Population Dynamics of Western Atlantic Bluefin Tuna:

Modeling the Impacts of Fishing using Differential Equations

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Abstract:

West Atlantic Bluefin tuna (*Thunnus thynnus*) present a classic case study in the dynamic interaction between ecological function and impact by humans. As a species, tuna are important to marine ecologies in many regions and to global fishing industries. Better understanding of tuna population dynamics is therefore important not just for predicting future ecological impacts as populations change, but also for forecasting economic impacts to the fishing and seafood industry. We model population dynamics of West Atlantic Bluefin tuna from 1970-2000 using both (1) a logistic growth differential equation, and (2) a set of three coupled differential equations reflecting the three age classes within the population structure of tuna. Regardless of the initial value, the tuna population under the logistic model approaches an equilibrium population of 595,000 individuals. This value does not accurately reflect the population of tuna in the year 2000; therefore, we also develop a set of three differential equations for three size classes of tuna defined as *J*, juvenile (years 1-2), *A*, adolescent (years 3-7), and *M*, mature (years 8+). Both analytical and numerical solutions of these three equations grow exponentially. Finally, we add complexity to our second model using Euler's Method solutions of three additional scenarios: (1) a carrying capacity, (2) seasonally variable fishing rates, and (3) both a carrying capacity and seasonal fishing combined. The carrying capacity and combined scenarios approach equilibrium population sizes, while the seasonal fishing scenario alone exponential growth like the original third order differential equation. Therefore, while seasonal fishing may be important for tuna populations within the year, it does not affect the overall behavior of populations over a multi-year timescale.

Problem Statement:

Tuna population dynamics are important to fishing industries and global economies, as well as to maintaining fully functional marine ecosystems. However, as with many economically important fish populations, tuna numbers have declined substantially with the advent of commercial fishing practices. In particular, the western Atlantic Bluefin Tuna has declined from an estimated 1,200,000 individuals in 1970 to approximately 595,000 individuals by the year 2000 (Reynolds and Jennings, 2005, Porch, 2005). Furthermore, the number of mature individuals has declined from 200,000 to 20,000 over the same time span, which may indicate that the population decline will be even more dramatic in the future (Porch, 2005). The western Atlantic Bluefin Tuna represents a particularly threatened population as sexual maturity is not reached until the fish is approximately 175 kg at about the age of 10 years, while fishing regulations allow any fish above 6.4 kg (equivalent to an age of 1-2 years) to be harvested (Fromentin, 2006, Porch, 2005).

In light of the importance of the tuna populations to both conservation ecology and the economy, we develop a model which will analyze the effects of fishing and the interaction between fishing practices and natural parameters which may help to establish sustainable fishing guidelines. Such a model could be used to evaluate the current health of tuna stocks in the West Atlantic, and to predict future changes in these stocks with and without changes in regulations. Ultimately, this will allow us to comment on the sustainability of published recommendations for target harvest levels and provide input to policy agencies such as the International Commission for the Conservation of Atlantic Tunas (ICCAT).

Model Design:

Model 1: Logistic growth of tuna with no age structure

The first model relies on the following assumptions:

1. The tuna population grows logistically.
2. There is only one age group of tuna.
3. The number of fishermen is constant.
4. The number of fish removed by fishing is proportional to the size of the tuna population.

Therefore, the change in the population of western Atlantic Bluefin Tuna may be represented by the differential equation

$$\frac{dF}{dt} = r\left(1 - \frac{F}{K}\right)F - bF, \tag{1}$$

where F is the size of the fish population, t is time in years after 1970, r is the population growth rate, K is the environmental carrying capacity, and b is the fishing rate. Estimated values and units for these parameters are provided in Table 1.

Parameter	Estimated Value	Units	Source
r	1.13	tuna per year	Reynolds and Jennings, 2000
K	1200000	# tuna (total)	Reynolds and Jennings, 2000
b	0.2329	# tuna caught/# total tuna/year	Porch, 2005

Table 1: The parameter values listed below were used in equations 1-3 to determine the dynamics of the tuna population. The value for r was assumed to be the same as that for Northern Cod (Reynolds and Jennings, 2000). While the population growth rate for Northern Cod may not be identical to that of western Atlantic Bluefin Tuna, the populations have shown similar responses to fishing over the 1970-2000 interval and have similar life-histories. Therefore, in the absence of actual data on the r value for tuna, the population growth rate for Northern Cod should be an adequate substitute.

Solutions for the equilibrium points of the model as well as an analytical solution are discussed in the Model Implementation and Analysis Section.

Model 2: Age structure of tuna populations

While the previously described model gives a first order estimate of the effects of fishing on tuna populations, age structure may play an important role in determining the susceptibility of western Atlantic Bluefin Tuna to overfishing because of the delayed sexual maturity. Therefore, the next model employs three coupled differential equations to account for age structure. The following assumptions are made:

1. The three age classes include the juveniles (J), adolescents (A), and mature adults (M).
2. These age classes each have specific natural mortality rates, fishing rates, reproductive rates, and growth rates. Note that reproductive rates for the juvenile and adolescent age groups are both zero.
3. Fish which are captured and then released survive. Therefore, any excess fish that are caught beyond quotas are thrown back and they all survive.
4. No juvenile fish will be harvested to reflect the moratorium on harvesting fish under 6.4 kg, which corresponds to an age of approximately 2 years (Porch, 2005).
5. Within each age class, tuna have a uniform age distribution. Thus, in any given year, the number of fish that grow to the next age class will be proportional to both the

number of fish in that age class and inversely proportional to the number of years that it takes for an individual to grow out of that stage. For example, $g_{J\text{-}A}$ is ½ years^{-1} and $g_{A\text{-}M}$ is 1/8 years^{-1}, where $g_{i\text{-}j}$ is the rate of growth from age group *i* to *j*.

6. The number of fishermen is constant.

Using these assumptions, the following three differential equations represent the growth (or decline) of tuna populations:

$$\frac{dJ}{dt} = \alpha M - J\left(g_{J-A} + m_J\right) \quad (2)$$

$$\frac{dA}{dt} = g_{J-A}J - A(g_{A-M} + m_A + h_A) \quad (3)$$

$$\frac{dM}{dt} = g_{A-M}A - M(m_M + h_M) \quad (4)$$

where α is the reproductive rate, m_i is the age specific natural mortality rate for age group *i*, h_i is the age specific harvest rate for age group *i*, and *J*, *A*, and *M* are the sizes of the juvenile, adolescent, and mature subgroups, respectively. Estimates for these parameters are provided in Table 2.

