PROPERTIES OF AGE STRUCTURE MODELS FOR HARVESTED POPULATIONS WITH APPLICATIONS TO YELLOWFIN TUNA Thunnus albacares (BONATERRE) AND HARP SEALS Pagophilus groenlandicus (ERXLEBEN)

by

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A Thesis Submitted In Partial Fulfilment Of The Requirements For The Degree Of Doctor Of Philosophy in the Department of Zoology

We Accept This Thesis As Conforming To The Required Standard

THE UNIVERSITY OF BRITISH COLUMBIA September, 1972
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Abstract

Dynamic population models that incorporate the age structure of the population can be used as a powerful tool for fisheries management. In this thesis some of the properties and potential uses of a class of these models is examined. This class can be described as a life table operating on a population with a stock-recruit relation that is formed by multiplying the egg production by a function of a linear combination of the numbers of fish of different ages.

The study of the properties included an analysis of the stability and the non-equilibrium behaviour of the model. This behaviour was related to some types of fluctuations observed in fish populations. Special attention was given to the limit cycles that occur in populations with an unstable equilibrium and this is considered as a possible mechanism causing the regular fluctuations known as cyclic dominance in sockeye salmon Oncorhyncus nerka (Walbaum).

The fisheries for yellowfin tuna in the eastern Pacific Ocean, and harp seals in the western North Atlantic were used as examples to show how these models might be used by a management body.

In the case of the yellowfin tuna the model agreed with results obtained using surplus production models and in addition suggested it is possible to increase both catch and catch per unit effort by changing the open season from the beginning of
the year to later in the year. The yield could also be increased by using a fishing method that increased the age of first capture. However, this would suffer from the disadvantage of producing a much greater variability in the yield because of the consequent reduction in the number of year classes making a substantial contribution to the yield.

The analysis of the harp seal population showed that this population is being over-harvested, and that if the size of the pup harvest is not reduced the entire pup production would be harvested by 1980. If the harvest rates are substantially reduced a sustained harvest could be taken, the best estimate of a sustained kill of pups only was 172,000. Because the estimates of the parameters are not very precise an analysis of the sensitivity of the results to changes in the parameters was made, and this showed if the estimates are not very accurate considerable errors could be made in the predictions of the model. This analysis was used to compare several possible observations that could be used to check the effect of a reduced harvest on the population, and of these the catch curves of the younger age groups offered the best compromise between sensitivity to changes in population size and ease of measurement.
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Introduction

In this thesis I shall explore the uses and properties of dynamic models which represent a population as a series of year classes, the members of which are reduced each year by natural and fishing mortality. By dynamic I mean non-equilibrium models, that is models in which the population in any year depends on the previous history of the population. This type of model is of most value when the relative year class size is more or less fixed, apart from fishing mortality, soon after it is produced. Essentially the model is a life table operating on a population with a stock-recruit relation.

This approach combines the best features of the yield per recruit and logistic models which are the most commonly used models at the present. These features are the identification of elementary processes which can be independently estimated in the yield per recruit models, and the dynamic nature of the logistic models.

There are several advantages that can be gained from using dynamic models that incorporate age structure. One of the most important of these is that they can be used to examine the effects of a wide range of harvest policies. Traditionally harvest policies have been primarily dictated by the nature of the fishery, with restrictions on types of gear, total effort or catch, being introduced after it became obvious that stocks were being seriously depleted. Size limits were introduced initially to protect the spawning stock, and more recently to attempt to allow year classes to reach their maximum biomass before being
harvested. Partly because of this earlier models as a rule have only allowed for management by changing the age of first capture and overall fishing effort. Dynamic age structure models can be used to study the effects of these policies as well as a wide range of alternatives such as harvesting only a few of the year classes present or policies that fluctuate in time.

A second use of the information on age structure is that harvest policies may be designed to ensure that the age structure of the stock is kept near some desirable structure. Often an intensive fishery on a short lived fish results in the reduction of the spawning stock to only one or two year classes of substantial abundance. This coupled with poor spawning conditions over one or two years could cause a drastic decline in the stock. It is likely that this was a contributing factor in the decline of the California sardine *Sardinops caerulea* (Girard) fishery (Clark 1952), and could easily happen in other major fisheries where the spawning stock consists of very few year classes such as the anchoveta *Engraulis ringens* (Jenyns) fishery of Peru (Schaefer 1967a), or the menhaden *Brevoortia tyrannus* (Latrobe) fishery on the Atlantic coast of U.S.A. (Schaaf and Huntsman 1972). Another advantage of keeping as many year classes as possible in the stock is that it reduces the effect of variation in individual year class sizes on the population size and the yield.

