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Marine Prey Vulnerability versus Resilience to Human Foragers

Insights from Agent-Based Modeling

Alex E. Morrison and Melinda S. Allen

Abstract: The resilience and susceptibility of key marine organisms to human predation and environmental change is a topic of importance to archaeologists, wildlife managers, and conservation biologists. While contemporary studies are useful for linking managerial strategies to prey population patterns, zooarchaeological assemblages when combined with computer-based simulation methods provide additional insights into marine prey resilience or susceptibility to harvesting pressures over the long-term. In this paper we generate a set of predictions, drawing on concepts from life-history theory, and then build an agent-based model to examine how energetic return rate and age at reproductive maturity influence prey resilience to foraging pressures. Our agent-based model results are then compared with archaeological observations from a limited number of Pacific island assemblages to assess the validity of the model. The results of the simulation indicate that prey taxa with low energetic return rates which reach reproductive maturity at young ages are more impervious to human predation than those which reach reproductive maturity later in life and have greater energetic returns. The archaeological assemblages examined support these key findings and suggest that the susceptibility of marine organisms to human predation is likely to be multi-faceted and context dependent. Our results also demonstrate the utility of agent-based modeling as a technique for establishing the dynamic sufficiency of competing explanations and for generating new hypotheses.

Keywords: agent-based modelling, marine mollusks, resilience, foraging dynamics, Pacific Islands.

***Vulnérabilité des proies marines* versus *résistance aux prédateurs humains :
résultats d'une modélisation multi-agents***

Résumé : La capacité de résilience et la vulnérabilité de certains organismes marins face à la prédation humaine et aux changements environnementaux sont des sujets d'importance tant pour les archéologues que les biologistes. Si les études actuelles permettent de relier les stratégies de conservation des espèces aux profils démographiques des populations exploitées, les assemblages archéozoologiques combinés aux méthodes de simulation assistées par ordinateur fournissent un aperçu de la résilience et de la vulnérabilité des proies marines aux pressions de collecte sur le long terme. Dans cet article, nous proposons un ensemble de prédictions et développons un modèle multi-agents pour documenter la manière dont les taux de rendement énergétique et l'âge de reproduction influencent la résilience des proies aux pressions de collecte. Les résultats issus du modèle sont ensuite mis en rapport avec des observations archéologiques relevées dans plusieurs assemblages dans le Pacifique afin d'évaluer sa validité. Il apparaît dans notre simulation que les espèces à faible retour énergétique et ayant une maturité reproductive précoce sont plus résistantes à la prédation humaine que celles ayant une maturité reproductive tardive et un plus grand retour énergétique. Les assemblages archéologiques étudiés soutiennent ces résultats et suggèrent que la vulnérabilité des organismes marins à la prédation anthropique dépend du contexte. Nos résultats montrent également l'utilité de modèles multi-agents en tant que technique pour établir l'autonomie d'explications concurrentes et pour générer de nouvelles hypothèses.

Mots-clés : modélisation multi-agents, mollusques marins, résilience, dynamiques d'approvisionnement, Pacifique.

THE RESILIENCE of marine organisms to human predation is of considerable concern to archaeologists, conservation biologists, and wildlife managers (Jackson et al., 2001; Dulvy et al., 2003; Hutchings and Reynolds, 2004). Current estimates suggest that at least 133 marine populations and species worldwide have gone extinct, with the majority of cases caused by human predation (Dulvy et al., 2003, p. 27). In an extensive study

of 232 marine populations, J. Hutchings and J. Reynolds (Hutchings and Reynolds, 2004, p. 298) found an average maximum population decline of 83% during the historic period. These estimates are likely conservative given the absence of long-term records that might provide reliable ecological baselines from which to measure population trajectories (Pauly, 1995). Contemporary studies that document relationships between managerial strategies and resilience in prey populations can provide important insights into the short-term consequences of enforcing size and catch restrictions. We further suggest that diachronic records derived from archaeological studies, especially when combined with computer-based simulation methods, provide additional and unique insights into marine prey resilience or vulnerability to harvesting by human foragers. Usefully, archaeological studies provide the time depth necessary to examine long-term predator-prey dynamics, as well as informing on predator-prey interactions in a variety of marine ecological settings. Often representing several centuries of marine resource use, these data sets in combination with ethnographic and ecological information can track the development and outcomes of customary marine tenure practices (Aswani, 2014; Aswani and Hamilton, 2004; Thomas, 2007), traditional ecological knowledge regarding the vulnerability of specific taxa to overharvesting (Berkes et al., 2000; Drew, 2005), and long-term human adaptations to marine ecosystems variation (Fitzpatrick and Keegan, 2007; Rick and Erlandson, 2008)..

D. O'Sullivan and G. Perry (O'Sullivan and Perry, 2013, p. 14) have recently suggested that one of the difficulties associated with contemporary research on predator-prey dynamics is the inability to separate the complex causes of resilience and population-scale impacts when examining the interaction of multiple factors over long time periods. Quite simply, the majority of these studies are short-term and not capable of identifying the key variables that operate over multi-decadal or centennial time scales. Moreover, the interaction of multiple variables may result in population level consequences that are impossible to predict from analyses made over short temporal scales.

While numerous archaeological studies demonstrate how humans have impacted marine species across the globe (e.g., Allen, 2002 and 2003; Braje et al., 2007; Erlandson et al., 2008; Mannino and Thomas, 2002; Morrison and Hunt, 2007), the processes responsible for changes in marine ecosystems often are difficult to determine. These may include not only human predation but also variation in habitats and regional climate fluctuations. Agent-based computer modeling has proven useful in a range of scientific analyses where the phenomena that make up the empirical record are the result of multiple processes occurring over different temporal scales and from the interaction of many variables (e.g., O'Sullivan and Perry 2013, p. 52; Premo, 2010, p. 31).