Parameter	Estimated Value	Units	Source
α	4.5	New *J*/total *M*/year	Fromentin and Powers, 2005
$g_{J\text{-}A}$	0.5	1/year	Rooker et al., 2007
$g_{A\text{-}M}$	0.125	1/year	Rooker et al., 2007
m_J	0.6	*J* dead/total *J*/year	Rooker et al., 2007
m_A	0.14	*A* dead/total *A*/year	Rooker et al., 2007
m_M	0.14	*M* dead/total *M*/year	Rooker et al., 2007
h_J	0	*J* caught/total *J*/year	See assumptions
h_A	0.2329	*A* caught/year	Porch, 2005
h_M	0.2329	*M* caught/total *M*/year	Porch, 2005

Table 2: The parameter values below will be used with Equations 4-6 to determine the behavior of the tuna population when age structure is taken into account. The value of *α* was determined by multiplying the number of eggs produced per tuna by the number of eggs that survive to the juvenile stage. As in the main text, *J*, *A*, and *M* refer to the number of tuna in the Juvenile, Adolescent, and Mature age groups.

After the analysis of the age structured model, two possible modifications are proposed. The first of these is a growth that is regulated by a carrying capacity for mature adults. The second is seasonal variation in hunting rates. The effects that these modifications have on the original model are discussed individually and then are analyzed together.

Model Implementation and Analysis

Model 1: Logistic growth of tuna with no age structure

Recall Equation 1 from the preceding section, which represents logistic growth of tuna populations with a constant number of fishermen, but does not account for age structure. According the existence and uniqueness theorem which states that for a first order, initial value problem, where $f(x, y)$ and $\frac{\partial f}{\partial y}$ are both continuous on some rectangle *R* such that $(x_o,y_o)\epsilon R$, there exists and interval I centered at x_o and a unique solution $y(x)$ on I such that $y(x)$ is a solution to the initial value problem. Therefore, for Equation 1,

$$f(t,F) = r\left(1 - \frac{F}{K}\right)F - bF,$$

$$\text{and } \frac{\partial f\,(t,F)}{\partial F} = r - \frac{2r}{K}F - b.$$

Therefore, both $f(t\,,F)$ and $\frac{\partial f\,(t,F)}{\partial F}$ are continuous on R^2, and so there exists a unique solution F for any given initial value of F.

Having determined that unique solutions exist for any initial value problem in our model, the next step is to determine what equilibrium solutions exist. By setting $\frac{dF}{dt}$ equal to zero and solving for F, the following two equilibrium solutions are obtained:

$$F = K\left(1 - \frac{b}{r}\right) \text{ and } F = 0. \tag{5}$$

It is possible to solve this equation explicitly for F. Separation of variables in Equation 1 yields

$$\frac{dF}{\left(1 - \frac{b}{r} - \frac{F}{K}\right)F} = rdt.$$

After partial fraction decomposition, the following equation is obtained:

$$\frac{1}{1 - \frac{b}{r}}\left(\frac{1}{F} + \frac{\frac{1}{K}}{1 - \frac{b}{r} - \frac{F}{K}}\right)dF = rdt.$$

Integration of the above equation yields the equation

$$\frac{1}{1 - \frac{b}{r}}\left[lnF - ln\left(K - \frac{bK}{r} - F\right)\right] = rt + C.$$

where C is an integration constant dependent on the initial values. Once the equation has been simplified by combining the natural logarithms and e is raised to the power of each side, the following equation is obtained:

$$\left[\frac{F}{K - \frac{bK}{r} - F}\right]^{\frac{1}{1 - \frac{b}{r}}} = Ce^{rt}.$$

Raising both sides to the power of $\left(1 - \frac{b}{r}\right)$ and multiplying by the denominator yields:

$$F = Ce^{rt\left(1 - \frac{b}{r}\right)}\left[K - \frac{bK}{r} - F\right].$$

It is then relatively simple to solve algebraically for F:

$$F = \frac{Ce^{rt\left(1 - \frac{b}{r}\right)}\left[K - \frac{bK}{r}\right]}{1 + Ce^{rt\left(1 - \frac{b}{r}\right)}}. \tag{6}$$

We used the parameter values listed in Table 1, an initial population size of 1,200,000 individuals based on the population size in 1970, and Equation 3 to calculate that C = -4.852. Using this value in Equation 3 yields a population size after 30 years of 952,673 total individuals

(Figure 3). This estimate is clearly too high to represent the actual data, which indicate that there were only approximately 595,000 individuals by the year 2000. The MATLAB® code for this analysis, as well as all other analyses, is provided in Appendix 1.

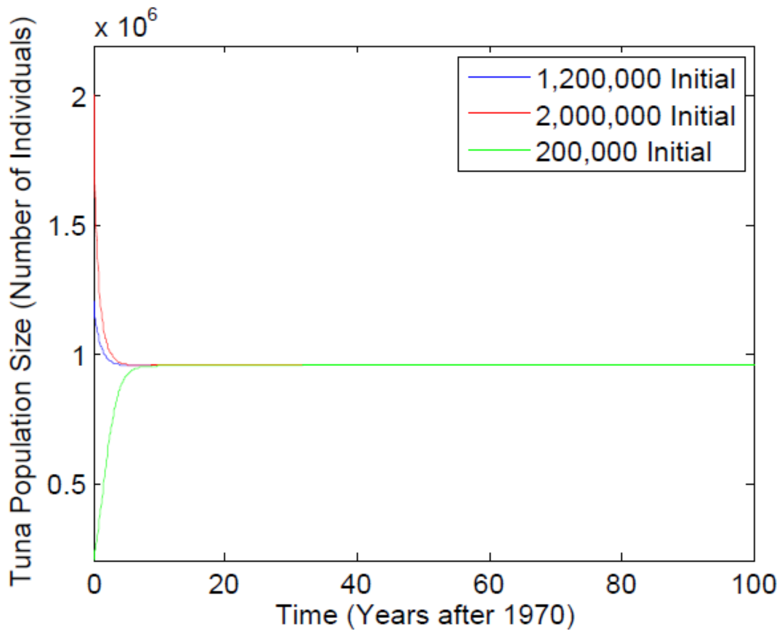

Figure 1: The graph above shows the dynamics of tuna populations over time using the parameter values given in Table 1 and initial populations of 1,200,000 tuna (blue), 2,000,000 tuna (red), and 200,000 tuna (green). The long term behavior is the same for all initial values; the population size approaches 952,673 tuna for large values of t.

