between control groups (Table 2).

Experiment 2: repeated predation probes

The fixed and random effects together accounted for 65.63% of the variation in observed clam hiding time across multiple probes, but there was no significant effect of treatment on hiding time directly or through an interaction (Table 2; Fig. 1). Size, observer, and depth all explained significant variation in clam hiding time (Table 2). Clam size was positively associated with hiding time (estimate = 0.074 ± 0.039 SE, $P = 0.002$). Depth was negatively associated with hiding time (estimate = -0.047 ± 0.039 SE, $P = 0.002$).

Table 1 Results (fixed and random effects) from a Gaussian model explaining the log₁₀ hiding times (s) in experiment 1

| Fixed effects | Chi-squared | <i>P</i> -value | Marginal part. <i>R</i> ² | Conditional part. <i>R</i> ² |
|----------------------------|-------------|-----------------|--------------------------------------|---|
| Treatment | 4.223 | 0.121 | 0.006 (0.000–0.126) | 0.055 (0.000–0.175) |
| Scaled (size) | 47.172 | <0.001 | 0.000 (0.000–0.120) | 0.048 (0.000–0.169) |
| Experimental day | 78.563 | <0.001 | 0.000 (0.000–0.120) | 0.048 (0.000–0.169) |
| Scaled (depth) | 0.025 | 0.875 | 0.001 (0.000–0.121) | 0.048 (0.000–0.170) |
| Treatment*scaled (size) | 0.596 | 0.743 | 0.104 (0.039–0.210) | 0.153 (0.025–0.268) |
| Treatment*experimental day | 25.228 | <0.001 | 0.189 (0.128–0.285) | 0.237 (0.119–0.345) |
| Random effect: | | Variance | SD | — |
| Individual ID | (Intercept) | 0.001 | 0.027 | — |

Table 2 Results (fixed and random effects) from a Gaussian model explaining the log₁₀ hiding times (s) in experiment 2

| Fixed effects | Chi-squared | <i>P</i> -value | Marginal part. <i>R</i> ² | Conditional part. <i>R</i> ² |
|-------------------------|-------------|-----------------|--------------------------------------|---|
| Treatment | 2.246 | 0.325 | 0.009 (0.000–0.281) | 0.361 (0.156–0.522) |
| Scaled (size) | 9.305 | 0.002 | 0.000 (0.000–0.274) | 0.352 (0.145–0.515) |
| Probe | 2.597 | 0.107 | 0.000 (0.000–0.274) | 0.352 (0.145–0.515) |
| Observer | 7.392 | 0.025 | 0.072 (0.000–0.333) | 0.424 (0.242–0.575) |
| Scaled (depth) | 5.536 | 0.019 | 0.054 (0.000–0.318) | 0.406 (0.217–0.560) |
| Treatment*scaled (size) | 0.610 | 0.737 | 0.130 (0.055–0.383) | 0.482 (0.317–0.623) |
| Treatment*probe | 2.806 | 0.246 | 0.031 (0.000–0.289) | 0.382 (0.186–0.541) |
| Random effect: | | Variance | SD | — |
| Individual ID | | 0.014 | 0.118 | — |

Discussion

Nutrient enrichment altered giant clam anti-predator behaviour over time as seen by the significant interaction between treatment and experimental day. This is consistent with giant clam risk assessment being state-dependent. Overall, clam hiding time decreased over the course of the experiment regardless of treatment (Fig. 2) which is likely explained by clams habituating to repeated experimental probes because these manipulations were not associated with a true predatory threat (Dehaudt *et al.*, 2019).

Contrary to our prediction of shorter hiding times, clams that received additional nutrients had significantly longer hiding times over time compared to clams without nutrient enrichment. This finding is not consistent with the observation by Hayes *et al.* (2021) that energetically limited clams had longer hiding times. Fundamental differences in experimental design should be noted. The study conducted by Hayes *et al.* (2021) sought to deprive clams of energy through light manipulation, while the clams in our study were enriched with nutrient supplementation. Therefore, the non-light deprived control group of clams in Hayes *et al.* (2021) were more energetically comparable to the unenriched clams in our study. Thus, the energetically limited clams in Hayes *et al.* (2021) and the energetically limited clams in our study had fundamentally different energetic states.

