# **Exploring a Marine Ecosystem with a General Complex Adaptive System Model**

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#### Abstract

Lotka-Volterra equations The classic present mathematically robust and well-validated set of idealized equations for describing the predator-prey relationship found in many domains. Here we present results of formulating these equations using a Complex Adaptive Systems model, simulated using Agent-based Modeling techniques. This method allows for (a) closer study of the complex dynamics that are found in these systems, (b) greater understanding of the agent interactions, and (c) more realistic simulation outputs. In so doing, we have uncovered a novel relationship between the amount of resources found at the lowest tropic level of a hypothesized ecosystem and the highest tropic level predators. explore these results in detail, and highlight their applicability to a real-world marine ecosystem.

## Introduction

It is becoming increasingly evident that certain stocks of fish are becoming severely depleted, are in danger of collapse, or have already collapsed in many parts of the world. To meet these challenges it is incumbent on researchers and industry experts to better understand the complex dynamics of marine ecosystems, as well as the impact of the fishing industry upon these ecosystems, in order to promote more sustainable practices.

One of the foundations of ecology dynamics is the Lotka-Volterra equations for predator-prey populations. These equations are both mathematically robust and widely accepted, but are also general in nature. Thus, they are limited by the assumptions imposed upon them, including, for example, the assumption of unlimited resources available to the prey population.

In order to address this limitation, we have adapted our general Complex Adaptive Systems model (32) to the domain of a marine ecosystem. By simulating the classic Lotka-Volterra equations in a stochastic, Agent-based

Model (ABM), the complex dynamics of predator and prey interactions can be more fully explored.

# **Background**

First proposed in 1925-1926, the Lotka-Volterra (LV) equations are a pair of first-order, non-linear differential equations that govern the relationship between two types of interacting species. The equations have periodic solutions, such that an increase in the prey population generates a temporary increase in the predator population, which increases predation levels. Increased predation reverses the growth of the prey population, which in turn reduces the predator population. Once the prey reverses again to a growth phase, the cycle is complete.

Let x equal the prey population and dx equal the rate at which the prey population increases. In the expression of LV, dx = Axdt, where A is the growth rate of the prey and dt is the change in time t, the prey population x continues to increase exponentially in the absence of some predator.

We define y as the predator population, and dx = -Bxydt as the rate of prey consumption by the predators. Thus the overall growth rate in the prey population is given by combining these two equations:

$$\frac{dx}{dt} = Ax - Bxy$$

For the predator population, growth is dependent on C, the rate of predator removal from the system (either by death or migration), and D, the growth rate for predators. Predators therefore also have two equations to express the change in population over time: 1) dy = -Cydt, and 2) dy = Dydt, which combine to form the following equation:

$$\frac{dy}{dt} = -Cy + Dxy$$

The solution to these two equations is periodic, with the predator population curve always following the prey curve. Figure 1 gives a graphical example of typical LV solution. These dynamics are well-understood and have been validated in both computer simulations and real-world studies.

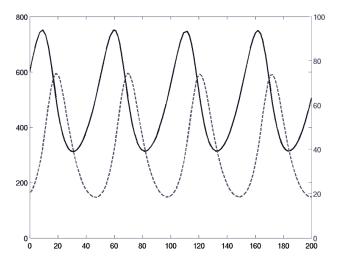


Figure 1. Graphical illustration of a periodic solution to a typical LV equation, showing the change in population levels for the predator (dashed) and prey (solid) populations.

# **Complex Adaptive Systems**

A Complex Adaptive System (CAS) is a collection of autonomous, heterogeneous agents, whose behavior is defined with a limited number of rules. These rules govern the type and number of interactions among agents. The power of the system mainly comes from agents' interactions, not the agents themselves. Each individual interaction generally has only a small or limited direct effect on the outcome of the system. However, the aggregate product of the thousands of these interactions and the accumulated feedbacks among the agents can have a large effect.