Model 2: Age structure of the tuna populations

Recall Equations 2-4, which represent age structured tuna populations with no carrying capacity. It is possible to solve for the equilibrium points again by setting all three derivatives to zero. However, because all three equations are linear, it is possible to simply read off that the only equilibrium point will be:

$$J=A=M=0.$$

Euler's Method can be used to find a numerical solution to Equations 2-4. Euler's Method uses the assumption that for small changes in t, the change in the value of the variables will also be small. Therefore, for small Δt,

$$J(t) \approx J(t-\Delta t) + \Delta t\left[\alpha M(t) - \left(g_{J-A} + m_J\right)J(t)\right], \tag{7}$$

$$A(t) \approx A(t-\Delta t) + \Delta t\left[g_{J-A}J(t) - (g_{A-M} + m_A + h_A)A(t)\right], \tag{8}$$

$$\text{and } M(t) \approx M(t-\Delta t) + \Delta t[g_{A-M}A(t) - (m_M + h_M)M(t)]. \tag{9}$$

Approximate solutions for Equations 2-4 using the Euler Method are plotted in Figure 2a. Because Equations 2-4 are all first order linear differential equations, it is also possible to simplify them into a single higher order differential equation which can then be solved analytically. The first step in obtaining an exact solution is to solve Equation 2 for M and Equation 3 for J:

$$M = \frac{J' + (g_{J-A} + m_J)J}{\alpha}, \qquad (10)$$

$$\text{and } J = \frac{A' + (g_{A-M} + m_A + h_A)A}{g_{J-A}}. \qquad (11)$$

Taking the derivative of *M* and the first and second derivatives of *J* with respect to *t* yields:

$$M' = \frac{J'' + (g_{J-A} + m_J)J'}{\alpha}, \qquad (12)$$

$$J' = \frac{A'' + (g_{A-M} + m_A + h_A)A'}{g_{J-A}}, \qquad (13)$$

$$\text{and } J'' = \frac{A''' + (g_{A-M} + m_A + h_A)A''}{g_{J-A}}. \qquad (14)$$

Substituting these equations into Equation 4 yields a single higher order linear differential equation:

$$\frac{A'''}{g_{J-A}*\alpha} + \left(\frac{g_{A-M} + m_A + h_A + g_{J-A} + m_J}{g_{J-A}*\alpha}\right)A'' + \left(\frac{(g_{J-A} + m_J)(g_{A-M} + m_A + h_A)}{g_{J-A}*\alpha}\right)A' = g_{A-M} * A - (m_M + h_M)\left[\frac{A''}{g_{J-A}*\alpha} + \left(\frac{g_{A-M} + m_A + h_A + g_{J-A} + m_J}{g_{J-A}*\alpha}\right)A' + \left(\frac{(g_{J-A} + m_J)(g_{A-M} + m_A + h_A)}{g_{J-A}*\alpha}\right)A\right].$$

Combining like terms and multiplying by $g_{J-A} * \alpha$ yields a homogeneous, third order differential equation:

$$aA''' + bA'' + cA' + dA = 0,$$

where the coefficients are given by:

$$a = 1,$$

$$b = [g_{A-M} + m_A + h_A + g_{J-A} + m_J + m_M + h_M],$$

$$c = [(g_{J-A} + m_J)(g_{A-M} + m_A + h_A) + (m_M + h_M)(g_{A-M} + m_A + h_A + g_{J-A} + m_J)],$$

$$d = [(g_{J-A} + m_J)(g_{A-M} + m_A + h_A)(m_M + h_M) - g_{A-M} * g_{J-A} * \alpha].$$

Using a solution of the form

$$A = e^{mt},$$

it then follows that the roots can be solved using the cubic equation:

$$am^3 + bm^2 + cm + d = 0.$$

Using the parameter values listed in Table 2 and a cubic equation calculator (1728 Software Systems, 2010), the following roots were found:

$$m \approx 0.1267, \text{ and}$$

$$m \approx -1.049 \pm 0.5562i.$$

Therefore, the equation for A is given by:

$$A = c_1 e^{0.1267t} + e^{-1.049t}[c_2 \cos(0.5562t) + c_3 \sin(0.5562t)]. \qquad (15)$$

Taking the first and second derivatives of A with respect to *t* and substituting Equation 15 into Equations 10 and 11 yields equations with the general forms:

$$J = [ae^{m_1 t} - be^{m_2 t}\{c\cos(kt) + d\sin(kt)\} + ke^{m_2 t}\{\cos(kt) - \sin(kt)\} + g(he^{m_1 t} + e^{m_2 t}[j\cos(kt) + l\sin(kt)])], \qquad (16)$$

$$M = [{m_1}^2 e^{m_1 t} + {m_2}^2 e^{m_2 t}\{j\cos(kt) + l\sin(kt)\} - 2km_2 e^{m_2 t}\{j\cos(kt) - l\sin(kt)\} - k^2 e^{m_2 t}\{l\cos(kt) + j\sin(kt)\}] + n[m_1 p e^{m_1 t} + m_2 e^{m_2 t}\{j\cos(kt) + l\sin(kt)\} + ke^{m_2 t}\{l\cos(kt) - j\sin(kt)\}] + q[m_1 e^{m_1 t} - m_2 e^{m_2 t}\{j\cos(kt) + l\sin(kt)\} + ke^{m_2 t}\{l\cos(kt) - j\sin(kt)\}], \qquad (17)$$

where a, b, c, d, g, h, j, k, l, m_1, m_2, n, p, and q are constants. See Appendix 2 for the values of these coefficients. Using the parameter values listed in Table 2, Equations 15-17 are plotted in Figure 2b. Note the similarity of long term behavior in the numerical and analytic solutions. In both, the tuna populations increase exponentially with time. The predicted population sizes of all three age groups are provided in Table 3 (below), and indicate that population sizes for juveniles, adolescents, and mature adults in the year 2000 should exceed 4 million, 3.6 million, and 1.0 million individuals, respectively. Since this is even less representative of the observed behavior of the tuna populations since 1970 than the logistic model proposed in Model 1, two improvements to the model are suggested below. These will be dealt with individually first, and then will be implemented together to observe their combined effect.