Agent-based modeling (ABM) is a computer simulation approach used to examine population scale patterns and outcomes which arise from multiple interacting autonom-

ous (individual) entities. Here we utilize a combination of life-history theory, ABM, and archaeological observations to examine how marine mollusk characteristics contribute to prey population resilience or vulnerability in the face of human predation pressures. Our aim is not only to explore factors contributing to prey vulnerability/resilience, but also to illustrate how ABM can augment theoretical models from foraging theory. Of note, our model does not include real life taxa and their specific life history and ecological traits; rather we evaluate a set of hypothetical taxa which vary in these dimensions. We begin by outlining a simple foraging model that stipulates the relationships between prey energetic return rates and reproductive ages, based on principles from life history theory. Our theoretical model provides a set of expectations about prey resilience and vulnerability to human predation. We then generate an ABM to explore the temporal dynamics of this theoretical foraging model, manipulating interactions between two key variables, energetic returns and reproductive age, at variable settings across multiple model runs. Finally, we compare our ABM results with empirical records of marine mollusk use in the prehistoric past, as derived from Pacific archaeological studies.

GENERAL MODEL

The agent-based model described below focuses on two primary variables: first, the probability that a prey item will be pursued upon encounter, based on its energetic return rate; and second, the age of reproductive maturity of each hypothetical molluscan taxon. We discuss the relevance of each of these variables in greater detail below.

Prey return rate

The prey choice model, originally developed in evolutionary ecology, identifies which taxa should be pursued by predators upon encounter and which should be ignored, all else being equal (Stephens and Krebs, 1986). The model stipulates that predators choose prey based on their post encounter return rates, relative to other potential resources encountered during a foray. Prey therefore are ranked according to their post encounter return rate or Θ, defined as: the ratio of energy gained (E_g) over energy spent (E_s) while foraging (Weimerskirch et al., 2003).

$$\Theta = E_g/E_s \text{ (equation 1)}$$

Often in human behavioral ecology studies, energy spent (E_s) can be further defined as the sum of:

$$E_s = T_h + T_s \text{ (equation 2)}$$

In most archaeological studies, energy gained (E_g) is approximated using prey body size (P_s; Broughton et al., 2011) or based on ethnographic studies where handling and search time can be directly observed and measured (e.g., Bird and Bliege-Bird, 1997; Codding et al., 2014; Thomas, 2007). Prey return rate can be defined as the expected caloric gain per unit of handling cost (a combination of handling time and search time). If we make a further simplify-

ing assumption that all prey of the same taxon are handled in the same way, then a prey item can be ranked based on the simple ratio of energy gained over search time.

The decision of whether to pursue an item also depends on the encounter rate of other potential resources in the environment. For example, if high ranked (i.e., large-bodied) resources are common, and frequently encountered, lower ranked items should be ignored. However, as higher ranked resources are less frequently encountered, diet breadth will expand to include lower ranked prey that provide lower energetic returns. The increased abundance of lower ranked items in the diet often is taken to signal a change in the encounter rate of high ranked resources, although with some technologies (e.g, mass harvesting) collection of small-bodied prey can be quite efficient (Madsen and Schmitt, 1998; Ugan, 2005). Hypothetically, if taxa with varied return rates were available in equal amounts, lower ranked items would be pursued less frequently and therefore be less susceptible to human foraging through time. However, as the highest ranked prey are depleted, foragers typically move to those of intermediate rankings; in other words, prey rankings vary over time and ultimately are influenced by the encounter rate of the suite of possible prey in any particular setting.

Prey reproductive age

While energetic return is clearly an important variable in prey population resilience, life-history characteristics (e.g., reproductive features, life span, etc.), along with prey habitat preferences and mobility, also play significant roles. The age at which a prey taxon reaches reproductive maturity is negatively correlated with population growth (Roff, 2002), and this characteristic provides an estimate of the potential resilience of taxa to predation. In other words, high recovery rates following perturbations are associated with prey that reach reproductive maturity at a young age (Denney et al., 2002; Hutchings and Reynolds, 2004; Reynolds, 2003; Reynolds et al., 2001). Moreover, T. Lasiak (Lasiak, 1991) notes that the population level effects of size-at-sexual-maturity are closely linked to the size preferences of foragers. Prey taxa that reproduce at sizes below those preferred by their predators are less susceptible to exploitation resource depression because reproducing individuals are more likely to escape predation and remain in the population. In contrast, when foragers target prey organisms at sizes below reproductive maturity, prey populations are placed at greater risk of demographic instability. Thus, assuming the correlation between prey size and prey age is robust, and holds across taxonomic groups, then prey size may provide useful information on prey age at sexual maturity.

However, there are reasons to suspect that body size in mollusks may not be a reliable indicator of age, and by extension, reproductive maturity. This is because mollusk size can be affected by food supply and other ecological conditions, which affect prey population density. Individuals living in less dense populations may grow more

rapidly, leading to large but reproductively immature individuals. Dense clustered living conditions, in contrast, may potentially result in prey reaching reproductive age at smaller body sizes. Ultimately, reproductive maturity should be assessed by determining individual age rather than size alone (Swadling, 1976; Morrison and Allen, 2014).

Interactions between variables

Combining information regarding the relationship between human prey choice criteria and reproductive biology allows us to make the following general predictions about prey resilience to human predation (fig. 1):
– prey taxa that have high energetic return rates and reach reproductive maturity at older ages should be the most vulnerable to human impacts;
– prey taxa that have low energetic return rates and reproduce at younger ages should be the most resilient prey populations;
– prey taxa with intermediate return rates will vary in resilience, depending on their corresponding age at reproductive maturity and interaction between the two variables.

