THE EFFECT OF PURSE SEINE VESSEL HARVESTING IN THE EASTERN TROPICAL PACIFIC YELLOWFIN TUNA STOCK

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Abstract

In the eastern tropical Pacific, the purse-seine vessels captures yellowfin tuna as target species under three different fishing modes. We are interested in modeling the influence of these three different fishing modes in the tuna stock. We propose a system of differential equations to model the stock dynamics with proportional harvesting. We analyze a rescaled version of the model where a basic reproductive number was obtanied and interpreted in terms of the original parameters. The basic reproductive number was analyzed to study the effect of critical harvesting levels for each fishing mode. Finally we developed some numerical solutions using approximated parameters to study the effect of harvesting on the tuna stock dynamics.

1 Introduction

Marine fisheries are based on stocks [1] of wild animals such as fish, mollusks or crustaceans, living in their natural environment. Commonly, fish stocks are affected by fishing activities and possibly by other factors like evironmental pollution, etc. (Pitcher and Hart, 1982; Gulland, 1983).

In fishery management, the success of a fishery depends critically on the state of the fish stocks. The study of the possible effects of different fishing methods on a species stock (and on future catches) is therefore a very important topic for research and must take account of all other relevant factors like the multiple species relations and the change in natural environmental conditions (Pitcher and Hart, 1982; Laevastu and Favorite, 1988; National Research Council, 1998). The analysis of the direct impact of a fishery on a single species is an essential basis for more complex and more realistic analysis.

During the 1950's, the eastern tropical Pacific tuna fisheries began utilizing a purse-seine net. This method works by making a circle around the school of tunas with a large net (approximately one mile long), then the bottom of the net is closed catching a large amount of tunas. This revolutionary method enabled fisherman to catch tunas in high quantities (Joseph and Greenough, 1979). Today, this purse-seine fishery captures yellowfin tuna as the target species, under three different circumstances:

Tuna log-school fishing:

Tuna fish are collected under or near floating objects, usually some species of fish are attracted to floating objects for food and for protection against predators. This fishing method generally catches very small yellowfin tuna that have not reproduced, as well as other unwanted species called bycatch. The bycatch is generally returned to the ocean and therefore called discards. The bycatch for log-school fishing is an especially wide variety of animals, including other tuna like fishes, sharks, occasionally billfishes (marlin, swordfish, sailfish, etc.) and turtles (Arenas *et al*, 1992; Hall *et al*, 1992).

Tuna free school fishing:

[1] A fish stock can be defined as a collection of individual fish belonging to a given species that live in a particular geographic area at a particular time. The stock may contain only part of a population. Most importantly, the stock defined on a fishery management basis is managed as a unit whether or not it is identical to a genetic stock.(National Research Council, 1998. "Improving Fish Stock Stock Assessment". National Academy Press, Washington D.C., USA 177pp.)

Tuna fish are captured swimming by themselves or with some other like-sized tuna. In this stage, tunas have faster movements and do not stay behind a slow moving flotting object. This method catches small yellowfin tuna with a low proportion of reproductive fish. The bycatch is generally less varied than that of the log-school fishing, primarily other tuna like fishes (Hall et al, 1992).

Tuna-dolphin school fishing:

Tuna fish are found swimming with dolphins, this relation has not been fully understood. Some hypothesis establish that the tunas follow the dolphin herd because they have a higher ability of finding food, some others suggest that swimming with dolphins represents some kind of protection against predators. This fishing method generally catches large yellowfin. We assume that all of them have reproduced at least once. In this fishing mode, the bycatch are only dolphins.

During the 1960's, the incidental mortality of dolphins was very high, oscillating above 100,000 and sometimes reaching 500,000 animals killed in 1961 (Lo and Smith, 1986). In attempting to reduce the incidental mortality, fishermen developed special procedures and some technological improvements with which 99% of dolphins are released alive. As a result, in the 1990's, the incidental dolphin mortality is very low (less than 4,000 annualy since 1993).

In this project, we study possible effects of these three purse-seine fishing modes on the eastern tropical Pacific yellowfin tuna stock as a closed system. To achieve this, a system of differential equations was generated to model the stock dynamics, a basic reproductive number was obtained and a study related the effect of harvesting for each fishing mode was developed.

2 The Proposed Model

In this model, we assume the following sequence of school formation. The sequence starts in the formation of log schools with small non-reproductive tuna fish entering to the stock. Then at a fixed maturing rate, the medium size fish go to the free school stage where the reproduction starts at a low rate with a small proportion of sexually mature fish. In the same way, large sexually mature fish progress to the final dolphin school stage, where all fish have been reproduced at least once representing the highest reproductive rate.