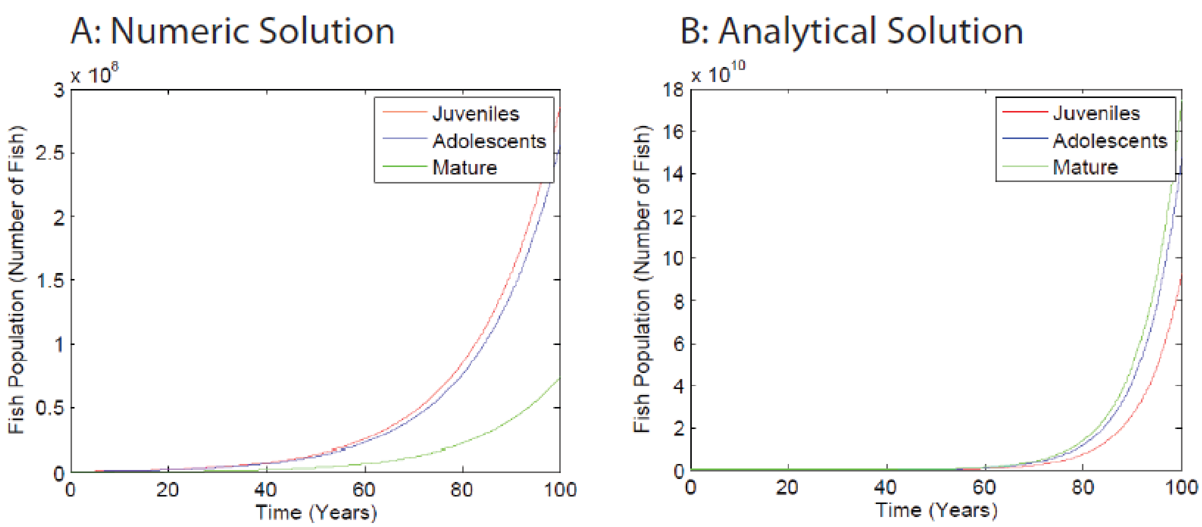

Figure 2: The graphs above show the results of (A) the numeric solution and (B) the analytical solution to Model 2, which is an age structured model without carrying capacity or seasonal variations in parameter values. Both solutions indicate similar long term behavior of the model, and indicate that the population size approaches infinity over long time scales. Modifications to the model to better represent actual population dynamics are suggested below.

Model 2 with carrying capacity

The first modification to the age-structured model is the incorporation of a carrying capacity. In order to accomplish this, Equation 2 is modified to:

$$\frac{dJ}{dt} = \alpha M\left(1 - \frac{M}{K}\right) - J(g_{J-A} + m_J + h_J), \qquad (18)$$

Where K is the carrying capacity for mature tuna (in number of fish), and all other variables and parameters are defined as above. The differential equations for change in adolescent and mature population sizes over time are still given by Equations 3 and 4, respectively. These equations can be solved numerically, again using the Euler Method described above, with the slight modification that:

$$J(t) \approx J(t-\Delta t) + \Delta t\left[\alpha M(t)\left(1-\frac{M(t)}{K}\right) - \left(g_{J-A} + m_J\right)J(t)\right]. \tag{19}$$

Using Equation 19 together with Equations 8 and 9 (the Euler approximations for $A(t)$ and $M(t)$, a numerical solution was found and is provided in Figure 3. The effect of adding a carrying capacity is that, after initial fluctuations in the population sizes, the juvenile, adolescent, and mature populations approach constant sizes of 162,000, 163,000, and 55,000 individuals, respectively. See Table 3 below for predicted population sizes after 30 and 100 years.

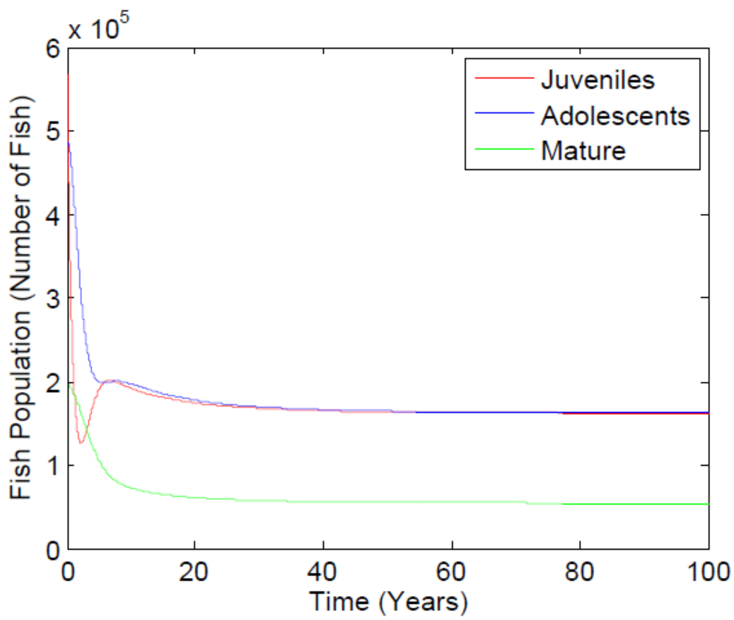

Figure 3: The graph above is the numeric solution to Model 2 after the growth rate is modified to reflect a mature adult carrying capacity. These results indicate a stable equilibrium, with relative abundances of juveniles, adolescents, and adults of approximately 163,000, 163,000, and 55,000 individuals, respectively. While not an exact match, this compares relatively well with observed population sizes in the year 2000 of 243,000, 347,000, and 30,000 individuals.

Model 2 with seasonal hunting

Equations 3 and 4 can also be altered to incorporate a seasonal hunting pattern. As a first approximation, we assume that hunting rate over the course of a year can be parameterized by a sin curve. Thus, the hunting rate at time *t* is

$$h = h_{1i}(\sin(h_{2i}t) + 1),$$

where h_{1i} is a constant to represent the amplitude of the fishing rate for age class *i* and h_{2i} is a constant to represent the frequency of the changes in fishing rate for age class *i*. The 1 is added to ensure that the minimum fishing rate is never less than zero. Because there is only one open fishing season and one closed fishing season per year (NOAA, 2009), then one complete cycle of fluctuation in fishing rates should occur between t=0 and t=1. Thus, for $\sin(h_2 t)$ to go through one entire cycle, h_2 must equal 2π. The value of h_1 must be such that the average fishing rate over the course of the year equals the average annual fishing rate from Table 2. Therefore,

$$h = \int_0^1 h_{1i}(\sin(2\pi t) + 1)\,dt.$$

Evaluating the integral yields:

$$h = h_{1i}(-\cos(2\pi t) + t)|_0^1 = h_{1i}.$$

Thus, the value of h_1 for each age group is the average annual fishing rate for that age group. When incorporated into Equations 3 and 4, this yields the new differential equations

$$\frac{dA}{dt} == g_{J-A}J - A(g_{A-M} + m_A + h_A(\sin(2\pi t) + 1)), \qquad (20)$$

and $$\frac{dM}{dt} = g_{A-M}A - m_M M - h_M M = g_{A-M}A - M(m_M + h_M(\sin(2\pi t) + 1)). \qquad (21)$$