It is important to note that while organisms with high energetic return rates are hypothesized to be more vulnerable to foraging-induced resource depression (because foragers typically pursue these items more frequently upon encounter), the effect of energetic return rate is best conceptualized in relationship to the entire set of prey items which are potentially available at a given locality. This is because although energetic returns are more or less constant (assuming predation pressure has not affected changes in the overall population structure), prey
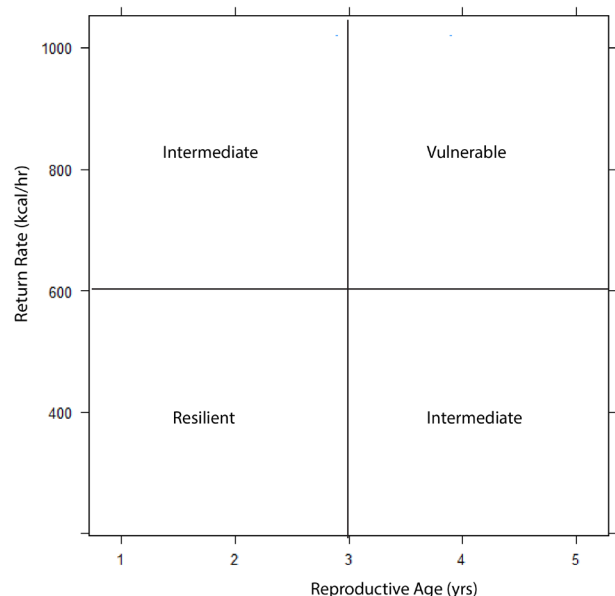
Fig. 1 – The relationship between return rate, reproductive age, and population resilience.
Fig. 1 – Le rapport entre le taux de rendement, l'âge de maturité reproductive et la résilience de la population.

rankings are relative and context specific to some degree. We return to this issue in the discussion section.

A number of ethnographic and archaeological studies have explored the dynamics of reproductive age and prey population resilience in marine mollusk populations (e.g., Catterall and Poiner, 1987; Codding et al., 2014; Giovas et al., 2013; Poiner and Catterall, 1988; Thomas, 2007). Here we augment these studies by simulating prey population dynamics under varied return rate and reproductive age settings across multiple model runs. Our aim is not simply to replicate outcomes from the foregoing studies, but also to assess phenomena which emerge over long time periods. The following section describes the ABM structure, model details, and design concepts, following Grimm and colleagues (Grimm et al., 2006 and 2010).

AGENT-BASED MODEL STRUCTURE

ABM is a computer simulation based approach that has recently seen wide-scale application in ecology, urban planning, archaeology, and a variety of other fields. A fundamental assumption of the approach is that population scale phenomena arise from the interactions of the individual entities that exist at lower organizational scales. For example, in ecological ABM applications it is common to include different agents that represent both predators and prey. Each individual may have different life history characteristics, such as age, size, and feeding strategies. These individual autonomous entities interact with each other according to a series of scheduled actions. Macroscale patterns, which emerge at the population level, then can be tracked and the primary causative factors potentially deduced from the model structure.

In the following agent-based simulation, we model two primary types of entities: human foragers and immobile mollusk taxa with various life-history characteristics and return rates. Human foragers are represented as mobile agents and prey are characterized as immobile properties of patches. In all of the models discussed below, the initial predator population size is 50 and the prey population starting size is set at 10,000. These starting parameters were chosen to create relatively stable frequencies of prey which would not be immediately susceptible to resource depression from human exploitation. The state variables, their parameters, symbols, and parameter settings are presented in tables 1 and 2. The environment consists of a 101 × 101 square grid, represented as a torus in order to avoid edge effects. Iterations of the model correspond to one day, although foraging trips only occur every three days. The model was allowed to run for 10,000 iterations across twenty different possible parameter combinations. Prey population mortality and reproduction occurs once a year, and prey grow and age with every iteration of the model. Ecological studies suggest that some mollusk species, such as *Tridacna maxima*, may reproduce during distinct seasons and are influenced by environmental factors such as sea surface salinity and temperature (Tan and Yasin, 2000), but these variables are not varied in the current analysis. In the present study, once individual prey reach a minimum maturity age, they are reproductively viable and then can participate in a reproduction sub-model described in detail below. Importantly, we hold human population growth and reproduction constant in these models.

Process overview and scheduling

Human foragers participate in several foraging related activities. First, a forager can move according to two different movement types, a correlated random walk (f_2), or an area restricted search, ARS (f_1), depending on if they were successful at capturing a prey item on their previous foray (following Bailleul et al., 2013). Foragers are allowed to capture up one item per foraging trip. Prey growth and aging occur at daily increments, while both crude mortality and reproduction are scheduled at annual time scales. The model's schedule is shown in figure 2.

We model prey return rate by defining different probabilities of being captured based on a return rate parameter R_k that varies from 1000 to 250 kcal/hr. The return rate setting determines the probability that an item will be harvested upon encounter. As a result, items with higher energetic return values are foraged more frequently than items with lower energetic return rates (see table 1). The energetic return rate parameter varies across model runs and is one of the primary analytic variables in our model.

Design concepts

This section describes the design concepts of emergence, adaptation, prediction, memory, learning, and stochasticity. Emergence is modeled as the prey population size at the completion of a given model run and its overall resilience to predation. Individual foragers adapt by changing their movement strategy after they are successful at capturing a prey item. Human foragers use very simple sensing upon encounter of prey items and therefore predict that more resources are located in close proximity to the items they have recently encountered and adjust their movement strategy accordingly. Empirical and computer simulation studies demonstrate that foraging return rates can be influenced by the ability of predators to remember the location of prey (Barraquand et al., 2009). Consequently, for simplicity we chose not to include memory and learning in the model. Stochasticity is included through the use of random variables that control the location of hard substrates and therefore the location of prey resources. Prey mortality, reproduction, and initial age also vary randomly upon initialization of the model. Prey population size is observed and reported twice a year, once after crude mortality and once after reproduction.