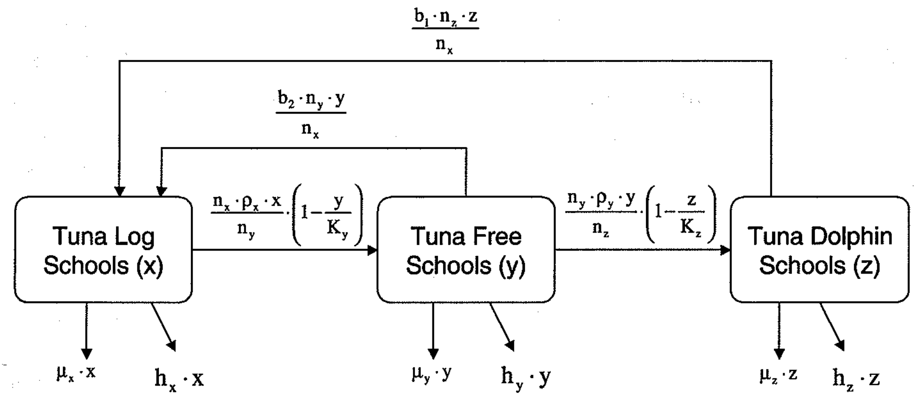

Figure 1. Tuna schooling model.

We proposed the following model of differential equations using the Verhulst logistic growth with proportional fishing (harvesting) terms:

$$
\begin{aligned}
\frac{dx}{dt} &= \frac{b_1 n_z z}{n_x} + \frac{b_2 n_y y}{n_x} - \rho_x x - \mu_x x - h_x x \\
\frac{dy}{dt} &= \frac{n_x}{\rho}{}_x x n_x \left(1 - \frac{y}{K_y}\right) - \rho_y y - \mu_y y - h_y y \\
\frac{dz}{dt} &= \frac{n_y \rho_y y}{n_z} \left(1 - \frac{z}{K_z}\right) - \mu_z z - h_z z
\end{aligned}
\tag{1}
$$

Table 1: The variables and parameters of the model

x number of schools (log school type)	μ_x tuna death rate of log schools
y number of schools (free school type)	μ_y tuna death rate of free schools
z number of schools (dolphin school type)	μ_z tuna death rate of dolphin schools
b_1 reproductive rate of tunas in dolphin schools	n_x average of tunas per log school
b_2 reproductive rate of tunas in free schools	n_y average of tunas per free school
K_y carrying capacity of tuna (free schools)	n_z average of tunas per dolphin school
K_z carrying capacity of tuna (dolphin schools)	h_z fishing rate on tuna log schools
ρ_x tuna maturing rate of log schools	h_y fishing rate on tuna free schools
ρ_y tuna maturing rate of free schools	h_z fishing rate on tuna-dolphin schools

We assume that $n_x > n_y > n_z$, i.e. the number of fish in each schooling stage is progresively less. We also assume, $\mu_x > \mu_y > \mu_z$, so that the natural mortality of fish on each schooling stage is reduced progresively.

With respect to the reproduction rates, $b_1 > b_2$ because the proportion of reproductive fish in the free school stage is lower compared with the tuna-dolphin schools (where all are sexualy mature).

Rescaling the system (1), we obtain the following adimensional system of equations:

$$\begin{aligned}\frac{d\overline{x}}{d\tau} &= a\overline{z} + b\overline{y} - (c_1 + H_1)\overline{x} \\ \frac{d\overline{y}}{d\tau} &= \overline{x}(1 - \overline{y}) - (c_2 + H_2)\overline{y} \\ \frac{d\overline{z}}{d\tau} &= m\overline{y}(1 - \overline{z}) - (1 + H_3)\overline{z}\end{aligned} \tag{2}$$

The rescaling details can be found in Appendix A.

3 Analysis of the Model and the Basic Reproductive Number

In this section we analyzed the rescaled version of the model. Initially the calculation of the resulting three equilibrium points of the system was performed. The analysis of equilibrium points was based on the trivial point $(x, y, z) = (0, 0, 0)$. We could not investigate the stability of the other two points analytically due to the number of parameters. The proof of the existence of a non-trivial point can be found in Appendix C. So, it was necessary to prove that the stock of tunas does not have stability at the trivial point to show that the stock size does not approach zero.