Light deprivation in giant clams can create physiological constraints and lead to behavioural responses. First, Hayes *et al.* (2021) alluded to the idea that the “shaded” treatment used to reduce giant clam photosynthesis in their experiment

may have had an effect on clams’ circadian rhythms. Shaded clams potentially responded to the lack of light as “night-time,” and Soo and Todd (2014) described how giant clams are often lethargic and inactive during the night. Second, shaded clams in Hayes *et al.* (2021) may have been so energetically limited that basic movements, such as mantle retractions, were not physiologically possible. This could explain why energetically limited clams in Hayes *et al.* (2021) did not respond according to traditional risk assessment models. The methodological distinction between light deprivation and nutrient enrichment could have led to the seemingly contradictory results between our study and Hayes *et al.* (2021). Further research should investigate changing diel light cycles on clam behaviour and the specific energetic requirements of mantle retractions.

Our finding aligns with traditional models of risk assessment where individuals with higher satiation levels, and presumably higher energetic states, will take fewer risks while foraging (McNamara & Houston, 1986). This model has been supported by multiple studies across taxa. For instance, hungry graybelly salamanders (*Eurycea multiplicata griseogaste*) attacked prey faster than satiated salamanders in the presence of predatory stimuli (Whitham & Mathis, 2000). Similarly, well-fed earthworms (*Lumbricus terrestris*) took fewer risks while foraging (Sandhu *et al.*, 2018).

In our second experiment, we tested whether manipulating an energetic state would modify clam risk assessment of repeated probes in a trial that was designed to fatigue the clams. Compared to the single predation probe experiment, this experiment was a more direct test of the inference that we had

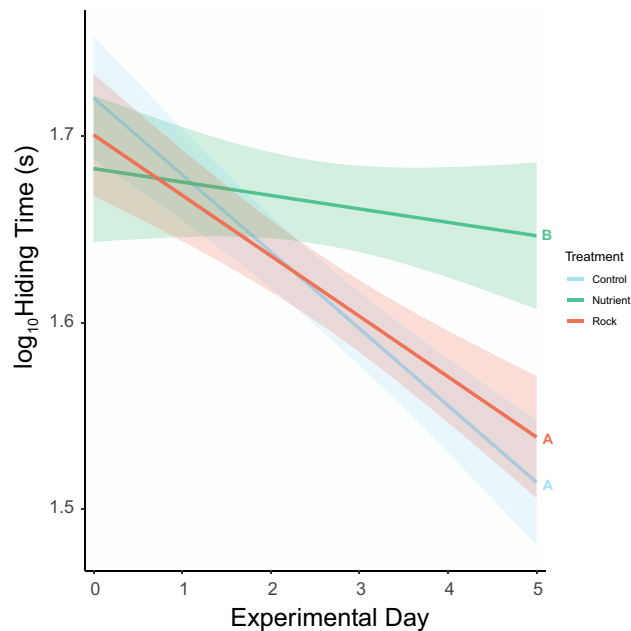


Figure 1 Interaction plot of giant clam hiding time across experimental days. Lines illustrate average response by treatment (+N, +R, C), shaded areas represent 95% confidence interval of associated line. Letters adjacent to each line represent statistically significant differences in the \log_{10} hiding times between treatments by experimental day ($P < 0.001$). “A” indicates statistically indistinguishable treatments, while “B” corresponds to a significantly different treatment.

manipulated clam energetic state through nutrient enrichment. We hypothesised that clams at lower energetic states would remain closed for longer durations as they would not have the energy required to rapidly open and close. Previous research has shown that clams with lower energetic states due to parasitic infestations would remain closed for shorter periods of time, returning to a “gaping” posture more quickly as a result of weakened adductor muscles (Ellis, 2000). However, we found no significant effect of treatment on hiding time after multiple probes, so we could not confirm any modifying effect of nutrient enrichment on clam energetic state and neither claim was supported.

Our nutrient manipulation was an indirect method to manipulate clam energetic state. Since zooxanthellae are symbionts, they rely on their host, the clam, for nutrients siphoned out of the water column (Norton et al., 1992). Clams are capable of exerting control on zooxanthellae growth by limiting access to certain nutrients and expelling excess algal symbionts as waste (Belda et al., 1993; Muscatine & Pool, 1979). Nutrient enrichment, in the form of ammonium and phosphate, has been observed to increase zooxanthellae numbers and size, while the chlorophyll *a* levels of each individual zooxanthellae decreases (Belda et al., 1993). Despite the smaller size and decreased chlorophyll *a* content of an individual zooxanthellae, the overall photosynthetic rate of the clam ultimately increases given enough time (Belda et al., 1993). Belda et al. (1993) observed