Movement and collection

Predator forays consist of two different sub-models which make up the overall foraging activity; movement

State Variables	Description	Initial Parameter Range
Predator		
Current location	The current x, y coordinates corresponding to the location of the agent	–
Success on last forage	Boolean variable indicating TRUE or FALSE	FALSE
Prey captured	The number of prey captured by each predator on a single foray	0
Number of moves	The total number of forays an agent has participated in	0
Capture probability	The probability that a prey will be captured based on kcal/hr	0.10–1
Prey		
Location	The x, y coordinates corresponding to the patch a prey resides within	n of hard substrate patches
Number of prey on patch	The number of prey residing within a patch	0–8,000
Age	The age of the prey items	0–15 years
Maturity	If the prey age is greater than M_k then the value is TRUE	TRUE or FALSE
Substrate	Boolean variable indicating either hard substrate of soft substrate	–
Reproductive age	The age parameter (M_k) at which prey participate in the reproductive sub-model	1–5 years
Energy/Kcal	The modeled energetic return rate for prey agent	250–1,000

Table 1 – State variables and parameter settings used in the agent-based model.
Tabl. 1 – *Variables d'état et paramètres utilisés dans le modèle multi-agents.*

Symbol	Description	Initial Parameter values and ranges
f_1	Movement Strategy 1 ; Area Restricted Search	–
f_2	Movement Strategy 2 : Correlated Random Walk	–
A_k	Prey age	0 to 25 years
M_k	Prey age at reproductive maturity	1–5 years
P	Prey population	10,000
k	Carrying capacity	$d * E_h$
E_h	The number of patches with hard substrate	0–10,201
d	Density limit	8,000
P_p	Number of prey on a patch.	0–8,000
P_w	Prey mortality rate	0.15
R	Predator population size	50
R_k	Prey return rate (kcal/hr)	250–1,000

Table 2 – Simulation symbols, description, and initial model values.
Tabl. 2 – *Symboles de simulation, description et valeurs initiales du modèle.*

and collection. These subroutines run once every three iterations. Upon initialization, all foragers move approximately in a straight line (f_2) until they reach a prey resource, after which they switch their movement strategy to an area restricted search radius (f_1). The area restricted search radius is meant to increase the probability of prey encounter by assuming that prey resources are aggregated in space. Only one predator is allowed to occupy a single grid cell at a time.

Capture

After the movement sub-model is completed, foragers check for the presence of any prey resources within the patch they are residing in. Resource units vary according to return rate and the return rate determines the probability that an item will be foraged once encountered. If there is no prey present, the forager simply stops without capturing any items.

Age

Immobile prey organisms have a corresponding life history attribute of age (A_k). Prey items age at a rate of one day per each iteration. When items reach a reproductively mature age (M_k) they are separated into a mature subset of the population. The reproductively mature age (M_k) parameter is varied across model runs from a minimum age of one year to a maximum of five years.
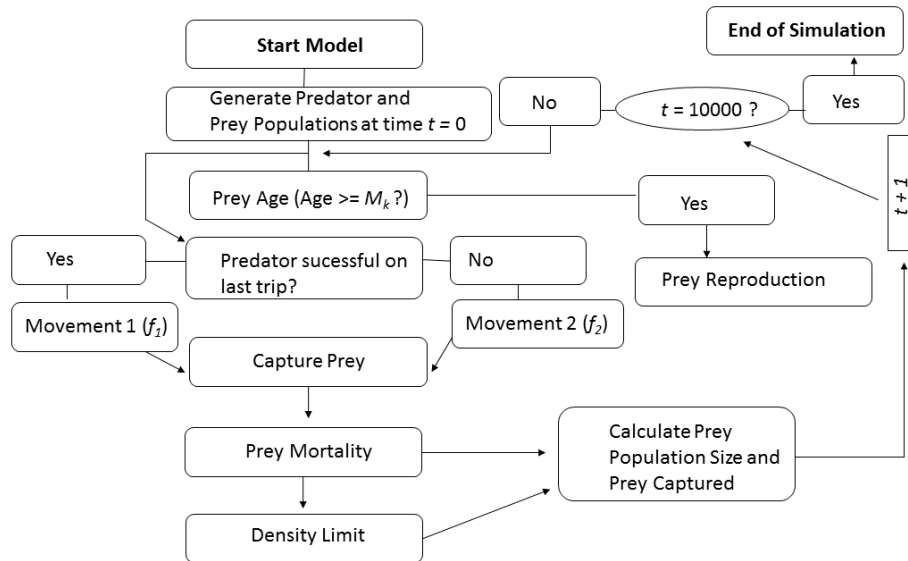
Fig. 2 – The agent-based model schedule. Note that the prey mortality and reproduction sub-models only run at annual time steps.
Fig. 2 *– Le modèle multi-agents. À noter que les sous-modèles de mortalité et de reproductivité des proies ont été appliqués par tranche annuelle.*

Birth

Prey items are able to reproduce if two criteria are satisfied. First, individual prey must be reproductively mature, a criterion which is satisfied by reaching a specified prey age of (M_k). Secondly, two reproductively mature organisms must be located within a patch. If these criteria are met, a mature prey reproduces one offspring, which is then distributed randomly on any hard substrate patch in the environment.

Mortality

The prey population (P) is subjected to a specified adult mortality rate (P_w), which for simplification occurs once every three hundred sixty iterations. The mortality sub-model is run by calculating the prey population at t + 1 or (P'): P' = P - (P * P_w).

While mollusk mortality and survivorship can vary dramatically depending on age, habitat, and taxonomic characteristics (Black et al., 2011; Mekawy and Madkour, 2012; Mies et al., 2012; Smith 2011), for simplification prey mortality is fixed at 15% in all of the models following the general results of R. Black and coworkers (Black et al., 2011).