CAS is a method developed in physics, mathematics, and computational sciences (1–6) to deal with the issue of complexity and complex systems, and has been redefined by a growing number of applications in domains as diverse as biology, political science, economics, and health care. Complex, dynamical systems are comprised of parts that interact with each other. They are complex because it is impossible to predict their behavior by simply understanding the function of each part, primarily because the function of the overall system depends on the way these parts interact with each other. The diversity of these parts and the richness of their interactions endow a complex system with its capacity to innovate, adapt, and sustain itself. At the same time, these global, emergent

properties cannot be studied or readily understood by only inspecting the parts in isolation.

Agent-Based Modeling (ABM) denotes a method for implementing a CAS in order to provide a computational environment for exploring characteristics of complex systems in a controlled setting. The Santa Fe Institute was one of the pioneers in this field. Since the mid-20th century there has been a steady effort to apply CAS to areas as diverse as economics, business, political science, government, military, archeology, biology, and ecology (7–30). Designing CAS applications is challenging because researchers often do not know what key variables need to be captured to successfully model the system. There has been some evidence that the CAS method itself can be used to identify key system variables (31).

# The General CAS Model

We have previously applied our current general CAS model to soft-tissue cancer, the immune system response, and political dissent in a polity (32). This model uses only a few simple agents that act with only local knowledge. Although the micro rules these agents follow are simple, the macro system exhibits multiple levels of agent feedback, is self-organizing and self-regulating, and exhibits non-linear behavior for substantial regions of the parameter space. The simplicity of the model gives it the flexibility to be adaptable to different application domains. It also suggests that common fundamental principles may be working across these domains.

# **Experimental Design**

This general CAS model has been adapted here for application to a marine ecosystem. In this paper we show the results from a simple Complex Adaptive System (CAS) model of two species interacting in a predator-prey relationship. By utilizing the CAS framework for simulating this relationship our model can easily incorporate more realistic stochastic elements than one would find in a purely mathematical solution to these phenomena. Nevertheless, as seen in Figure 2, our model easily captures the cyclical nature of this well-understood dynamic.

#### **Model Details**

The key assumptions of the Lotka-Volterra equations are: 1) unlimited food availability to the prey population; 2) the predator population depends entirely on the prey for food; 3) the natural growth rates for both populations are proportional to their sizes; and 4) the environment doesn't change to the benefit of either population.

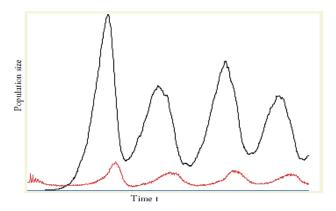


Figure 2. The periodic oscillations of a typical setup for the marine ecosystem model. As in Figure 1, the predator cycles (red, lower curve) follow the prey cycles (black, upper curve).

Our investigation into a deeper understanding of the predator-prey dynamics began by changing assumption (1) above: we tailored the general simulation model so that the food available to the prey population is adjustable. The simulation environment is a torus grid with 151\*151 grid cells, with a total number of 22,801 cells.

There are four populations in this model: food (generated by the simulation stochastically as a constant rate per grid cell); fish (the prey population); eggs (generated by the fish as a positive function of the amount of food consumed); and predators (which reproduce as a positive function of the number of fish consumed). This model is not intended to be thoroughly realistic, but rather to capture the basic properties of the predator-prey-food relationship. As such, the environment is largely homogeneous: that is, there are no variations in sea temperature, depth, or ocean currents. Furthermore, each tropic level is represented by a single species, without the complex dynamics of functionally similar, individual species. These refinements can be selectively added to future models in an iterative process, to ensure that the basic dynamics at each level are well-understood before proceeding to the next level of complexity.

As with the environment, both the fish and the predator populations are largely homogeneous, different only in their current state variables: individual age, x-y coordinates, and current amount of food consumed.

#### Results

When the simulation is run with a baseline test-case (food production set to 20% chance of positive growth per cell, per simulation time step) it settles to an equilibrium relationship between the fish and predator populations. The fish population is somewhat more variable than the predators, stabilizing generally between ~1100 and ~1200

individuals. The predator population stabilizes at  $\sim$ 170 individuals.