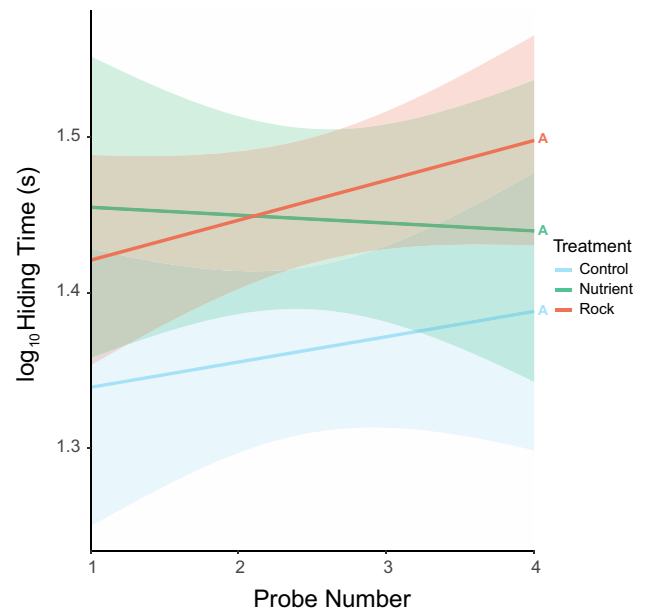


Figure 2 Giant clam hiding time across successive probes. Lines illustrate average response by treatment (+N, +R, C), shaded areas represent 95% confidence interval of associated line. Letters adjacent to each line signify statistically indistinguishable differences in the \log_{10} of hiding times between treatments by probes ($P > 0.05$). “A” indicates statistically indistinguishable treatments.

a doubling of the zooxanthellae population in clams enriched by both ammonium and phosphate over 7–12 days, a relatively rapid shift in growth strategy. However, it is unclear how quickly clams begin to retain more zooxanthellae to increase their density (Belda et al., 1993). If in the initial stages of nutrient enrichment giant clam hosts continue to expel algal symbionts at the same rate prior to nutrient enrichment there may not be enough of a net gain in zooxanthellae density to achieve a threshold level that would lead to a marked increase in photosynthetic activity. Because previous work on nutrient enrichment in clams were conducted over a longer time scale, the relatively short duration of our experiment may have limited this increase in energetic state (Ambaryanto & Hoegh-Guldberg, 1996; Belda et al., 1993; Hastie et al., 1992). Therefore, we may not have seen as large of an increase in energetic state as possible because the difference in energetic state may become more pronounced given more time and nutrient exposure. For our second experiment, this minimal increase in energetic state may not have been sufficient to create an observable difference to repeated mantle retractions, which we assumed are relatively more costly than a single retraction and closure. In contrast, the single retractions studied in our first experiment may have been more sensitive to the variation in energetic state created by the nutrient addition.

Further study is warranted to examine the response of giant clams and their algal symbionts to nutrient enrichment. Minimally invasive repeated tissue sampling over months could quantify changes in zooxanthellae density following nutrient enrichment (Bucciarelli et al., 2014). Studies using respirometry

techniques could further quantify changes in photosynthetic rate, and therefore energetic state, during this same period (Anthony & Hoegh-Guldberg, 2003).

Further study of giant clam and other marine invertebrate behaviours under nutrient-rich conditions is necessary among continuing environmental changes. Anthropogenic land use and rainfall events can drive fluxes of nutrient and sedimentation in marine ecosystems (Fabricius, 2005; Fong *et al.*, 2020). Particularly, increased rainfall flushes sediments from deforested and agricultural lands, leading to large eutrophication events (Maina *et al.*, 2013). The addition of excess nutrients can lead to harmful effects on coral reef systems, including algal blooms and oxygen minimum zones (Bell, 1992; Hallegraeff *et al.*, 1995; Hallegraeff, 2003). Although run-off may generate pulses of nutrients to the reef that enhance the growth of giant clams and other photosynthetic organisms, it can also limit light penetration because sediment and algal blooms increase water turbidity (Sanseverino *et al.*, 2016). Following a 10-day storm, a recent study in Moorea found dissolved nitrite and nitrate concentrations in the reef to be more than 100 times higher than average, and phosphate concentrations to be 25 times higher than average (Fong *et al.*, 2020). As agricultural land use increases and climate change predictions suggest that extreme rainfall events will become more frequent, it is vital to understand the effects of nutrient run-off on the behaviour of giant clams, and, by extension, coral reef ecosystems.

Acknowledgements

We thank the UC Berkeley Gump South Pacific Research Station for logistical support, the government of French Polynesia for research permits, the UCLA Department of Ecology and Evolutionary Biology for partial funding, Peggy Fong for advice on aquatic nutrient manipulations, and two very constructive reviewers.