In the analysis of stability for the trival point, a linearization using the Jacobian matrix was performed, the characteristic equation was obtained and the Routh-Hurwitz criteria was applied to the rescaled model (see appendix B). From the characteristic equation, the corresponding coefficients we need that a_1, a_3 and $a_1a_2 - a_3$ must be greater than zero for stability. We take a_3 and by further manipulation, the basic reproductive number R_0 can be found, this condition is expressed as:

$$(-b + (c_1 + H_1)(c_2 + H_2))(1 + H_3) - am > 0 \tag{3}$$

Which is equivalent to:

$$b + am - (c_1 + H_1)(c_2 + H_2)(1 + H_3) < 0$$

Then, by further manipulations we arrive to

$$R_0 = \frac{am + b(1 + H_3)}{(c_1 + H_1)(c_2 + H_2)(1 + H_3)} < 1 \tag{4}$$

If $R_0 < 1$, then the trivial point $E_0 = (0, 0, 0)$ is stable, which in turn implies that the population goes to the zero (biologically it means that the tuna stock will go to zero).

So let $R_0 > 1$, this means that the trivial point is not stable, which implies that the tuna stock survives at catchable levels.

4 Interpretation of the Basic Reproductive Number

In terms of the original parameters, the basic reproductive number is given by:

$$\begin{aligned} R_0 &= \left(\frac{b_2}{\rho_y + \mu_y + h_y}\right)\left(\frac{\rho_x}{\rho_x + \mu_x + h_x}\right) + \cdots \\ &\quad + \left(\frac{b_1}{\mu_z + h_z}\right)\left(\frac{\rho_x}{\rho_x + \mu_x + h_x}\right)\left(\frac{\rho_y}{\rho_y + \mu_y + h_y}\right) \end{aligned} \tag{5}$$

R_0 represents the expected new schools generated during life span. We can rewrite as: $R_0 = R_{0y} + R_{0z}$ where

$$R_{0y} = \left(b_2 \frac{1}{\rho_y + \mu_y + h_y}\right)\left(\frac{\rho_x}{\rho_x + \mu_x + h_x}\right),$$

$$R_{0z} = \left(b_1 \frac{1}{\mu_z + h_z}\right)\left(\frac{\rho_x}{\rho_x + \mu_x + h_x}\right)\left(\frac{\rho_y}{\rho_y + \mu_y + h_y}\right),$$

where R_{0y} is the expected number of free schools produced by a free school during life span, and R_{0z} is the expected number of tuna dolphin schools produced by a tuna-dolphin school during life span. We can see that for R_{0y} the reproductive rate of the free schools b_2 is multiplied by the mean life span of the free schools $\frac{1}{\rho_y+\mu_y+h_y}$, which depends on the harvesting rate h_y. Since the new individuals enter to the stock in log school mode, we need to multiply this reproductive term by the probability of success from log school to free school mode, $P_{x,y} = \frac{\rho_x}{\rho_x+\mu_x+h_x}$, which also depends on the harvesting rate h_x.

Similarly, we can see that the reproductive rate of tuna-dolphin schools b_1 is multiplied by the mean life span of the tuna-dolphin schools $\frac{1}{\mu_z+h_z}$, which depends on the harvesting rate h_z. Again, we need to multiply this term by the probability of success from log schools to free schools, $P_{x,y} = \frac{\rho_x}{\rho_x+\mu_x+h_x}$, and by the probability of success from free schools to tuna-dolphin schools $P_{y,z} = \frac{\rho_y}{\rho_y+\mu_y+h_y}$, both depending on their respective harvesting rates h_x and h_y.

5 Critical Harvesting Levels

In this section we find the maximum values of h_x, h_y, h_z for which the stock survives at harvestable levels.

Let
$F(h_x, h_y, h_z) = \left(b_2\frac{1}{\rho_y+\mu_y+h_y}\right)\left(\frac{\rho_x}{\rho_x+\mu_x+h_x}\right)+\left(b_1\frac{1}{\mu_z+h_z}\right)\left(\frac{\rho_x}{\rho_x+\mu_x+h_x}\right)\left(\frac{\rho_y}{\rho_y+\mu_y+h_y}\right)$
If we harvest all the tuna-dolphin schools, that is, if we take,

$$\lim_{h_z\to\infty} F(h_x, h_y, h_z)$$

then we have:

$$\lim_{h_z\to\infty} F(h_x, h_y, h_z) = \overline{F}(h_x, h_y) = \left(b_2\frac{1}{\rho_y + \mu_y + h_y}\right)\left(\frac{\rho_x}{\rho_x + \mu_x + h_x}\right) = R_{0_y}$$

Now we have the function, $\overline{F}(h_x, h_y)$ that depends only on h_x, h_y. This means that the tuna stock depends on the harvesting done in the log and free schools. Note that the new R_0has to be greater than one for the tuna stock to survive at a catchable levels, this is

$$R_{0y} = \left(b_2\frac{1}{\rho_y + \mu_y + h_y}\right)\left(\frac{\rho_x}{\rho_x + \mu_x + h_x}\right) > 1.$$

If this is true, we can harvest all possible amounts of tuna-dolphin schools without endangering the stock.