In many fisheries, estimates of year class strength are made routinely and these estimates can be used either as data for the model or as a check on how well the model is describing
the behaviour of the population. When year class size is measured before or shortly after a year class is first exploited the estimates can be used with the model to provide short term predictions of yield. With this information a management body should be able to take full advantage of a large year class or to ensure that a weak incoming year class is not over exploited.

The main disadvantage of these models is their complexity. They are not usually amenable to analytic treatment and as a rule require a large amount of computer time both for fitting the model and for examining the properties of the model. An associated problem is their need for more parameters than are required for either the logistic or yield per recruit models.

Review of earlier work

A simple logical foundation for yield models was provided by Russell (1931) in his statement that the surplus yield is the sum of growth and recruitment minus the natural mortality. On the basis of this, yield models can be classified as belonging to one of two types. These are the yield per recruit models in which parameters for the three processes are estimated separately and their effects combined in the model; and the logistic types in which parameters that describe the summed effects of all processes in the fish population are estimated from catch and effort data.

Although Russell's statement provided the logical basis for yield models, it was preceded by Baranov (1918) who produced the first yield per recruit yield model. Baranov introduced the idea
of instantaneous mortality and used a cubic function of time to describe growth of a fish. His approach received little attention in the Western world until the late 1950s when the method became popular following the work of Beverton and Holt (Hulme et al. 1947, Graham 1952, Beverton 1953). Although Baranov's mathematical formulation was ignored, the yield per recruit model was employed in a tabular form notably by Thompson and Bell (1934) and Ricker (1945). Since the publication of Beverton and Holt's book (Beverton and Holt 1957), both methods of applying the model have been used as a guide for management (Hennemuth 1961b, IPHC 1960, Ketchen and Forrester 1966).

The logistic model was derived by Verhulst (1838) and independently by Pearl and Reed (1920). Many important developments of this simple model were made principally by Lotka (1924) and Volterra (Scudo 1971), one of the most important of these being the multispecies form of the model which has for a long time been the major model used in studies of multispecies fisheries (Larkin 1963). The simple model was used as a yield model by Hjort et al. (1933) and by Graham (1935). Schaefer (1954, 1957) provided a method of estimating the parameters for this model and his methods have been the basis for the management of yellowfin tuna in the eastern Pacific by the Inter-American Tropical Tuna Commission. Modifications of this model have been suggested by Pella and Tomlinson (1969) who introduced a third parameter which allows the surplus production curve to be skewed, and by Fox (1970) who used an exponential relation between catch per unit effort and effort.
In the Pacific salmon fishery a different management approach was dictated by the life history of salmon and the nature of the coastal fishery. For the coastal fishery, salmon are only susceptible to capture during a brief time span before they spawn and die. In this case the aim is to capture as many fish as possible subject to the constraint of allowing sufficient spawners to provide for subsequent generations. The problem was then to find a relation between the number of spawners in a given spawning area and the number of offspring that would return to spawn in later years. Ricker (1954) suggested such a relationship and several variants of this were described later (Larkin et al. 1964). As well as focusing attention on the relation between stock and recruitment these studies have stimulated work on the problem of what management policies are best in the face of uncertainty about the fish stocks. (Ricker 1958, Tautz et al. 1969, Allen 1972).

Leslie (1945, 1948) developed the use of the life table as an animal population model. Most of Leslie's work was concerned with linear equations and was applied to the properties of age structure when populations exhibit exponential growth. However Leslie showed that certain types of density dependent growth that produced stable or bounded populations could be handled using his method. The important difference between Leslie's models and the tabular forms of the yield per recruit models is that Leslie's model has a stock-recruit relation, albeit a very simple one. Leslie's model has been used mainly in the analysis of population numbers (Leslie 1966, Mertz 1971), but can equally well be used as a yield model (Lefkovitch 1970). The effect of
variation of the rates of mortality and reproduction in a Leslie model have been examined by Demetrius (1969) and Goodman (1971).