The Euler Method was used as above to find a numerical solution to Equations 20 and 21 were used with Equation 2 to determine the effect of adding seasonal variability in hunting rates. The following modifications were made to Equations 8 and 9:

$$A(t) \approx A(t - \Delta t) + \Delta t\left[g_{J-A}J(t) - (g_{A-M} + m_A + h_A(\sin(2\pi t) + 1))A(t)\right],$$

and $$M(t) \approx M(t - \Delta t) + \Delta t[g_{A-M}A(t) - (m_M + h_M(\sin(2\pi t) + 1))M(t)].$$

Equation 7 was still used to approximate $J(t)$. The results of the numerical solution are shown in Figure 4. The model predicts that population sizes for each age class will be the same after 30 and 100 years as reported for Model 2 without any modifications (Table 3).

The seasonal hunting and carrying capacity modifications can also be made in conjunction with each other. The Euler Method was used to find numerical solutions to Equations 18, 20, and 21, using their respective approximations (see above). The population sizes predicted using the combined model are the same as when a carrying capacity is used without the seasonal fishing variability (Table 3). These results are plotted in Figure 5.

Model 2 version	**Juveniles after 30 years**	**Adolescents after 30 years**	**Mature tuna after 30 years**	**Juveniles after 100 years**	**Adolescents after 100 years**	**Mature tuna after 100 years**
Euler approximation	4,050,500	3,625,100	1,044,800	285,330,000	255,360,000	73,360,100
Euler carrying capacity	167,940	169,670	57,476	162,720	163,410	54,779
Euler seasonal	4,050,500	3,625,100	1,044,800	285,330,000	255,360,000	73,601,000
Euler combined	167,940	169,670	57,476	162,720	163,410	54,779

Table 3: The table above provides the results from an Euler approximation of each of the different variations of the model described above. "Euler approximation" indicates Model 2 (an age structured model without a specified carrying capacity), and the subsequent rows represent the population sizes after 30 or 100 years for Model 2 with modifications for a mature adult carrying capacity, seasonal variation in fishing rates, or both.

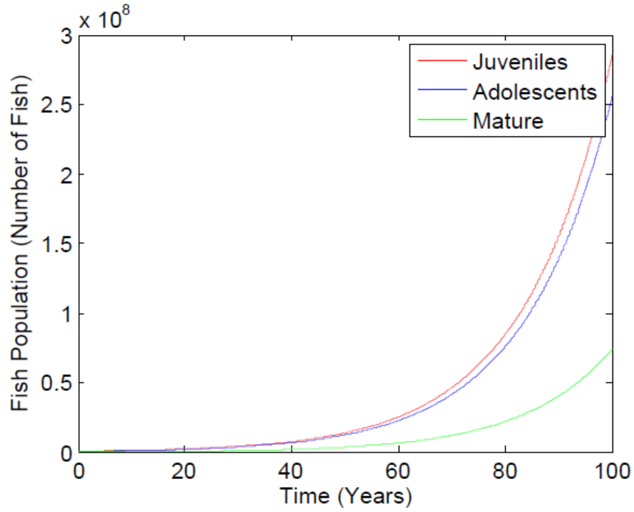

Figure 4: The graph above shows the results from the analytical solution of the age structured Model 2 with modifications to incorporate seasonal variation in fishing rates. The results are identical to those for the unmodified age structured model.

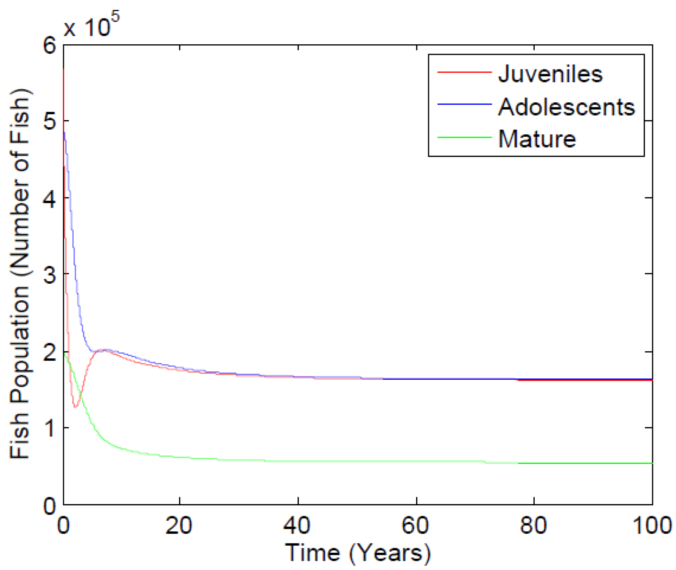

Figure 5: The graph above provides the results for the age structured model when both a mature adult carrying capacity and seasonal variation in fishing rates are accounted for. The results are identical to the age structured model with only a carrying capacity.

Discussion

Model 1: Logistic Growth

Our first model provides results that could be intuitively reasonable; however, the results do not match empirical evidence. Our model predicts that an equilibrium population level is possible in the presence of fishing, although this equilibrium is at a lower number of tuna individuals than without fishing. Specifically, the total population size according to our model using empirical parameter estimates is 952,673 individuals, while actual data indicate that the total population size is actually closer to 595,000 individuals. This discrepancy suggests that there are aspects of tuna population dynamics that are not accounted for using a simple logistic model. One likely reason for this is the delay in sexual maturity in tuna, which could result in many individuals being harvested prior to spawning. Thus, an age structured model could help to better describe the dynamics of tuna populations when harvesting of adolescent individuals is permitted.

Model 2: Age structure of the tuna populations

The second model accounts for the delay in sexual maturity in order to better describe the tuna population dynamics. However, the model predicts exponential increase in the size of all three population sizes, regardless of the initial population sizes. This result is clearly not representative of the dramatic decline in tuna populations between the years 1970 and 2000, and so indicate that further modifications are required to account for the long term behavior of tuna populations.