In order to find the ranges of h_x, h_y, that make $R_{0_y} > 1$, we solve for one of the variables.

$$h_y < b_2 \frac{\rho_x}{\rho_x + \mu_x + h_x} - (\rho_y + \mu_y) \tag{6}$$

The maximum h_y is obtained when $h_x = 0$. Thus the range of h_y is

$$0 < h_y < b_2 \frac{\rho_x}{\rho_x + \mu_x} - (\rho_y + \mu_y)$$

Similarly the range of h_x is

$$0 < h_x < b_2 \frac{\rho_x}{\rho_y + \mu_y} - (\rho_x + \mu_x)$$

In order to make a graphical representation of these values we define the function

$$G(h_x) = b_2 \frac{\rho_x}{\rho_x + \mu_x + h_x} - (\rho_y + \mu_y).$$

The graph of $G(h_x)$ is

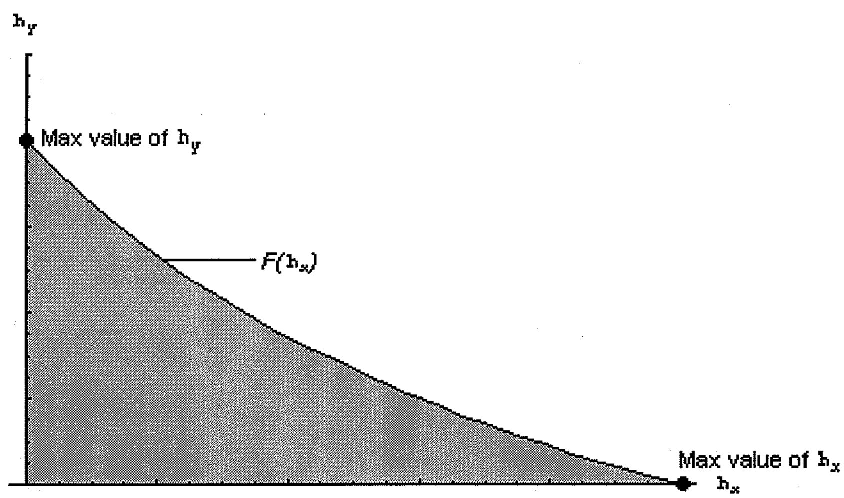

Figure 2. Stock survival values of h_x and h_y.

The shaded region of the graph represents the values of h_y and h_x for which the fish stock in general will always survive at sustainable levels.

6 Numerical Solutions

In order to represent explicitly the influence of the harvesting in the modeled tuna dynamics, we ran several numerical solutions of our system. These solutions were based on approximated parameters to better understand the functionality of the system equations.

The first numerical solution was run without harvesting, $(h_x, h_y, h_z) \to (0, 0, 0)$

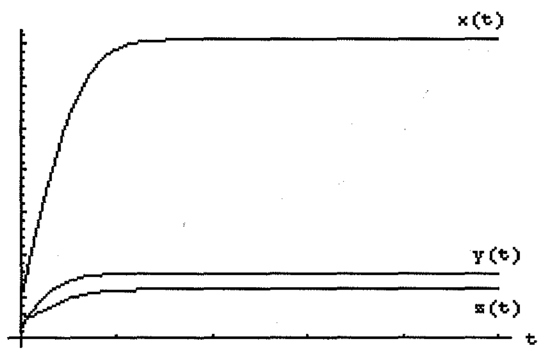

Figure 3. Non-harvesting numerical solution.

This graphical representation shows that the number of schools of those three types reach to their own maximum number of schools that remains theoretically constant.

The second representation is the case when $(h_x, h_y, h_z) \to (\infty, 0, 0)$

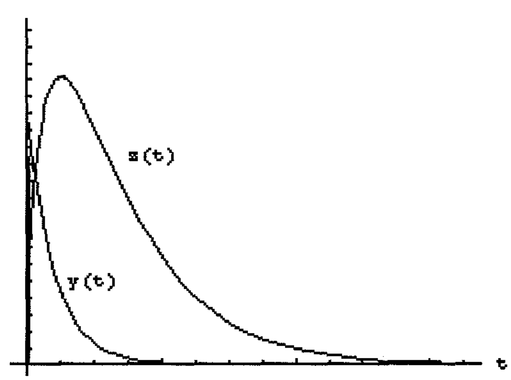

Figure 4. Only log schools harvested at high rates.