The next logical step in the development of this group of models was to replace the simple stock-recruit relation with more complex ones, such as those used by Southward (1968) and Walters (1969). The parts of these models dealing with the numbers in the population are very similar to the population models used for the study of problems of stock and recruitment by Ricker (1954) and Ward and Larkin (1964).
The Model

For a single species the basic population model I shall use is

\[ N(1,t) = \sum_{j} [h(j) \cdot N(j,t-1)] \cdot S(1,t) \]  

(1a)

\[ N(j,t) = S(j) \cdot N(j-1,t-1) \quad j=2,3,\ldots,k. \]  

(1b)

where \( N(j,t) \) is the number of fish that have just completed their \( j \)th year of life at the end of year \( t \). Throughout year \( t \) I shall refer to these fish as being of age \( j-1 \). The symbol \( S(j), (j = 2,\ldots,k) \) represents the proportion of fish of age \( j-1 \) that survive to age \( j \), while \( S(1,t) \) is the proportion of eggs that survive to become fish of age \( 1 \), and \( h(j) \) is the age specific fecundity. In general all the coefficients \( S(j) \) and \( h(j) \) could be functions of the population structure but I shall take all but \( S(1,t) \) to be constants.

There are many possibilities for the form of \( S(1,t) \), but I shall consider only those of the form \( S(1,t) = f(V(t)) \) where \( V(t) \) is a linear combination of the numbers of fish in each age group at that time, that is \( V(t) = \sum l(j) \cdot N(j,t) \). \( V(t) \) can be thought of as a measure of population density that is associated with egg or larval mortality. Of the possible set of combinations a frequently arising subset will be \( S(1,t) = f(U(t)) \), where \( U(t) = \sum h(j) \cdot N(j,t) \) which is the number of eggs produced by the population. This situation is likely to arise when density dependent mortality is the result of
competition between eggs or between the young of the year. This type of regulation is the basis of the stock-recruit models of Ricker (1954) and Beverton and Holt (1956), and has been used in simulation studies by Southward (1968) and Walters (1969). At the opposite extreme there is the possibility that some of the age groups which contribute to $V(t)$ do not contribute to egg production for that year. For example, this is a characteristic in the biology of pink salmon *Oncorhyncus gorbuscha* (Walbaum) populations (Ricker 1962). Other examples of the general case $S(1,t) = f{V(t)}$, could be the result of predation by adults of the same species, or by other predators whose numbers are determined by the number of juveniles in previous years. These mechanisms have been suggested by Regier et al. (1969) and Larkin (1972). Finally an important special case is that where $f{V(t)} = c$ where $c$ is a constant. This is simply the case of Leslie's model.

The magnitude of unexplained or unpredictable variation in recruitment to some fish stocks (Hjort 1926, Murphy 1966, Hylen and Dragesund 1972) is sufficiently large to make it important to look at the effect of random fluctuations in recruitment, and consequently in some cases $S(1,t)$ is multiplied by a random variable.

The model is the result of combining a set of assumptions describing the growth of a population. Of necessity these assumptions simplify the processes involved. For example, the fecundity is assumed to be a function of age alone. This should not be interpreted as assuming that the effects of density, or
other factors not even included in the model such as environmental conditions, are not important but rather as saying that the effect of variation from these sources is of less importance than the variation in survival of eggs to recruits. Thus it is assumed that the effects of variation in any of the processes that are summarised by the constants $S(j)$, $h(j)$, and $l(j)$ will have effects that are of secondary importance in comparison with the effects of the changes in $S(1,t)$ that are due to changes in density, or equivalently as far as the model is concerned with the effects of changes in fecundity. Many workers (for example Nikolsky 1969) have stressed the importance of conceiving of population size and changes in size as being a response to factors such as fecundity, viability of eggs and larvae, mortality, and growth, which in turn vary in a complicated manner in response to environmental changes. From this point of view my assumptions will appear to be an over simplification of the true situation. However, before the effects of changes in all these processes can be appreciated it is necessary to look at the situation when they are assumed to be constant.