Because the result indicates that tuna populations grow exponentially over large time scales, the failure of Model 2 to describe actual population patterns is most likely due to the assumption of unbounded growth. Therefore, adding a carrying capacity could have a significant impact in making the results more reasonable. Therefore, the expression for growth was modified to include a carrying capacity for mature individuals. It would be simple to instead incorporate a carrying capacity based on the total number of individuals; however, the mature individuals are the only breeding individuals and are by far the largest individuals (Rooker et al., 2007). Therefore, we used the assumption that the number of juveniles and even adolescents has a relatively smaller impact on resource availability than the number of mature individuals, and so a carrying capacity based on mature individuals only has a stronger theoretical justification than a carrying capacity based on all age classes. A possible avenue for future research is to determine both the validity of and the model sensitivity to this assumption. Furthermore, the carrying capacity could instead be incorporated as a fourth differential equation in terms of the total population and the set of four differential equations could then be solved analytically in order to compare the results with our present model.

The effect of adding a carrying capacity for mature individuals is that the tuna population reaches an equilibrium value. Using a numerical solution, our model predicts that after 30 years, representing the year 2000, the population sizes for juveniles, adolescents, and mature adults are 170,000, 168,000, and 57,000 individuals, respectively. The data for actual Western Atlantic Bluefin Tuna are that by the year 2000, the population sizes were approximately 243,000, 347,000, and 30,000 individuals, respectively, assuming that individuals are evenly distributed through the 2-4 year age class. Furthermore, the populations sizes in 2000 were all significantly different from the nearly constant population sizes over the preceding 20 years. During this earlier time, the population sizes were 123,000, 217,000 and 40,000 individuals, respectively.

While there are obvious differences between the results of Model 2 with a carrying capacity and empirical data on tuna population sizes, the overall similarity between these results is encouraging. Thus, this model is a strong candidate for further exploration. The possible uses and interpretations of this model will be discussed further after the effects of adding a seasonal fishing component to Model 2 are addressed.

When an expression to represent seasonal fishing is added to the model without a carrying capacity, the results are nearly identical to Model 2 without any modifications. Again, the population size of all three age groups increases exponentially regardless of initial conditions. This is due to the continued assumption of unbounded growth.

Equations incorporating seasonal variation in fishing rates can also be used in conjunction with a mature adult carrying capacity. In this case, the long term behavior of the model is very similar to that when a carrying capacity is incorporated without seasonal harvesting. This raises the question as to why seasonal variation in fishing rates has very little effect on the results of our model. The most likely explanation for these trends is that tuna reproduce and grow on multiannual time scales. Because the long term behavior of tuna populations depends on how many fish in each age group survive long enough to move into the next age class, the population dynamics depend on how many fish are removed over the course of a year, regardless of when during that year they are removed. In other words, concentration of fishing during only part of the year has very little, if any, effect on long term population dynamics.

It is possible that the effects of adding seasonal fishing variability would be more pronounced if seasonal breeding were incorporated into the model. Thus, if fishing could occur either before or after annual spawning events, variability in fishing rates could have a much more dramatic impact on tuna population dynamics.

These results indicate that Model 2 with a mature adult carrying capacity most accurately describes the empirical data for the behavior of tuna populations over the time since 1970. Therefore, this is the model that we recommend for further explorations. As mentioned above, one possible avenue for further research is to incorporate seasonal breeding into the model, and then determine the effects that seasonal fishing have on the population dynamics. Furthermore, many of the parameter values presented in Table 2 have considerable uncertainty. Sensitivity tests of our model could provide policy makers with a range of potential outcomes given any set fishing policy. The results of both our first and second model indicate that stable equilibria are possible for tuna populations, even in the presence of significant fishing, and Model 2 provides a means for determining the approximate size of this equilibrium population. Therefore, by altering parameter values, it is possible for environmental planners to determine the optimal level of fishing to maintain ecologically functional population sizes while continuing to support the fishing industry. In particular, we recommend consideration of adjustments to the fishing rate of adolescent individuals in order to maintain a larger breeding population of tuna.

Conclusions

We develop two models to model Western Atlantic Bluefin Tuna (BFT) population for 1970 to 2000. The first model is a simple logistic growth model which produces population estimates that are too high to accurately represent tuna population in the year 2000. We believe this is due to the model not reflecting the delayed sexual maturity of BFT such that overall population is severely affected when tuna individuals are harvested before they reach the reproductive age and can contribute to tuna population. To improve the model and account for the delay in sexual maturity for BFT, we develop a second model that incorporates three age groups: juvenile, adolescent and mature. Each age class is associated with specific mortality, fishing, reproductive and growth rates. When Euler's method is applied to produce numeric solutions for this model, we observed that tuna population was predicted to increase exponentially with time. To add additional complexity to the age structured model, we modified the differential equation to account for a carrying capacity for mature individuals, preventing exponential growth at large time values. Under this iteration of the second model, populations for each age class approached a constant size that approximated but did not fully match observed populations values for 2000. In addition to carrying capacity, seasonal fishing patterns were also added to the age structured model. However, this modification approximated long term behavior exactly as did the original age structured model without a seasonal harvest component. This indicates that seasonal fishing rates do not have an effect on long term population growth, unless perhaps some other factor was taken into account such as seasonal breeding.

The age structured model with carrying capacity included was the model that best accounted for trends in tuna population dynamics of all the models developed in this paper. Thus the age structured, carrying capacity model most closely modeled BFT population dynamics. While this simple model accounts for trends and patterns in tuna population growth reasonably well for 1970 to 2000, it fails to predict values for tuna population in 2000 that match observed data. Therefore further exploration and expansion of this model could produce a more accurate means of predicting population growth. Investigation into the parameters used in the differential equations and the degree to which their variation affects predicted population size could yield a more accurate model. The resulting model could then be used by policymakers, environmental analysts and industry members to improve tuna fishing regulations to maximize conservation of this ecosystem and species.

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Author Contribution

Marie Hoerner and Esther Bowen conceived of the initial differential equations. All authors contributed to collecting data for parameters and revising equations to account for more variables. Marie Hoerner typed up equations and contributed most to data analysis. All authors helped with MATLAB®, with Marie Hoerner contributing most. Esther Bowen wrote Appendix 1 and created multiple figures presented in the paper. Cassie Kontur compiled references. All authors discussed results and contributed to writing.