Here we see that if all of the log-schools are caught, even though the other kind of schools, free schools and dolphin schools are not harvested, the stock will be reduced theoretically to zero.

The case where $(h_x, h_y, h_z) \rightarrow (0, \infty, 0)$ is plotted in the following graph:

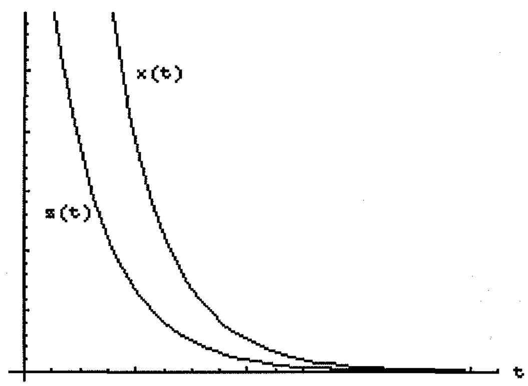

Figure 5. Only free schools harvested at high rates.

In this case we can clearly see that if we harvest all of the free schools the entire tuna stock will approach zero.

The last solution is where $(h_x, h_y, h_z) \rightarrow (0, 0, \infty)$ and is plotted in the following graph:

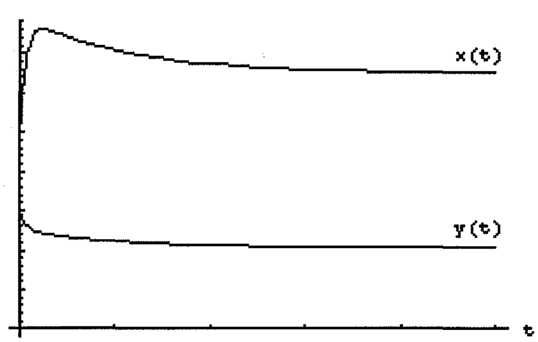

Figure 6. Only tuna-dolphin schools harvested at high rates.

In this plot, we can see that even though all the tuna-dolphin schools are being removed, the log-schools and the free-schools prevail at catchable levels.

7 Fish Stock Assessment Considerations

The use of this mathematical model in the study of fish stocks and the effects of harvesting are helpful to understand the biological implications in a fishery. However, any mathematical model has limitations. The use of the concept of stock may be required, since in the fishery, all the animals belonging to the tuna population may not be available. This situation introduces a level of uncertainty to a demographically based model (Pitcher and Hart, 1982; Gulland, 1983; Laevastu and Favorite, 1988; National Research Council, 1998).

Other biological implications as the dynamics of fish stock growth, together with fluctuations in environmental conditions, result in stochastic variations in fish abundance. These situations represent unexpected variability to the stock dynamics.

This study represents the fist step in building a model to understand the effects of different proportions of harvesting on these three fishing modes. Further studies may be oriented in the estimation of model parameters using some probability distributions that could help control the varability of the stock, and other alternative ways of finding parameters. At this point, we place the model in a statistical framework that includes assumptions about the type of errors that occur. These errors can be characterized in process errors or observational errors (National Research Council, 1998).

For further studies, the use of stochastic models is recommended Bayesian approaches or any other robust methods for modeling can incorporate in some way the inevitable uncertainty.

At this point, we only refer to the biological implications of the fishery, but the fishery management also includes economical, social and political aspects that must be incorporated to achieve a global view of the problem. So, fishery management involves decision making in the presence of uncertainty. The model proposed here is a different way to understand the biological implications of purse-seine fishing for tunas in the eastern tropical Pacific.

8 Conclusions

The simplification and rescaling of the model provided us with a simpler more manageable system of equations that was easier to manipulate. By analyzing the simplified model we were able to obtain the basic reproductive number by using the Routh-Hurwitz criteria.

It was imperative that the basic reproductive number was put in terms of the original parameters in order to be interpreted. When it was rewritten in terms of to the original parameters, it was confirmed that it depended on the reproduction of the free and dolphin schools as it was expected. Most importantly, it was noted that this number depended mainly on the factor that represented the free schools rather than the dolphin schools. This means that even if the dolphin school term of the basic reproductive number desappeared, the tuna stock could still prevail provided that the free school term remained greater than one.