The standard formula for calculating annual yield from the $j$th age group in year $t$ is

$$Y = F \cdot N(j, t) \int_0^t w(j+x) \cdot \exp[-(F+M) \cdot x] \cdot dx$$

where $w(x)$ is the weight at age $x$, and $F$ and $M$ are the instantaneous rates of fishing and natural mortality for that age group. If growth is also approximated by an instantaneous
rate i.e. $w(j+x)$ is replaced by $w(j) \cdot \exp(G \cdot x)$ then

$$Y = P \cdot N(j,t) \cdot w(j) \left\{1 - \exp[G-F-M]\right\} / (G-F-M)$$

The equilibrium population

Suppose there is an equilibrium population with $N(1,t) = n$. Then time may be dropped from equations (1b) giving, say

$$N(2) = S(2) \cdot n = P(2) \cdot n$$

$$N(3) = S(3) \cdot S(2) \cdot n = P(3) \cdot n$$

and $N(j) = P(j) \cdot n$

That is $P(j)$ is the fraction of those fish that survive from age 1 to age $j$. Setting $P(1) = 1$, and substituting the expressions above in equation (1a) gives

$$n = \sum [h(j) \cdot P(j) \cdot n] \cdot f\left[\sum [l(j) \cdot P(j) \cdot n]\right]$$

Or by writing $E = \sum [h(j) \cdot P(j)]$, and $D = \sum [l(j) \cdot P(j)]$

$$n = E \cdot n \cdot f(D \cdot n.$$ 

That is $n = f^{-1}(1/E) \cdot D$ providing $f^{-1}$ exists.

For the case that $f$ is a non-negative monotonically decreasing function, $f^{-1}$ exists only for non-negative arguments less than $f(0)$, and thus the population becomes extinct if $E$ the
average number of eggs produced by a recruit falls to \((f(0))^{-1}\).

The stock-recruit relation

The most convenient measure of stock size is the egg production, and in this and the next section the two terms are used synonymously. For a given stock size \(U(t) = \sum h(j) \cdot N(j,t)\) there is a range of values of density \(V(t) = \sum l(j) \cdot N(j,t)\). This implies that the stock-recruit relation \(N(1,t+1) = U(t) \cdot f(V(t))\) is described by a region rather than by a curve as is the case for the Ricker or Beverton and Holt stock-recruit relations. This region is bounded above provided there is no value of \(j\) such that \(l(j) = 0\) while \(h(j) > 0\).

A stock-recruit relation of this type would be very difficult to detect from an examination of spawner-recruit data, and the estimation of such a relation would be impractical without prior estimates of "weighting coefficients" \(l(j)\). In view of this it is not surprising that models of the relation between stock and recruits have with few exceptions been limited to the type \(N(1,t+1) = U(t) \cdot f(U(t))\).

In practice, the variation that is typically shown by stock-recruit data makes it difficult to decide which functional form best describes the data. For examples of curves fitted to stock-recruit data, see Figures 18-24 of Ricker (1954), and Figures 15.14-15.18 of Beverton and Holt (1957). Because of the difficulty of choosing a particular form of stock-recruit relation from a wide possible range of relations it seems to be best to make the choice from a restricted set that contains the
major features that may be required in a particular relation. Such a set is generated by the following three survival functions

(a) \( f(U) = c \)  

Leslie

(b) \( f(U) = a \cdot (1 + b \cdot U)^{-1} \)

Beverton and Holt

(c) \( f(U) = a \cdot \exp(-b \cdot U) \)  

Ricker

When the decision as to the type of stock-recruit function to be used is made solely on the basis of the spawner-recruit data, the following rules will help in choosing an appropriate relation. If recruitment appears to increase proportionally with stock size over the whole range of the data, the Leslie type should be used. If for large stock sizes recruitment increases at a slower rate than stock size or appears to be independent of stock size, the Beverton and Holt relation should be used, while the Ricker relation should be used if recruitment declines after the stock surpasses some critical size.

It is of course probable that the choice of stock-recruit relation will depend on the range of the data. For example, data from a population with a Ricker relation would be taken as an indication of the Leslie relation if the data only showed the ascending left hand limb, while data that extended to the dome of the curve could be taken as coming from a Beverton and Holt relation. This problem cannot be avoided without getting additional information on the form of the relation, and shows the possible dangers in extrapolating outside the range of the
data. Within the range of the data it is unlikely that the relation chosen will make much difference to the results obtained from the model if it is impossible to discriminate between the three types.

The equilibrium stock-recruit relation

The arguments about the stock-recruit region and its bounds extend to the equilibrium relation which is in general described by a region, though for any given mortality schedule there is a fixed equilibrium point or set of equilibrium points. Suppose the natural survival is \( P(j) \), and fishing mortality alters the survival to \( Q(j) \). The new value of \( E \cdot n = \sum [h(j) \cdot Q(j)] \cdot n \) is subject to the constraint

\[
Q(j+1)/Q(j) \leq P(j+1)/P(j)
\]

as well as to

\[
0 \leq Q(j+1) \leq Q(j)
\]

thus the region of possible equilibrium positions is contained within the region describing the stock-recruit relation.