# **Changes to Baseline Test-Case**

This model's settings are designed to de-emphasize the cyclical volatility of that found in Figure 2, in order to more clearly see the overall population trends of each species. In terms of age, the equilibrium age for predators is about 50% higher than that of fish. These outcomes can be adjusted by changing the parameters and the environment to more realistically capture real-world species. However in the current simulation, what is important to note is how the food supply – the lowest trophic level – affects the relationship between the midand high-trophic level populations. Figure 3 shows the change in population counts as the food supply is increased from 20% to 30%, and again to 40%.

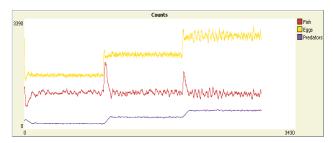


Figure 3. 3000 simulation time-steps showing population counts at 20%, 30% and 40% food levels (1000 steps per level).

Initially the fish population increases in response to an increased food supply. The predator population also increases as their food supply (the fish) becomes more abundant. Remarkably however, the gains in fish population are only temporary, and are quickly offset by the increased predation rates (as shown by the temporary spikes in fish population in Figure 3). Thus, the fish population returns to the same equilibrium level as that found with a lower supply of food: only the predator population remains elevated. This result indicates that all the gains resulting from the increased food supply are transferred to the high-trophic-level predators.

## **Average Age of Populations**

When we examine the changes in the average age for each population, we see that the fish – though reproducing at a faster rate – don't live as long as they do at a lower food supply. Even as they reproduce faster, they are also consumed faster, so that their average age is much lower, thus preserving the equilibrium population size. The predators, faced with an increased food supply, are much more efficient in catching the fish; thus, their population increases. Unlike the fish however, their average age – after stabilizing at a higher population – is essentially

unchanged. Figure 4 shows changes in the mean population age for each of the three populations.

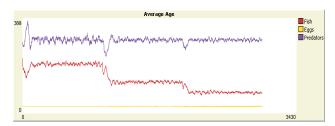


Figure 4. 3000 simulation time-steps showing mean population age at 20%, 30% and 40% food levels (1000 steps per level); same simulation run as in Figure 2.

Though we suspect that other factors will ultimately influence these dynamics to some degree, the overall picture is clear: the highest trophic level – the predators – are greatly affected by the food available at the lowest trophic level, while the species in the mid-trophic level – the fish – are affected only in average age, not in population. This is a surprising and new result not found in the literature for a three-trophic-level simulation.

#### **Continued Food Increase**

The previous results revealed what happens when the lowest tropic level – the fish food supply – changes from 20%, to 30%, and again to 40%. As noted previously, the LV equations assume an infinite food supply for the fish. What happens when this food supply is continually increased, even beyond 40%?

Figure 5 shows the results as the food supply is incrementally increased, from the initial 20% as before, with 1% added each 100 simulation time steps.

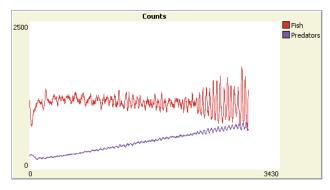


Figure 5. Food supply increased by 1% every 100 ticks, from 20% to 49% (3000 ticks total).

As we can see, both populations become more volatile at the 42% rate. At this point the increased food still seems to translate into only the predators becoming more populous. The prey population, while much more volatile than the predators, seems to still oscillate around a stable level.

Figure 6 shows the average age of each population. Again, the predators are holding fairly stable, while the fish tend to die quicker as the simulation progresses and their food increases. However, Figure 6 also shows that the average age of the fish, while still decreasing, is doing so at a slower rate. That is, the fish average age seems to be approaching some minimum, which may account for the increased volatility in their population numbers.

Spatially, the simulation environment is becoming less homogenous at this point. Up until the critical point of 42% food growth, the environment indicates very little variability, and the four populations are well-mixed throughout. Once the volatility in the fish and predators becomes apparent, we can see the effect this has on the spatial relationships between these populations. Figure 7 shows that the food is allowed to grow unconsumed in places, and that the agent populations begin to cluster.

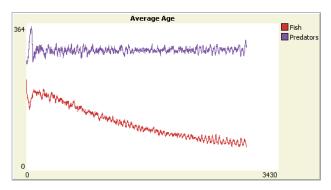


Figure 6. Food supply increased by 1% every 100 ticks, from 20% to 49% (3000 ticks total).