Having concluded that the basic reproductive number was not dependent on the imput from the dolphin schools, we found the existence of some levels of harvesting on log and free schools under which the tuna stock will remain healthy and harvestable.

Finally, the numerical solutions gave a pictorial representation of the behavior of the system of equations where the favorable situations could be easily differentiated from the situations where the tuna stock became endangered.

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Appendix A

Model simplification and rescaling

The simplification of parameters in the model arrive to the folowing system:

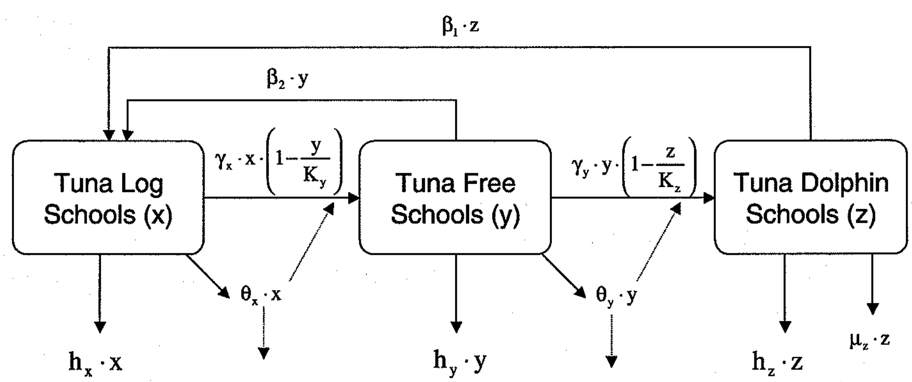

Figure 1A. Model with parameter simplification.

The resulting system of differential equations is the following:

$$\begin{aligned}\frac{dx}{dt} &= \beta_1 z + \beta_2 y - \theta_x x - h_x x\\ \frac{dy}{dt} &= \gamma_x x\left(1-\frac{y}{K_y}\right) - \theta_y y - h_y y\\ \frac{dz}{dt} &= \gamma_y y\left(1-\frac{z}{K_z}\right) - \mu_z z - h_z z\end{aligned}$$

Where the new coefficients are:

$\beta_1 = \frac{b_1 n_z}{n_x}$	birth rate of log schools generated from the dolphin school group
$\beta_2 = \frac{b_2 n_y}{n_x}$	birth rate of log schools generated from the free school group
$\gamma_x = \frac{\rho_x n_x}{n_y}$	rate of new free schools generated from the log schools
$\gamma_y = \frac{\rho_y n_y}{n_z}$	rate of new dolphin schools generated from the free schools
$\theta_x = \rho_x + \mu_x$	removal rate of log schools
$\theta_y = \rho_y + \mu_y$	removal rate of log schools

Rescaling this system yielded to the following model:

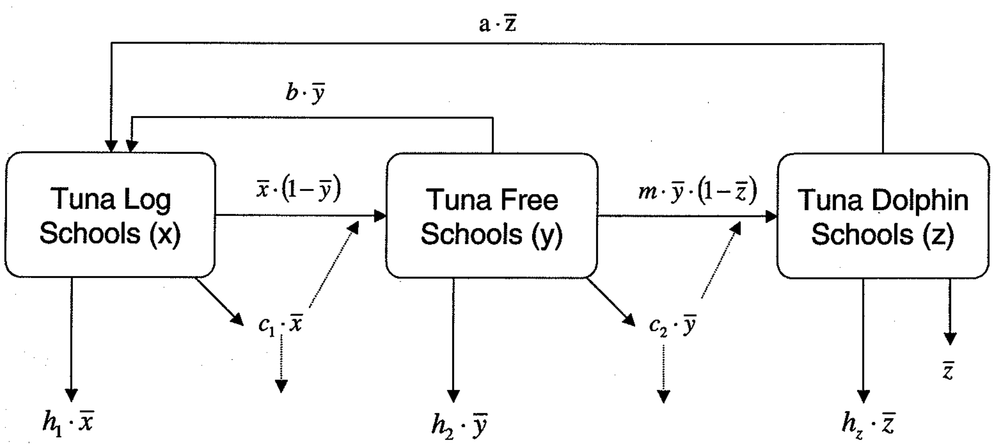

Figure 3. Model with reparameterization.