The stability of the equilibrium

Suppose at the equilibrium the stock size is \( U \), the density \( V \), and the population is \( N \). For small displacements from the equilibrium equations (1) may be approximated by a linear set of
equations consisting of the first terms of the Taylor series expansion of the terms in equations (1). Let $Z(t) = N(t) - N$ be the displacement of the population from its equilibrium, then

$$Z(t) = A \cdot Z(t-1)$$

(3)

where $A$ is the matrix $A(i,j)$ which consists of the partial derivatives of $N(i,t+1)$ with respect to $N(j,t)$. That is

$$A(i,j) = h(j) \cdot f(V) + l(j) \cdot u \cdot f'(V)$$

$$A(j+1,j) = s(j).$$

The stability of the equilibrium of equations (1) is the same as the stability of the equilibrium of equation (3), providing $A$ is not a critical matrix (Hahn 1967). Thus the equilibrium of (1) is stable if all the eigenvalues of $A$ have modulus less than one, and is unstable if there is an eigenvalue with modulus greater than one. If the modulus of the dominant eigenvalue is exactly one, $A$ is critical, and the stability of the equations must be investigated by other methods.

An outline of the computational procedures used to evaluate the behaviour of the model is given in Appendix 1.
Non-Equilibrium Behaviour Of The Model

In this section I will examine the behaviour of the model after the population has been perturbed from its equilibrium, and I shall relate this to some types of fluctuations shown by fish populations. Large scale fluctuations due to variation in year class size in important fisheries have attracted a lot of interest, and there have been many suggestions as to their causes (Hjort 1926, Nikolsky 1961, Ward and Larkin 1964, Hylen and Dragesund 1972). Undoubtedly there is a variety of causes of these fluctuations, and one possibility is that in some cases the type of density dependent population processes described by the model play a major part in causing the fluctuations. To check whether this is likely in a specific instance it is necessary to be familiar with the properties of the model in non-equilibrium situations.

Ricker (1954) made an empirical investigation of the case when $S(1,t) = f(U(t))$ and found that a perturbation from the equilibrium was frequently followed by oscillations which may either persist or die away. His main results relating to the unstable equilibrium can be summarised as:

1. Persistent oscillations only occur when the gradient of the stock-recruit relation at the replacement point is less than $-1$.

2. The "period" of the oscillations is approximately twice the mean age of reproduction, and is not much altered by changes in the stock-recruit curve.
(3) The "amplitude" of the oscillations decreases with increasing stock size, and also is larger when the age of first reproduction is delayed.

I have used quotation marks about the words period and amplitude as the oscillations shown in Ricker's paper are not strictly periodic. Nevertheless, the pattern of the fluctuations is sufficiently regular to make the terms useful in describing the motion.

The necessary condition for the unstable equilibrium was derived above but I do not know of an analytic expression of the second and third property. On the other hand these properties are intuitively reasonable, for the age structure in the model provides a time lag which produces oscillations which will have a period of the same order of magnitude as the lag, and the more year classes there are, the less a fluctuation in a single year class will affect the sum.

Near the equilibrium point, the behaviour of the solutions of equations (1) can be approximated by the solution of equation (3). It is more convenient to work with the companion matrix of the characteristic equation of A. That is the matrix B where

\[ B(1,j) = A(1,j) \cdot P(j) = b(j) \] say

\[ B(j+1,j) = 1, \]

with characteristic equation
\[ r - \sum_{i=1}^{k} r \cdot b(i) = 0. \] 

(4)

In most cases the eigenvalues will be distinct and can be denoted in order of decreasing modulus as \( r(1), r(2), \ldots, r(k) \), and then the general solution of (4) is

\[ z(t) = \sum_{j} K(j) \cdot r(j) \]

where the constants \( K(j) \) are determined by the initial conditions. In general the \( r(k) \) will be complex numbers which can be written as

\[ r(j) = R(j) \cdot \exp\{i \cdot \theta(j)\}. \]

The corresponding terms in the solution, that is those containing \( r(j) \) and its complex conjugate will oscillate with a period \( T(j) = 2\pi/\theta(j) \). These oscillations will be decreasing or increasing in amplitude depending on whether \( R(1) \) is less than or greater than one.