Density limit

To keep prey populations from growing to infinitely large numbers, and also to include some realistic population parameters in the model, a density limit (d) of prey items per patch (P_p) is specified. If $P_p > d$, then P_p is automatically reduced to d-1 by a random mortality procedure. The density limit sub-model has the ultimate effect of setting the prey population carrying capacity (k) = d * E_h, where E_h is the number of hard substrate patches available for resources.
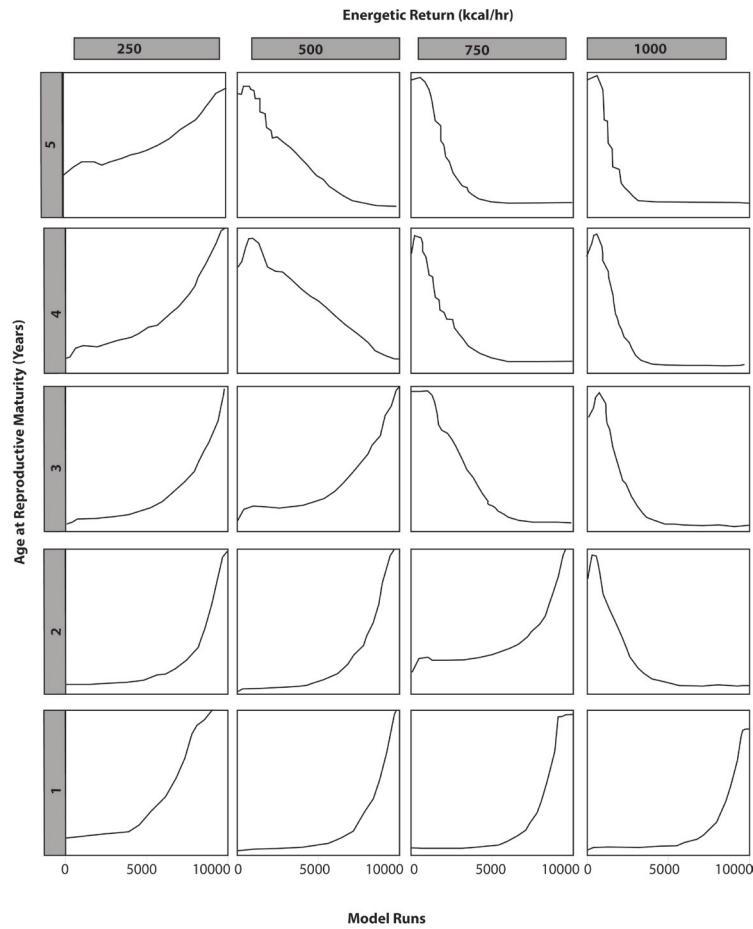
AGENT-BASED MODEL RESULTS

The results of the agent-based simulations (fig. 3) highlight a number of important trends. When return rate is set to 1,000 kcal/hr, only the youngest age at reproductive maturity groups (M_k) cohort (i.e., when one year-old individuals are reproductively mature) produces a resilient prey population. The effect of high foraging intensity reduces population sizes for all other reproductive ages, providing support for the idea that prey populations with high energetic return rates are more vulnerable. Similar results also were produced in model runs where the prey energetic return rate was set to 750 kcal/hr. However, resilient populations were present in the young reproductive age groups, those of one and two years.

At an intermediate prey return rate of 500 kcal/hr, the interaction of return rate and prey reproductive age also is apparent. When reproductive age is set to one, two, or three years, prey populations were resilient to foraging pressure. However, prey that reproduced at ages over three years ultimately were susceptible to human predation. Finally, when energetic return is set to the lowest parameter setting, 250 kcal/hr, individuals of all reproductive ages resulted in resilient populations. In other words, organisms with low energetic return rates are generally resilient, regardless of their inherent reproductive ages, because they are unattractive to human foragers, as long as prey with higher return rates are available in the local environment. Only when the latter decline and encounter rates fall, do we see prey switching behaviors (assuming all other factors are held constant).

Resilience analysis

Figure 4 displays the bivariate parameter space of resilient populations and non-resilient populations based on

Fig. 3 – Results of the agent-based model runs. Note that the Y axis values for each individual model pane refers to prey population size. The prey population size varies and for convenience is not shown on each model pane. All model prey population sizes began at 10,000 and the ending population sizes are presented in table 3.
Fig. 3 – Résultat des calculs du modèle multi-agents. Pour chaque volet du modèle, les valeurs sur l'axe y se réfèrent à la taille de la population de proies. La taille de la population de proies varie et n'est pas indiquée sur chaque volet du modèle pour des raisons de facilité. Toutes les tailles des populations de proies du modèle débutent à 10 000 et les tailles finales des populations sont indiquées dans le tableau 3.
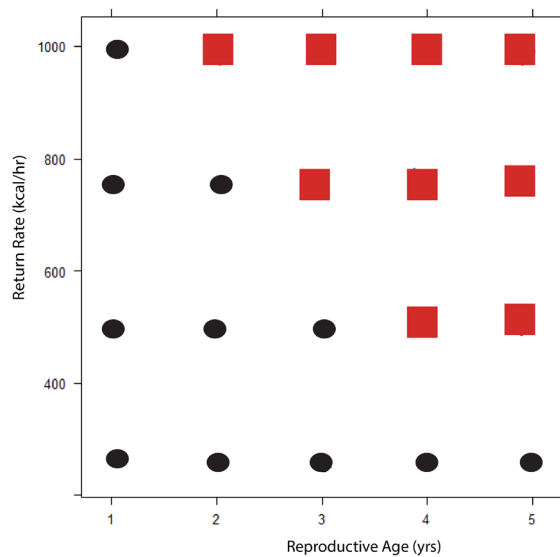
Fig. 4 – Black circles indicate resilient prey populations; red squares indicate heavily predated and susceptible populations.
Fig. 4 – Les cercles noirs indiquent les populations de proies résilientes et les carrés rouge indiquent des populations fortement touchées par la prédation et vulnérables.

the intersection of reproductive age and energetic return rate. The results demonstrate that organisms with young reproductive ages (one year) always produce resilient prey populations, regardless of energetic return rate. Identical results were produced when the energetic return parameter was set to the lowest setting of 250 kcal/hr. Low settings produced resilient prey populations with very little interaction between the two variables. However, as prey reproductive age increases, so does the interaction between energetic return and reproductive age. For example, when reproductive age is set to three years, only two possible parameter combinations produce resilient populations. These combinations correspond to low energetic return rates (250 kcal/hr, 500 kcal/hr). Moreover, as age of reproductive maturity increases, the number of parameter settings producing resilient prey populations decreases. Reproductive ages of four and five years result in resilient prey populations only when the energetic return rate is at the lowest setting: 250 kcal/hr.