The corresponding dimensionless system of differential equations is:

$$\begin{aligned}\frac{d\overline{x}}{d\tau} &= a\overline{z} + b\overline{y} - (c_1 + H_1)\overline{x}\\ \frac{d\overline{y}}{d\tau} &= \overline{x}(1-\overline{y}) - (c_2 + H_2)\overline{y}\\ \frac{d\overline{z}}{d\tau} &= m\overline{y}(1-\overline{z}) - (1 + H_3)\overline{z}\end{aligned}$$

Where:

$$\overline{x}=\frac{\gamma_x}{K_y\mu_z}x,\overline{y}=\frac{1}{K_y}y,\overline{z}=\frac{1}{K_z}z,\tau=\mu_z t$$

$a=\left(\frac{K_z\beta_1\gamma_x}{K_y\mu_z\mu_z}\right)$ adjusted birth rate due to dolphin schools
$b=\left(\frac{\beta_2\gamma_x}{\mu_z\mu_z}\right)$ adjusted birth rate due to free schools
$m=\left(\frac{K_y\gamma_x}{K_z\mu_z}\right)$ adjusted dolphin school formation rate
$c_1=\frac{\theta_x}{\mu_z}$ adjusted log school removal rate
$c_2=\frac{\theta_y}{\mu_z}$ adjusted free school removal rate
$H_1=\frac{h_x}{\mu_z}$, adjusted log school harvesting rate
$H_2=\frac{h_y}{\mu_z}$, adjusted free school harvesting rate
$H_3=\frac{h_z}{\mu_z}$, adjusted dolphin school harvesting rate

Appendix B

The Routh-Hurwitz Criteria at Trivial Point

The Routh-Hurwitz criteria was used to analyze the trivial equilibrium point of our system of equations (Edelstein-Keshet, 1988). This criteria is based specifically in the analysis of the coefficient of the characteristic equation.

Step1

Write the equations of the rescaled system for the tuna stock and let:

$$f(\overline{x},\overline{y},\overline{z})=\frac{d\overline{x}}{d\tau}=a\overline{z}+b\overline{y}-(c_1+H_1)\overline{x}$$

$$g(\overline{x},\overline{y},\overline{z})=\frac{d\overline{y}}{d\tau}=\overline{x}(1-\overline{y})-(c_2+H_2)\overline{y}\qquad(*)$$

$$h(\overline{x},\overline{y},\overline{z})=\frac{d\overline{z}}{d\tau}=m\overline{y}(1-\overline{z})-(1+H_3)\overline{z}$$

Step 2

Compute the Jacobian at the trivial equilibrium $E_0=(0,0,0)$. The Jacobian of the systemis given by

$$J = \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} & \frac{\partial f}{\partial z} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} & \frac{\partial g}{\partial z} \\ \frac{\partial h}{\partial x} & \frac{\partial h}{\partial y} & \frac{\partial h}{\partial z} \end{pmatrix},$$

and evaluated at the trivial equilibrium results is

$$J(E_0) = \begin{pmatrix} -c_1 - H_1 & b & a \\ 1 & -c_2 - H_2 & 0 \\ 0 & m & -1 - H_3 \end{pmatrix}$$

Biologists refer to the Jacobian as a community matrix, in this case tuna stock in schools by category (i.e. log schools, free schools, and dolphin schools).

Step 3

The characteristic equation is given by

$$det(J - \lambda I) = a_0\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$$

where

$$\begin{aligned} a_0 &= 1 \\ a_1 &= 1 + c_1 + c_2 + H_1 + H_2 + H_3 \\ a_2 &= -b + c_2 + H_1 + H_2 + H_1(c_2 + H_2) + H_3(c_2 + H_1 + H_2) + c_1(1 + c_2 + H_2 + H_3) \\ a_3 &= (-b + (c_1 + H_1)(c_2 + H_2))(1 + H_3) - am \end{aligned}$$

We use the Routh-Hurwitz criteria to analyze the stability of E_0.
The conditions for stability are

1. $a_1 > 0$,
2. $a_3 > 0$,
3. $a_1 a_2 - a_3 > 0$

The first condition is trivially satisfied since

$$a_1 = 1 + c_1 + c_2 + H_1 + H_2 + H_3 > 0.$$

The second condition is

$$a_3 = (-b + (c_1 + H_1)(c_2 + H_2))(1 + H_3) - am > 0,$$

Which is eqivalent to

$$-b+(c_1+H_1)(c_2+H_2) > \frac{am}{(1+H_3)}.$$

Adding b to both sides, and dividing by $(c_1+H_1)(c_2+H_2)$, we get the condition that represents the basic reproduction number (R_0) of the linearized system $\frac{dx}{dt}, \frac{dy}{dt}, \frac{dz}{dt}$.