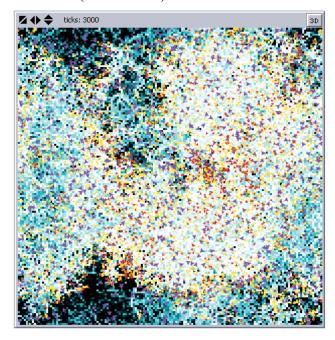


Figure 7. Spatial clustering of the four populations. Food is allowed to grow in areas (dark gray) where the fish are absent.

If the simulation is allowed to continue and the food levels are increased even more, then the volatility of the populations becomes even more pronounced. Also, the fish population, which had previously oscillated around a stable amount, now seems to be increasing somewhat. The dramatic swings between the high and low population levels are much more extreme, but the highs increase much more than the lows decrease. Further, the average age for the fish population seems to have bottomed out. Figures 8 and 9 illustrate this increased volatility.

The increased volatility is problematic for the fish and predator species. Due to the stochastic nature of the ABM, and the spatial clustering of the populations, there is an increased chance that one of the populations will drop to zero and completely die out. In this particular simulation, this occurred at approximately 4200 ticks, at a food growth rate of 61%. Repeated simulation runs confirmed that this level is indeed unsustainable.

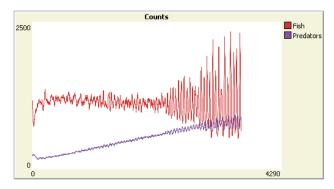


Figure 8. Graph of higher volatility of population size after 3600 simulation time steps. Food growth rater of 55%.

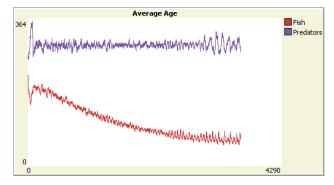


Figure 9. Graph of average population age for fish and predators after 3600 simulation time steps.

## **Discussion**

These results make it clear that, in this simulation at least, increasing the food at the lowest tropic level will eventually cause the fish and predator population levels to become highly unstable, to the point where they will eventually die out completely. In light of the assumption under the LV equations that food levels are not just large,

but infinite, it is worth exploring in more detail exactly how this ABM realization of the predator-prey dynamics differs from the idealized equations.

The first major difference is that the LV equations assume a "natural" level of population growth. This is a rate that is simply proportional to the size of the population. In the equations outlined previously, the term A is the growth rate for the fish, and D is the growth rate for the predators. Both of these terms are assumed to be constant in LV.

In our model, however, these terms are dependant upon consumption rates. Thus they are both stochastic and variable, based on the spatial distribution of the agents. Further, this has the effect of connecting the two equations, in that the consumption rate of the predators is directly proportional to the predators' rate of reproduction. The more the predators eat – and indeed, the same goes for the prey – the more they reproduce.

The spatial distribution, therefore, makes a noticeable difference. The fish continually move around the simulation environment looking for food and trying to avoid predators. If a fish finds itself on the same patch as a predator, it will move away without eating. If there is no predator, it will look for food. The fish will eat the food and not swim away as long as food is available. If there is no food, it will move away, without another chance to eat during the present "turn."

Likewise, the predators move around looking for prey. The predator will eat any fish found on the same patch, and move without eating if no fish are present. Therefore, both the consumption rates and the reproduction rates are not constant in this model, but rather dependent upon how efficiently both the fish and the predators can find food.

As food grows more on the patches (with the increased rate of growth), the fish have an easier time, and thus reproduce more. This is tempered by the fact that, as the fish population increases, the predators subsequently have an easier time finding food. Unlike the assumptions underlying the LV equations, neither the fish nor the predators are guaranteed to find food each time step. Therefore, the consumption rate of the predators eating the prey, coefficient B in the LV equations, is not a constant. Further, since the predators' growth is directly dependent on how much food is consumed, coefficient D is related to B.