Prey population size at completion of model run

Reproductive age and energetic returns also affect overall population size and therefore may render populations vulnerable to other external factors. These could include climate change, habitat destruction, or increased foraging pressure as a result of predator population growth. To assess how these variables influence overall prey population size, we conducted a bivariate sensitivity analysis with the twenty different parameter combinations of

reproductive age and energetic returns (fig. 5). The results are displayed as a three-dimensional contour plot with total population size set as the z value (see also table 3).

The prey population size after 10,000 model runs demonstrates that as reproductive age increases total terminal population size deceases. The lowest ending populations sizes, associated with reproductive ages of four and five, are zero. The parameter space corresponding to young reproductive age and low energetic return results in the largest prey population. The overwhelming influence of reproductive age on population size is indicated by the steep vertical nature of the contour lines in the parameter space corresponding to reproductive ages of one and two years. Moreover, the steep increasing contours also indicate that prey population size is sensitive to reproductive age, especially when reproductive age is set to low values.

The influence of energetic return also is visible in the contour plot. As previously mentioned, when reproductive age is set to mature age settings (four or five years), populations are resilient only at the lowest energetic return rate setting (250 kcal/hr). The interaction between energetic return and reproductive age is indicated by the diagonal direction of the contour lines in the parameter space corresponding to high energetic return rates and reproductive ages over two. Additionally, even though young reproductive ages produce large population sizes, there is a slight interaction effect with high energetic return rates, which produces population sizes at lower abundances than those characterized by young reproductive ages and low energetic returns.
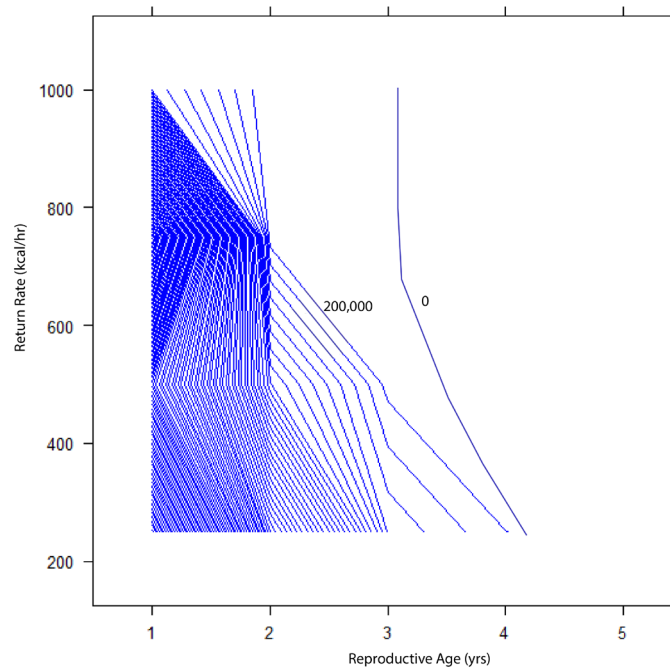
Fig. 5 – Population size as a function of energetic return rate and prey reproductive age after 10,000 iterations. The contour interval is 200,000 resources and the Z value is population size.
Fig. 5 – Taille d'une population en fonction du taux de rendement énergétique et de l'âge de procréation des proies après 10 000 itérations. L'intervalle entre deux lignes de courbes correspond à 200 000 ressources et la valeur Z indique la taille de la population.

Model	Return Rate k/cal	Reproductive Age	Ending Population Size
1	250	1	14,741,780
2	500	1	9,259,847
3	750	1	1,609,102
4	1,000	1	1,373,486
5	250	2	5,215,601
6	500	2	1,821,728
7	750	2	77,030
8	1,000	2	0
9	250	3	774,325
10	500	3	125,392
11	750	3	0
12	1,000	3	0
13	250	4	202,069
14	500	4	1,512
15	750	4	0
16	1,000	4	0
17	250	5	77,376
18	500	5	224
19	750	5	0
20	1,000	5	0

Table 3 – The twenty different model parameter combinations and the ending prey population sizes. All models began with a prey population size of 10,000.
Tabl. 3 – *Les vingt combinaisons de paramètres du modèle et les tailles finales des populations de proies. Tous les modèles ont été lancés avec une taille de la population de proies de 10 000.*

Agent-based model summary

The results of the ABM support the hypotheses outlined in the general behavioral ecology model we presented above. First, resilience to human predation in prey populations is strongly influenced by age of reproductive maturity and energetic return rate. Specifically, taxa with lower return rates that reproduce at young ages are the most likely to be resilient to human predation. In contrast, taxa that reach reproductive maturity later in life and have greater energetic return rates are the most susceptible to human-induced resource depression. The strongest interaction between the two variables occurs at moderate parameters settings. Specifically, when reproductive age is set to three years, the influence of energetic return can lead to either a resilient or a susceptible prey population. Finally, terminal population size, like resilience, is strongly influenced by both age of reproductive maturity and energetic return rate.

Comparison of these results with those from archaeological assemblages provides a better understanding of why certain mollusk species remain stable though time and others are more susceptible to human foraging. In the following section we compare our ABM results with case studies from island archaeological contexts to assess how well they compare with actual sequences and assess the model's utility for understanding different prey responses to human foraging over long time scales.