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Appendix 1: Matlab codes used in modeling tuna populations

Code 1, “Fish:” The below code plots our Model 1 logistic equation for time 0 through 100 years. Three plots were created using C values reflecting three sets of initial conditions; code for a C value of ___ is shown below.

```
%t=time
%Fa=Fish population for initial value of 1,200,000 tuna
%Fb=Fish population for initial value of 2,000,000 tuna
%Fc=Fish population for initial value of 200,000 tuna
%Ca=Coefficient for initial value of 1,200,000 tuna
%Cb=Coefficient for initial value of 2,000,000 tuna
%Cc=Coefficient for initial value of 200,000 tuna
%r=Intrinsic growth rate of tuna
%K= Carrying Capacity for tuna
%b=Fishing rate

t=(0:0.1:100);
Fa=zeros(size(t));
Fb=zeros(size(t));
Fc=zeros(size(t));

Ca=-4.852;
Cb=-1.9096;
Cc=0.2657;

r=1.13;
K=1200000;
b=0.23;

Fa=(Ca*exp(r*t*(1-b/r))*(K-b*K/r))./(1+Ca*exp(r*t*(1-b/r)));
Fb=(Cb*exp(r*t*(1-b/r))*(K-b*K/r))./(1+Cb*exp(r*t*(1-b/r)));
Fc=(Cc*exp(r*t*(1-b/r))*(K-b*K/r))./(1+Cc*exp(r*t*(1-b/r)));

figure(1)
clf
plot(t,Fa,'b');
hold on
plot(t,Fb,'r');
plot(t,Fc,'g');
legend('1,200,000 Initial', '2,000,000 Initial', '200,000 Initial')

xlabel('Time (Years after 1970)')
ylabel('Tuna Population Size (Number of Individuals)')
```

Code 2, “Fish2:” The below code performs an Euler numerical approximation for given parameters for tuna population.

```
clear

%new model for group starting with fish.m
%J = Juvenile
%A = Adolescent
%M = Mature
%g_IJ = growth rate from state I to state J
%h_I = fishing rate of state I
%m_I = natural mortality rate of state I
%a = reproduction rate
%t = time

a = 4.5;
g_JA = 0.5;
g_AM = 0.125;
m_J = 0.6;
m_A = 0.14;
m_M = 0.14;
h_J = 0;
h_A = 0.2329;
h_M = 0.2329;

dt = 0.001;
T = 100;
tot_dt = (T/dt)+1;

t = (0:dt:T);

J = zeros(size(t));
A = zeros(size(t));
M = zeros(size(t));

J(1) = 567000;
A(1) = 483000;
M(1) = 200000;

for n = 1:tot_dt-1

J(n+1) = J(n) + dt*(a*M(n) -J(n)*(g_JA+m_J+h_J));
A(n+1) = A(n) + dt*(g_JA*J(n)-A(n)*(g_AM+m_A+h_A));
M(n+1) = M(n) + dt*(g_AM*A(n)-M(n)*(m_M+h_M));

end
```

```
figure(1)
clf
plot(t,J,'r');
hold on
plot(t,A,'b');
plot(t,M,'g');

xlabel('Time (Years)')
ylabel('Fish Population (Number of Fish)')
legend('Juveniles','Adolescents','Mature');
```

Code 3, “Fish2carryingcap:” The below code performs an Euler numerical approximation for given parameters for tuna population, incorporating a carrying capacity of 200,000 individuals.

```
clear

%new model for group starting with fish.m
%J = Juvenile
%A = Adolescent
%M = Mature
%g_IJ = growth rate from state I to state J
%h_I = fishing rate of state I
%m_I = natural mortality rate of state I
%a = reproduction rate
%t = time
%K=Mature carrying capacity

a = 4.5;
g_JA = 0.5;
g_AM = 0.125;
m_J = 0.6;
m_A = 0.14;
m_M = 0.14;
h_J = 0;
h_A = 0.2329;
h_M = 0.2329;
K=200000

dt = 0.001;
T = 100;
tot_dt = (T/dt)+1;

t = (0:dt:T);
```

```
J = zeros(size(t));
A = zeros(size(t));
M = zeros(size(t));

J(1) = 567000;
A(1) = 483000;
M(1) = 200000;

for n = 1:tot_dt-1

J(n+1) = J(n) + dt*(a*M(n).*(1-M(n)/K)-J(n)*(g_JA+m_J+h_J));
A(n+1) = A(n) + dt*(g_JA*J(n)-A(n)*(g_AM+m_A+h_A));
M(n+1) = M(n) + dt*(g_AM*A(n)-M(n)*(m_M+h_M));

end

figure(1)
clf
plot(t,J,'r');
hold on
plot(t,A,'b');
plot(t,M,'g');

xlabel('Time (Years)')
ylabel('Fish Population (Number of Fish)')
legend('Juveniles','Adolescents','Mature');

J(30)
A(30)
M(30)
```

Code 4, “Fish2season:” The below code performs an Euler numerical approximation for given parameters for tuna population, incorporating a sine component to model seasonal hunting of tuna.

```
clear

%new model for group starting with fish.m
%J = Juvenile
%A = Adolescent
%M = Mature
%g_IJ = growth rate from state I to state J
%h_I = fishing rate of state I
%m_I = natural mortality rate of state I
%a = reproduction rate
```

```
%t = time

a = 4.5;
g_JA = 0.5;
g_AM = 0.125;
m_J = 0.6;
m_A = 0.14;
m_M = 0.14;
h_J = 0;
h_A = 0.2329;
h_M = 0.2329;

dt = 0.001;
T = 100;
tot_dt = (T/dt)+1;
t = (0:dt:T);

J = zeros(size(t));
A = zeros(size(t));
M = zeros(size(t));

J(1) = 567000;
A(1) = 483000;
M(1) = 200000;

for n = 1:tot_dt-1

J(n+1) = J(n) + dt*(a*M(n)-J(n)*(g_JA+m_J+h_J));
A(n+1) = A(n) + dt*(g_JA*J(n)-A(n).*(g_AM+m_A+h_A*(sin(2*pi*n)+1)));
M(n+1) = M(n) + dt*(g_AM*A(n)-M(n).*(m_M+h_M*(sin(2*pi*n)+1)));

end

figure(1)
clf
plot(t,J,'r');
hold on
plot(t,A,'b');
plot(t,M,'g');

xlabel('Time (Years)')
ylabel('Fish Population (Number of Fish)')
legend('Juveniles','Adolescents','Mature');
```