The growth of the fish is also no longer held constant. In this simulation, the variable nature of A is not only due to how much food is present locally, but also due to the presence of predators locally. If a fish sees a predator, it moves away without eating even if food is present. Further, local competition among the fishes can also affect A: as the number of fishes increases, finding food, even in the absence of predators, becomes more difficult.

Finally, both the fish and the predators in this simulation have a *lifetime*. The LV equations account for a lifetime for the predators – the C coefficient – but not

one for the fish. However, in an ABM even this coefficient is not held constant. As the predators are increasing in numbers, their average age decreases due to an influx of new agents. Conversely, as their numbers are decreasing their average age is increasing, and a higher percentage of them are therefore dying due to old age. This same mechanism occurs in the fish population, even though the LV equations assume that the *only* way fish can die is due to predation.

For the baseline model results, with food growth rate at 20%, the predators consume fish at an average rate of  $\sim 0.05$  fish per turn. Meanwhile, the fish consumption rate of food is an average rate of  $\sim 0.24$  times per turn ... that is, each fish successfully finds food approximately once every four turns.

Table 1 shows how these two rates change under different rates of food growth, after stabilizing at each new level.

Table 1. Consumption rates for fish and predators at various levels of food growth.

	Predator Rate	Fish Rate
0.20 food growth	0.049	0.244
0.30 food growth	0.049	0.364
0.40 food growth	0.048	0.485
0.50 food growth	0.049	0.600

These results confirm two previously noted observations. The first observation, that the predator population increases when resources for the fish are increased, may at first seem to contradict the fact that the predators consumption rate doesn't change. More predators would indicate more competition among them, and thus seem to warrant a lower consumption rate. However, the increased resources for the fish, as we have seen, help produce *more fish* that are consumed *more quickly*. Therefore, as the number of predators increases, so does the availability of prey. As these two factors balance out, competition among the predators remains stable under all four scenarios.

The previous result of the fish population not changing due to more resources is also consistent with these results. The amount of competition among the fishes is not affected by their population, as their numbers remain the same. Indeed, since there is more food available, but no more fish, we would expect that they find food much more readily. These results confirm this, as the fish consumption rate increases along with food growth. In fact, these two seem to increase by almost exactly the same amount. Food growth from 0.20 to 0.30 is a 50% increase, while the fish consumption rate is also a  $\sim$ 50% increase: from  $\sim$ 0.24 to  $\sim$ 0.36. Likewise, food growth from 0.20 to 0.40 is a 100% increase, and the fish consumption rate also doubles, from  $\sim$ 0.24 to  $\sim$ 0.48.

As with the total population numbers, the volatility of these consumption rates also begins to increase. Comparing Figure 10 and Figure 11 with Figure 5 illustrates this, as the food growth rate increases by 0.01 every 100 steps, ranging from 0.20 to 0.49 (3000 simulation steps, as in Figure 5). In Figure 12 and Figure 13 we continue to increase the food growth rate, so that this can be compared to Figure 8.

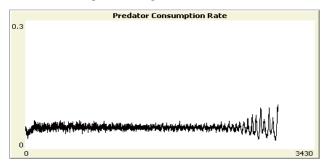


Figure 10. Predator consumption rates as food growth is slowly increased from 0.20 to 0.49 (3000 ticks). Y-axis range from 0 to 0.3.

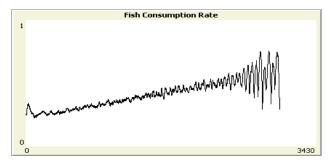


Figure 11. Fish consumption rates as food growth is slowly increased from 0.20 to 0.49 (3000 ticks). Y-axis range from 0 to 1.0

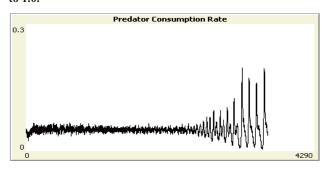


Figure 12. Predator consumption rates as food growth is slowly increased from 0.20 to 0.55 (3600 ticks). Y-axis range from 0 to 0.3.

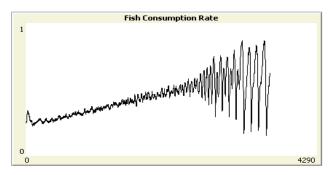


Figure 13. Fish consumption rates as food growth is slowly increased from 0.20 to 0.55 (3600 ticks). Y-axis range from 0 to 1.0.