COMPARISON WITH PACIFIC ARCHAEOLOGICAL SEQUENCES

The foraging model presented here is quite simple in that it explores the effects of, and interaction between, only two variables. Usefully the results do conform to expectations derived from foraging theory models (e.g., Broughton, 2002). In real life situations, however, a large number of cultural, ecological, and/or environmental factors might be at play and affect prey populations and long-term foraging outcomes. Nonetheless, our simple ABM serves as a null hypothesis which appears to account for multi-century outcomes predicted at the outset. In particular we have sought to understand how variation in energetic returns and reproductive age might singly, or in combination, factor into prey vulnerability (or resilience) to human predation over extended periods of time. In this section we compare theoretical predictions and simulated outcomes with empirical archaeological records relating to human use of three molluscan taxa which are common food resources in the Pacific, now and in the past: *Tridacna*, *Turbo* and *Nerita* (table 4). The aim is to assess how closely the archaeological records, from diverse geographic settings and variable time periods, conform to theoretical and model predictions and, where there are departures, potential causal factors.

Taxon	Energetic Return (kcal/hr)	Reproductive Age
Nerita	42 to 1,106	1–2 years
Turbo	520 to 606	3–4 years
Tridacna	2,622 to 13,064	4–5 years

Table 4 – Energetic return rates and age at maturity for common archaeological taxa (summarized from Codding et al., 2014).
Tabl. 4 – Taux de rendement énergétique et âge de maturité pour des taxons archéologiques (résumé d'après Codding et al., 2014).

Description of important mollusk taxa recovered from archaeological assemblages

Tridacna is the largest of the three selected taxa. This long-lived, sessile bivalve can reach sizes of 40 cm to 1.4 m and provides energetic return rates ranging from 2,622 to 13,064 kcal/hr, depending on the species under consideration (Codding et al., 2014, p. 242, table 1; Ellis, 1998). *Tridacna maxima*, one of the more common species, typically reach maturity between four to five years of age (Codding et al., 2014, p. 242, table 1). In terms of energetic returns, *Tridacna* not only provides the highest returns of the three taxa considered here, but also exceeds all of the hypothetical prey species modeled in our simulation. *Turbo*, a medium-size, browsing gastropod, provides energetic returns, between 520 to 606 kcal/hr, and reaches reproductive maturity between three and four years (Codding et al., 2014). *Turbo* is analogous to one of our model prey taxa, with a return rate of 500 kcal/hr and a reproductive age of three to four years. Usefully, the large and dense opercula of *Turbo* often preserve in archaeological sites and provide an independent means of assessing foraging impacts (Sealy and Galimberti, 2011, p. 408). Finally, *Nerita*, a small browsing gastropod, has the lowest return rates, ranging between 42 and 1,106 kcal/hr. (Codding et al., 2014, p. 242, table 1). *Nerita* reproduce at the very young age of one to two years. Although there is variability in average body sizes and reproductive ages within these three genera, this variation is less than inter-generic variability. It is worth noting that prey population spatial patterning associated with aggregation or dispersion also can impact on foraging return rates and vulnerability to predation (Broughton, 2002; Wolverton et al., 2012), however, we do not model these effects here. Given the foregoing, the expectation is that *Tridacna* will be the most susceptible to human predation, *Nerita* generally resilient and *Turbo* intermediate, as indicated by the ABM results and the position of these three taxa in figure 6, based on variation in energetic return rates and age of reproductive maturity. We consider trends in the abundance of these three species across three geographic contexts and in archaeological sequences which also vary in duration.
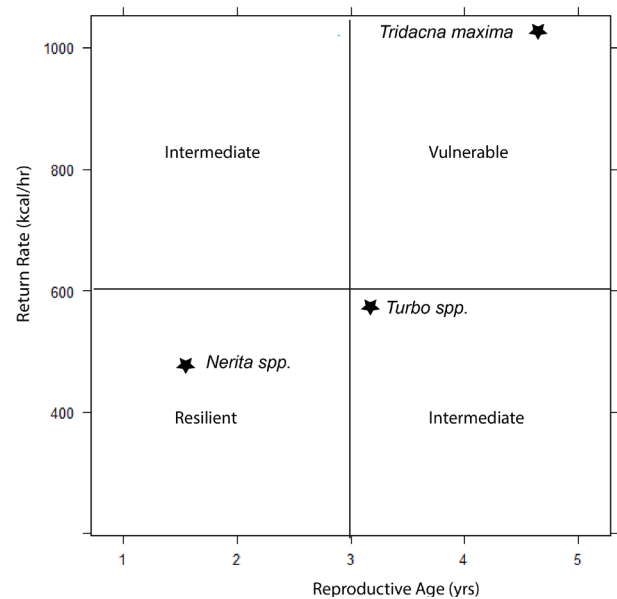
Archaeological case studies

Case study 1: Tikopia Island, Solomon Islands

Tikopia Island is a small Polynesian outlier of 5 km² located in the Western Pacific and provides the longest occu-

pation sequence of the case studies discussed here (Kirch and Yen, 1982). Drawing on assemblages from site TK-1 or the Sinapupu site, the authors document marked shifts in molluscan use over an approximately 1800-year period of human occupation. Of particular note are declines in the relative abundance of *Tridacna maxima* (Kirch and Yen, 1982, p. 300, fig. 117), a taxon which features prominently despite the fact that the heavy shell remains are often discarded at the site of collection (Bird and Bliege-Bird, 1997; Thomas, 2007). *Tridacna* appears to be sustainable for most of the 1800-year sequence, but declines markedly in the last few hundred years of occupation. This is most notable after layer III (dated to approximately 1200 BP), when *Tridacna maxima* declines from 2,333 grams/m³ (layer III) to 500 grams/m³ (layer I; approximately 500 BP). These changes also are reflected in the rank order of *Tridacna*, which moves from a rank of 2 to 6.5 during the corresponding period.