Code 5, “Fish2combined:” The below code performs an Euler numerical approximation for given parameters for tuna population, incorporating a sine component to model seasonal hunting of tuna as well as a carrying capacity for mature individuals.

```
clear

%new model for group starting with fish.m
%J = Juvenile
%A = Adolescent
%M = Mature
%g_IJ = growth rate from state I to state J
%h_I = fishing rate of state I
%m_I = natural mortality rate of state I
%a = reproduction rate
%t = time
%K=Mature carrying capacity

a = 4.5;
g_JA = 0.5;
g_AM = 0.125;
m_J = 0.6;
m_A = 0.14;
m_M = 0.14;
h_J = 0;
h_A = 0.2329;
h_M = 0.2329;
K=200000

dt = 0.001;
T = 100;
tot_dt = (T/dt)+1;
t = (0:dt:T);

J = zeros(size(t));
A = zeros(size(t));
M = zeros(size(t));

J(1) = 567000;
A(1) = 483000;
M(1) = 200000;

for n = 1:tot_dt-1

J(n+1) = J(n) + dt*(a*M(n).*(1-M(n)/K)-J(n)*(g_JA+m_J+h_J));
A(n+1) = A(n) + dt*(g_JA*J(n)-A(n).*(g_AM+m_A+h_A*(sin(2*pi*n)+1)));
M(n+1) = M(n) + dt*(g_AM*A(n)-M(n).*(m_M+h_M*(sin(2*pi*n)+1)));
```

```
end

figure(1)
clf
plot(t,J,'r');
hold on
plot(t,A,'b');
plot(t,M,'g');

xlabel('Time (Years)')
ylabel('Fish Population (Number of Fish)')
legend('Juveniles','Adolescents','Mature');
```

Code 6, “Fish3:” The below code plots the analytically-derived solution to our differential equation modeling juvenile, adolescent and mature tuna individuals for the global West Atlantic bluefin tuna for time 0 through 100 years with initial condition ____.

```
%t=time
%J=Juvenile population
%A=Adolescent population
%M=Mature population
%gij=Growth rate of i to j
%mi=natural mortality rate of i
%hi=fishing rate of i
%alpha=reproduction rate in juveniles/mature
%ci=constant i calculated from initial value problem

t=(0:0.01:100);

J=zeros(size(t));
A=zeros(size(t));
M=zeros(size(t));

ca=464446.5181;
cb=18553.48193;
cc=-20280.8933;

gja=.5;
gam=.125;
mj=.6;
ma=.14;
mm=.14;
ha=.2329;
hm=.2329;
```

```
alpha=4.5;

A=(ca*exp(.1266882286537815*t)+exp(1.0487441143268907*t).*(cb*cos(.556246133447245*
t)+cc*sin(.556246133447245*t)));

J=((ca*.1266882286537815*exp(.1266882286537815*t)-
1.0487441143268907*exp(1.0487441143268907*t).*(cb*cos(.556246133447245*t)+cc*sin(.55
6246133447245*t))+exp(1.0487441143268907*t).*(cc*.556246133447245*cos(.556246133447
245*t)*cb*.556246133447245*sin(.556246133447245*t))+(gam+ma+ha)*(ca*exp(.1266882286
537815*t)+exp(1.0487441143268907*t).*(cb*cos(.556246133447245*t)+cc*sin(.55624613344
7245*t)))));

M=((((ca*(.1266882286537815)^2*exp(.1266882286537815*t)+(1.0487441143268907)^2*exp(
1.0487441143268907*t).*(cb*cos(.556246133447245*t)+cc*sin(.556246133447245*t))2*1.048
7441143268907*exp(1.0487441143268907*t).*(cc*.556246133447245*cos(.556246133447245
*t)-cb*.556246133447245*sin(.556246133447245*t))+exp(-1.0487441143268907*t).*(-
cb*.556246133447245^2*cos(.556246133447245*t)-
cc*.556246133447245^2*sin(.556246133447245*t)))+(gam+ma+ha)*(ca*exp(.1266882286537
815*t)+exp(1.0487441143268907*t).*(cb*cos(.556246133447245*t)+cc*sin(.55624613344724
5*t))))/gja+(gja+mj)/alpha*((ca*.1266882286537815*exp(.1266882286537815*t)1.0487441143
268907*exp(1.0487441143268907*t).*(cb*cos(.556246133447245*t)+cc*sin(.55624613344724
5*t))+exp(1.0487441143268907*t).*(cc*.556246133447245*cos(.556246133447245*t)cb*.556
246133447245*sin(.556246133447245*t))+(gam+ma+ha)*(ca*exp(.1266882286537815*t)+exp
(1.0487441143268907*t).*(cb*cos(.556246133447245*t)+cc*sin(.556246133447245*t)))));

figure(1)
clf
plot(t,J,'r');
hold on
plot(t,A,'b');
plot(t,M,'g');

xlabel('Time (Years)')
ylabel('Fish Population (Number of Fish)')
legend('Juveniles','Adolescents','Mature');
```

Appendix 2: Analytical Solution to Model 2

The equations below are the analytical solutions with the full expressions for the coefficients for the Juvenile and Mature adult populations. The analytical solution for the Adolescents is included in the main text, as are values for all of the parameters in these equations.

$$J = \frac{1}{g_{J-A}}[0.1267 * c_1 e^{0.1267t} - 1.049e^{-1.049t}\{c_2 \cos(0.5562t) + c_3 \sin(0.5562t)\} + e^{-1.049t}\{0.5562c_3 \cos(0.5562t) - 0.5562c_2 \sin(0.5562t)\} + (g_{A-M} + m_A + h_A)(c_1 e^{0.1267t} + e^{-1.049t}[c_2 \cos(0.5562t) + c_3 \sin(0.5562t)])],$$

$$M = \frac{1}{g_{J-A}}[0.1267^2 c_1 e^{0.1267t} + 1.049^2 e^{-1.049t}\{c_2 \cos(0.5562t) + c_3 \sin(0.5562t)\} - 2.098e^{-1.049t}\{0.5562c_3 \cos(0.5562t) - 0.5562c_2 \sin(0.5562t)\} + e^{-1.049t}\{-0.5562^2 c_2 \cos(0.5562t) - 0.5562^2 c_3 \sin(0.5562t)\}] + \frac{(g_{A-M} + m_A + h_A)}{g_{J-A}}[0.1267 * c_1 e^{0.1267t} - 1.049e^{-1.049t}\{c_2 \cos(0.5562t) + c_3 \sin(0.5562t)\} + e^{-1.049t}\{0.5562c_3 \cos(0.5562t) - 0.5562c_2 \sin(0.5562t)\}] + \frac{g_{J-A} + m_J}{\alpha * g_{J-A}}[0.1267 * c_1 e^{0.1267t} - 1.049e^{-1.049t}\{c_2 \cos(0.5562t) + c_3 \sin(0.5562t)\} + e^{-1.049t}\{0.5562c_3 \cos(0.5562t) - 0.5562c_2 \sin(0.5562t)\}].$$