$$R_0 = \frac{am+b(1+H_3)}{(c_1+H_1)(c_2+H_2)(1+H_3)} < 1.$$

We will show that the 2nd condition impies the condition 3. It is not hard to see that:

$$a_1a_2 - a_3 = -b(d_1+d_2) + (d_1+d_2)(d_1+d_3)(d_2+d_3) + am$$

where:

$$\begin{aligned} d_1 &= (c_1+H_1) \\ d_2 &= (c_2+H_2) \\ d_3 &= (1+H_3) \end{aligned}$$

We have to prove that:

$$\begin{aligned} &-b(d_1+d_2) + (d_1+d_2)(d_1+d_3)(d_2+d_3) + am > 0 \\ &\Leftrightarrow -b(d_1+d_2) > -[(d_1+d_2)(d_1+d_3)(d_2+d_3) + am] \\ &\Leftrightarrow \tfrac{b(d_1+d_2)}{(d_1+d_2)(d_1+d_3)(d_2+d_3)+am} < 1 \end{aligned}$$

So, we take

$$a_3 = \frac{am+b(d_3)}{(d_1)(d_2)(d_3)} < 1.$$

$$1 > \tfrac{am+b(d_3)}{d_1d_2d_3} > \tfrac{b(d_3)}{d_1d_2d_3} = \tfrac{b}{d_1d_2} > \tfrac{b}{(d_1+d_3)(d_2+d_3)} = \tfrac{b(d_1+d_2)}{(d_1+d_2)(d_1+d_3)(d_2+d_3)}$$

$$> \tfrac{b(d_1+d_2)}{(d_1+d_2)(d_1+d_3)(d_2+d_3)+am} \Rightarrow \tfrac{b(d_1+d_2)}{(d_1+d_2)(d_1+d_3)(d_2+d_3)+am} < 1 \ \blacksquare$$

Appendix C

Proof the existence of a non-trivial point

To prove the existance of a non-trivial point, we take the rescaled system of equations:

$$\frac{d\overline{x}}{d\tau} = a\overline{z} + b\overline{y} - (c_1 + H_1)\overline{x}$$

$$\frac{d\overline{y}}{d\tau} = \overline{x}(1 - \overline{y}) - (c_2 + H_2)\overline{y}$$

$$\frac{d\overline{z}}{d\tau} = m\overline{y}(1 - \overline{z}) - (1 + H_3)\overline{z}$$

We first set $\frac{d\overline{x}}{d\tau} = 0$ and solve for the variable $\overline{x}$.

$$\overline{x} = \frac{a\overline{z} + b\overline{y}}{(c_1 + H_1)}$$

Then, we set $\frac{d\overline{z}}{d\tau} = 0$ and solve for the variable $\overline{z}$.

$$\overline{z} = \frac{m\overline{y}}{1 + H_3 + m\overline{y}}$$

The next step is to substitue $\overline{z}$ into $\overline{x}$ this way we have $\overline{x}$ in terms of $\overline{y}$. Now, substitute $\overline{x}$ into $\frac{d\overline{y}}{d\tau}$ and we have function in terms of $\overline{y}$. We call this function $H(\overline{y})$.

$$H(\overline{y}) = \frac{a\left(\frac{m}{1+H_3+m\overline{y}}\right) + b}{(c_1 + H_1)}(1 - \overline{y}) - (c_2 + H_2), 0 < \overline{y} < 1$$

A non-trivial point exists if $H(\overline{y})$ has a real root. This can be seen by evaluating $H(\overline{y})$ on the interval (0,1). For this, one of the following conditions have to be met:

$$H(1) < 0 \text{ and } H(0) > 0(i)$$

or

$$H(1) > 0 \text{ and } H(0) < 0(ii)$$

Now notice that

$$H(1) = -(c_2 + H_2) < 0$$

$H(0) = \frac{a\left(\frac{m}{1+H_3}\right)+b}{(c_1+H_1)} - (c_2 + H_2)$, it is not hard to see that this expresion is the basic reproduction number

$$\frac{\frac{am+b(1+H_3)}{1+H_3}}{(c_1 + H_1)} - (c_2 + H_2)$$

$$am + b(1 + H_3) - (c_2 + H_2)(c_1 + H_1)(1 + H_3)$$

$$R_0 = \frac{am + b\,(1 + H_3)}{(c_1 + H_1)(c_2 + H_2)(1 + H_3)}.$$

$H(1) < 0$ and $H(0) = R_0 > 1$

This means that condition (i) has been met. At the same time it tells us that the graph of $H(y)$ crosses the axis, which implies the existance of a real root for the equation, and the existance of a real root implies that there exists a positive non-trivial point for the system of equations.