The outputs of the simulation allow us to directly measure key parameters of both fish and predator growth, predator consumption of fish, and the rates that both species die due to limited lifetime. Further, we can see how each of these parameters is affected under different scenarios of food growth rates at the lowest tropic level. Table 2 shows these results for 0.20, 0.30, and 0.40 food growth rates.

Table 2. Fish and predator consumption rates (taken from Table 1), new fish and predator rates per turn, and rate of agent death due to limited lifetime, for three different levels of resource growth: 0.20, 0.30, and 0.40.

	0.20	0.30	0.40
Fish Consumption (table 1)	0.244	0.364	0.485
New fish rate per tick	73.6	144.1	223.9
Fish die rate (from old age)	9.3	1.6	0.2
Pred Consumption (table 1)	0.049	0.049	0.048
New Pred rate per tick	2.2	4.9	7.6
Pred die rate (from old age)	2.2	4.8	7.8

We know from Table 1 that the fish increase their consumption rates as the available resources increase, while the predators do not (due to an increase in the predator population). Table 2 shows that, similarly, the "new fish" rate increases along with this higher rate of consumption, even though we know from Figure 3 that the fish population does not increase. The "new predator" rate increases also; however, as with the "new fish" rate, this is an absolute measurement. As the population of predators has increased as well, this is to be expected. Also note the rate that fish die due to limited lifetime. This number is reduced greatly at each higher level of resources. We know from Figure 4 that the age of the fish population is dramatically lower. That fewer of them die from "old age" also reflects this fact. Under these conditions fish simply don't live as long.

## **Conclusions and Future Work**

The simulation model presented here represents a realization of the classic LV equations in the form of an ABM. Though not intended to be thoroughly realistic, this model does contain more realism than the idealized LV equations are intended to represent. For example, the agents – both predator and prey – have a limited lifetime. They also have consumption rates, along with the related rates of reproduction, that are stochastic: dependent on the spatial distribution of agents which represent a chance, rather than a guarantee, of finding resources.

While this model does present a degree of greater realism, there are many factors in a true marine ecosystem that have not yet been factored in. This was done purposefully, so that the complex dynamics of this system can be fully explored before additional complications are added to the model.

In general, the additional factors that will be added to future iterations of this model are ones that make either the environment, or the agent populations, more heterogeneous. For the environment, it may be useful to allow for variation of such factors as ocean depth and temperature, and ocean currents. For the agents, greater heterogeneity can be added by allowing each species to grow, perhaps moving from one tropic level to another. Also, a real-world ecosystem would contain multiple species at each level, rather than just one. Further, each of these species would have slightly different attributes than those found here, such as how fast they can move, how much food is required, and a varying ability to escape predators.

Finally, we note that the direct relationship between consumption of food and reproduction is not as clear-cut as represented in this model. While it seems clear that the lack of food in a real ecosystem would be a limiting factor on population growth, it is not as clear to what degree an *excess* of food is directly translated into *more* growth. This is also where considerations of seasonality would presumably make a difference as well, as many species of fish reproduce only during certain times of the year, or in certain places.

Nevertheless, this model's interesting and surprising main result – that the increased resources at the lowest tropic level accrue completely to the top-level predators – indicate that a more thorough investigation of this phenomenon is needed. Such behavior, if validated with real-world marine ecosystems, could have many practical implications for the management of ocean fisheries. For example, some fishing techniques include a method whereby the fishing nets are anchored on the seabed. As the net is dragged along behind the ship, the seafloor in this area is completely disrupted, and many decades worth of accumulated marine structures are destroyed. Previous generations of fisherman may have assumed this "doesn't matter" to the species being harvested, as such target

species are generally one or more levels away from these low-tropic-level life forms.

However, if a robust ecosystem at the lowest tropic level can accrue all the way up to the highest tropic level, then such fishing practices may in fact represent twice the disruption to their robustness: reducing the absolute numbers directly via harvesting, and reducing their future resources by destroying their ultimate source of food.

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