Turbo crassus, a second important taxon, is an intermediate size member of the Turbinidae family, varying in length from 50 to 80 mm (Alf and Kreipl, 2003). Contrasting with *Tridacna*, this species is relatively stable during the earliest Tikopia occupations but increases

Fig. 6 – Relationship between model results and common molluscan taxa described in the archaeological case studies.
Fig. 6 – Rapport entre les résultats du modèle et les taxons de mollusques communs décrits dans les cas d'études archéologiques.

in density in late prehistory as *Tridacna* declines. Both *Turbo crassus* and a second turban species, *Turbo marmoratus*, increase substantially in layer II, with densities of 3,750 grams/m^3 and 2,875 grams/m^3 respectively. Together these two taxa are ranked second in abundance in layers I and II. This shift from *Tridacna* to *Turbo* is consistent with our ABM results.

Case study 2: Aitutaki, Cook Islands

Aitutaki, a slightly larger island with 18 km^2 land area and a 54 km^2 lagoon, is an almost-atoll in the southern Cook Islands. Here a sequence of molluscan usage dating from the 12th century AD derives from four sites on the island, three open coastal sites on the mainland and one rockshelter site on an offshore basalt islet of Moturakau (Allen, 1992; Allen and Morrison, 2013; Allen and Wallace, 2007). *Tridacna* ranks first in the oldest occupation layers but over time decreases in abundance, although it remains a relatively high ranked taxon (Allen, 1992). *Turbo*, in contrast, is ranked relatively low early in time but by late prehistory is the top ranked shellfish at several sites. Analysis of *Turbo* opercula from Moturakau rockshelter revealed no significant changes in body size over time, suggesting that human exploitation had negligible effects on prey body size (Allen, 1992). In contrast, none of the three local *Nerita* species figure importantly in the mainland assemblages at any point in time. *N. plicata*, however, is moderately well represented in the Moturakau sequence, fluctuating between rank 6 and 7 (Allen, 1992, p. 343; also appendix E, table E5). Again, these findings are consistent with the ABM outcomes.

Case study 3: Nualolo Kai, Kauai, Hawai'i

The Nualolo Kai site (K3) on the windward coast of Kaua'i island in the Hawaiian Archipelago is relatively isolated, being situated in a narrow valley bounded by steep rocky cliffs which is difficult to access even from the sea. The molluscan assemblage here derives from a coastal rockshelter with an approximately 1.8 m deep stratified deposit, dating from the 15th century AD and into the post-contact period (Hunt, 2005; Morrison and Hunt, 2007, p. 31). Unlike the foregoing examples, the large *Tridacna* clams are not represented in the Hawaiian Islands. Here one of the largest species available to early Hawaiian colonists was *Turbo sandwicensis*, measuring up to 90 mm in length (in Morrison and Hunt 2007, p. 333).

Morrison and Hunt (Morrison and Hunt, 2007) found that the relatively large endemic *Turbo sandwicensis* was initially the top-ranking taxon at Nualolo Kai, comprising 64% of the earliest occupation layer. However, by the 19th century the species represented only 19% of the recovered remains by shell weight, and had dropped from 1 to 2 in rank order abundance. In contrast, the smaller *Nerita picea* (ca. 14 mm in length) increased in both absolute and relative abundance through time. In the earliest occupation it comprised only 3% of the assemblage but

by the late period had increased to 16% by weight, with an associated increase in rank from 5 to 4. In general, these findings are consistent with the intermediate position of *Turbo* in our ABM-modelled relative scale of vulnerability. However, it is more vulnerable in this Hawaiian context because of the lack of larger taxa. This third case illustrates that resilience is situational. While energetic return rates (essentially meat weights) may be relatively constant for a given taxon, prey rankings are defined by the array of taxa present within any given habitat.

DISCUSSION

In this final section we discuss how ABM, when integrated with theoretical expectations and archaeological observations, helps us build more refined understandings of human activities in the past. Notably the agent-based models are simple and lacking in realism, focusing on a limited number of variables. Nonetheless, they are invaluable for iteratively exploring particular sets of interactions and making predictions about what we might expect in archaeological contexts given limited and explicit assumptions. They assist in identifying empirical departures from theoretical expectations and in designing further tests with other variables to better understand past processes. With these general ideas in mind we identify three contributions of the current ABM analysis.

An initial result is that our ABM reproduces outcomes predicated by life history (e.g., Codding et al., 2014) and optimal foraging theory (e.g., Broughton, 2002). One specific prediction is that molluscan taxa which reach reproductive maturity comparatively late in life are more likely to be vulnerable to human foragers. Similarly, taxa of larger body size provide higher energetic returns but also are more vulnerable to anthropogenic resource depression. An advantage of the ABM analysis is that we have strictly specified the model conditions and can be confident that our results are not affected by taphonomic conditions, recovery procedures, spatial variability or sampling. Further, the ABM not only replicates expected outcomes but also gives insights into relative thresholds of vulnerability and the conditions under which resilience is maintained. These features are most visible through our use of different parameter settings which help define the points at which any given taxon moves from resilient to vulnerable.

The three archaeological case studies described herein, from Tikopia, Aitutaki, and Hawai'i, demonstrate that the predicted outcomes have been observed in multiple empirical contexts. Moreover, similar temporal declines and examples of prey switching are common elsewhere in Polynesia. For example, at the To'aga site on Ofu Island (American Samoa), *Turbo setosus* is the highest ranked taxon by weight (main trench) and remains so across an approximately 2,200-year occupation sequence (Nagaoka, 1993). Similarly, at the Fatumafuti site on Tutuila Island (American Samoa), Morrison and Addison (Morrison and Addison, 2008) observed a decline in *Tridacna* and

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