References

- Ambariyanto, & Hoegh-Guldberg, O. (1996). Nutrient enrichment and the ultrastructure of zooxanthellae from the giant clam *Tridacna maxima*. *Marine Biology*, **125**, 359–363.
- Anholt, B. R., & Werner, E. E. (1995). Interaction between food availability and predation mortality mediated by adaptive behavior. *Ecology*, **76**, 2230–2234.
- Anthony, K. R., & Hoegh-Guldberg, O. (2003). Kinetics of photoacclimation in corals. *Oecologia*, **134**, 23–31.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48.
- Belda, C. A., Lucas, J. S., & Yellowlees, D. (1993). Nutrient limitation in the giant clam-zooxanthellae symbiosis: Effects of nutrient supplements on growth of the symbiotic partners. *Marine Biology*, **117**, 655–664.
- Bell, P. R. F. (1992). Eutrophication and coral reefs—some examples in the Great Barrier Reef lagoon. *Water Research*, **26**, 553–568.
- Bucciarelli, G. M., Li, A., Kats, L. B., & Green, D. B. (2014). Quantifying tetrodotoxin levels in the California newt using a non-destructive sampling method. *Toxicon*, **80**, 87–93.
- Chambers, C. N. L. (2007). Pasua (*Tridacna maxima*) size and abundance in Tongareva Lagoon, Cook Islands. *SPC Trochus Information Bulletin*, **13**, 7–12.
- Dehault, B., Nguyen, M., Vadlamudi, A., & Blumstein, D. T. (2019). Giant clams discriminate threats along a risk gradient and display varying habituation rates to different stimuli. *Ethology*, **125**, 392–398.
- Dill, L. M., & Fraser, A. H. G. (1997). The worm re-turns: Hiding behavior of a tube-dwelling marine polychaete, *Serpula vermicularis*. *Behavioral Ecology*, **8**, 186–193.
- Doyle, R., Kim, J., Pe, A., & Blumstein, D. T. (2020). Are giant clams (*Tridacna maxima*) distractible? A multi-modal study. *PeerJ*, **8**, e10050.
- Ellis, S. (2000). Nursery and grow-out techniques for giant clams (Bivalvia: Tridacnidae). Center for Tropical and Subtropical Aquaculture Publication, 143.
- Fabricius, K. E. (2005). Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. *Marine Pollution Bulletin*, **50**, 125–146.
- Fankboner, P. V. (1981). Siphonal eyes of giant clams and their relationship to adjacent zooxanthellae. *Veliger*, **23**, 245–249.
- Fitt, W. K., Heslinga, G. A., & Watson, T. C. (1993). Utilization of dissolved inorganic nutrients in growth and mariculture of the tridacnid clam *Tridacna derasa*. *Aquaculture*, **109**, 27–38.
- Fong, C. R., Bittick, S. J., & Fong, P. (2018). Simultaneous synergist, antagonistic and additive interactions between multiple local stressors all degrade algal turf communities on coral reefs. *Journal of Ecology*, **106**, 1390–1400.
- Fong, C. R., Gaynus, C. J., & Carpenter, R. C. (2020). Extreme rainfall events pulse substantial nutrients and sediments from terrestrial to nearshore coastal communities: A case study from French Polynesia. *Scientific Reports*, **10**, 2955.
- Fox, J., & Weisberg, S. (2019). *An R companion to applied regression*. Third. Sage.
- Fraser, D. F., & Huntingford, F. A. (1986). Feeding and avoiding predation hazard: The behavioral response of the prey. *Ethology*, **73**, 56–68.
- Gazzola, A., Balestrieri, A., Martín, J., & Pellitteri-Rosa, D. (2018). Is it worth the risk? Food deprivation effects on tadpole anti-predatory responses. *Journal of Evolutionary Biology*, **45**, 67–74.
- Hallegraeff, G. M., Anderson, D. M., & Cembella, A. D. (1995). *Manual on Harmful Marine Microalgae, IOC Manuals and Guides No. 33* (p. 551). UNESCO.
- Hallegraeff, G. M. (2003). Harmful algal blooms: A global overview. In G. M. Hallegraeff, D. M. Anderson, & A. D. Cembella (Eds.), *Manual on Harmful Marine Microalgae* (pp. 25–49). UNESCO.
- Hastie, L. C., Watson, T. C., Isamu, T., & Heslinga, G. A. (1992). Effect of nutrient enrichment on *Tridacna derasa* seed: Dissolved inorganic nitrogen increases growth rate. *Aquaculture*, **106**, 41–49.

- Hayes, H. G., Hollander, E. N. R., Vydro, S. A., Williams, D. M., & Blumstein, D. T. (2021). Cautious clams? Energetic state modifies risk assessment in giant clams. *Journal of Zoology*, **313**, 208–215.
- Johnson, G. C., Karajah, M. T., Mayo, K., Armenta, T. C., & Blumstein, D. T. (2017). The bigger they are the better they taste: Size predicts predation risk and anti-predator behavior in giant clams. *Journal of Zoology*, **301**, 102–107.
- Klumpp, D. W., & Lucas, J. S. (1994). Nutritional ecology of the giant clams *Tridacna tevoroa* and *T. derasa* from Tonga: Influence of light on filter-feeding and photosynthesis. *Marine Ecology Progress Series*, **107**, 147–156.
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in linear mixed effects models. *Journal of Statistical Software*, **82**, 1–26.
- Lenth, R. (2022). emmeans: Estimated marginal means, aka least-squares means. R package version 1.7.2. Retrieved from <https://CRAN.R-project.org/package=emmeans>
- Lima, S. L. (1998). Stress and decision making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior*, **27**, 215–290.
- Lucas, J. S. (1994). The biology, exploitation, and mariculture of giant clams (Tridacnidae). *Reviews in Fisheries Science*, **2**, 181–223.
- Maina, J., de Moel, H., Zinke, J., Madin, J., McClanahan, T., & Vermaat, J. E. (2013). Human deforestation outweighs future climate change impacts of sedimentation on coral reefs. *Nature Communications*, **4**, 1986.
- Matuschek, H., Kliegl, R., Vasishth, S., Baayen, H., & Bates, D. (2017). Balancing type I error and power in linear mixed models. *Journal of Memory and Language*, **94**, 305–315.
- McNamara, J. M., & Houston, A. I. (1986). The common currency for behavioral decisions. *The American Naturalist*, **127**, 358–378.
- Middlebrooks, M. L., Pierce, S. K., & Bell, S. S. (2011). Foraging behavior under starvation conditions is altered via photosynthesis by the marine gastropod, *Elysia clarki*. *PLoS One*, **6**, e22162.
- Muscantine, L., & Pool, R. R. (1979). Regulation of numbers of intracellular algae. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **204**, 131–139.
- Norton, J. H., Shepherd, M. A., Long, H. M., & Fitt, W. K. (1992). The zooxanthellal tubular system in the giant clam. *The Biological Bulletin*, **183**, 503–506.
- Robson, A. A., Chauvaud, L., Wilson, R. P., & Halsey, L. G. (2012). Small actions, big costs: The behavioural energetics of a commercially important invertebrate. *Journal of the Royal Society, Interface / the Royal Society*, **9**, 1486–1498.
- Sandhu, P., Shura, O., Murray, R. L., & Guy, C. (2018). Worms make risky choices too: The effect of starvation on foraging in the common earthworm (*Lumbricus terrestris*). *Canadian Journal of Zoology*, **96**, 1278–1283.
- Sanseverino, I., Conduto, D., Pozzoli, L., Dobricic, S., & Lettieri, T. (2016). *Algal bloom and its economic impact*. JRC Technical Reports. European Commission Joint Research Centre, Italy.
- Soo, P., & Todd, P. A. (2014). The behaviour of giant clams (Bivalvia: Cardiidae: Tridacninae). *Marine Biology*, **161**, 2699–2717.
- Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2021). partR2: Partitioning R2 in generalized linear mixed models. *PeerJ*, **9**, e11414.
- Titlyanov, E. A., Leletkin, V. A., & Dubinsky, Z. (2000). Autotrophy and predation in the hermatypic coral *Stylophora pistillata* in different light habitats. *Symbiosis*, **29**, 263–281.
- Todd, P. A., Lee, J. H., & Chou, L. M. (2009). Polymorphism and crypsis in the boring giant clam (*Tridacna crocea*): Potential strategies against visual predators. *Hydrobiologia*, **635**, 37–43.
- Walker, S., & Rypstra, A. (2003). Hungry spiders aren't afraid of the big bad wolf spider. *Journal of Arachnology*, **31**, 425–427.
- Whitham, J., & Mathis, A. (2000). Effects of hunger and predation risk on foraging behavior of graybelly salamanders, *Eurycea multiplicata*. *Journal of Chemical Ecology*, **26**, 1659–1665.
- Wilkens, L. A. (1986). The visual system of the giant clam *Tridacna*: Behavioral adaptations. *The Biological Bulletin*, **170**, 393–408.