Simulations showed that the dominant root or pair of roots generally mask the others in the general solution, and consequently the period of small oscillations is as a rule be given by \( \theta(1) \), the argument of the dominant eigenvalue. The part of the solution involving the dominant eigenvalue is proportional to \( R(1) \cdot \cos(\theta(1) \cdot t) \). If \( R(1) \) is just slightly less than one, oscillations will persist for a long time after an initial disturbance, while if \( R(1) \) is small any oscillations will disappear swiftly.
The elements of the first row of $B$ may be positive or negative as $f'[V]$ is negative. In particular when $l(j) = 0$ whenever $h(j) = 0$ these elements will be positive for small populations, for as the stock size approaches zero $b(j)$ will approach $h(j) \cdot f[V]$. In this case the dominant eigenvalue will be real and positive, and will be greater than or less than one depending on whether the sum of the elements in the first row of $B$ is greater than or less than one. Now

$$\sum b(j) = \sum [P(j) \cdot [h(j) \cdot f(V) + U \cdot l(j) \cdot f'(V)]]$$

$$= E \cdot f(V) + D \cdot U \cdot f'(V)$$

$$= 1 + D \cdot U \cdot f'(V)$$

Thus the equilibrium is stable in this case when the survival curve has a negative gradient at the equilibrium. The other case, that is the survival curve increasing at the equilibrium corresponds to depensatory mortality (Ricker 1954), the result of a perturbation from such an unstable position is a move to the vicinity of a different equilibrium or extinction. Even though the dominant eigenvalue is real there still could be minor oscillations caused by the eigenvalues of smaller modulus.

In the special case where the number of eggs produced is the argument of the survival function then

$$b(j) = \{f(U) + U \cdot f'(U)\} \cdot P(j) \cdot h(j) \quad (5)$$
and thus all the elements in the first row of $B$ have the same sign which is of course the sign of the gradient of the stock-recruit curve. If the curve has a descending right hand limb then for an equilibrium in this region all the elements in the first row of $B$ will be negative, and the dominant eigenvalue may be complex indicating that motion near the equilibrium will be oscillatory. In fact this was the case in all the simulations I have examined.

If the stock-recruit curve is steep enough the modulus of the dominant eigenvalue could be greater than 1. and in this case the equilibrium would be unstable. A necessary but not sufficient condition for this to occur can be found by noting that a necessary condition for a root of equation (4) to have modulus greater than one is that

$$|b(j)| \geq 1$$

As $b(j) \leq 0$, for all $j$ this is equivalent to

$$\Sigma b(j) \leq -1$$

and using (5) we get

$$\Sigma \{b(j)\} = \left[f(U) + U \cdot f'(U)\right] \Sigma \{p(j) \cdot h(j)\}$$

$$= \left[f(U) + U \cdot f'(U)\right] \cdot E$$

Thus a necessary condition for an unstable equilibrium is
that $E^{-1} \leq -[f(U)+U\cdot f'(U)]$ which means that the gradient of the stock-recruit relation must be steeper than the replacement line $n = E^{-1}\cdot S$. This confirms the observations of Ricker (1954) and Basasibwaki (MS.) who found that a necessary condition for an unstable equilibrium when the replacement line had a gradient of 1.0 was that the gradient of the stock-recruit relation should be less than -1.0 at the equilibrium, and provides a basis for Ricker's (1954) assertion that a population that is unstable before harvesting can be stabilized by taking a sufficiently large harvest, provided no age groups contribute to density dependent mortality without contributing to egg production.

These points are illustrated by the examples shown in Figure 1. The three series shown in Figure 1(a)-1(c) show the fluctuations following a perturbation of a population with eight age classes and a stock-recruit relation of the form $n = a\cdot U\cdot \exp(-b\cdot U)$. This population shall be referred to as population A and its parameters are given in Appendix 1. With no fishing mortality the equilibrium is unstable and the oscillations following the perturbation grow swiftly, while with fishing mortalities of 0.5 and 1.0 applied from age 3 onwards the equilibrium is stable. With $F = 0.5$ the effects of the perturbation persist for a long time, as is expected on the basis of the dominant eigenvalue having a modulus (0.99) close to one. The period in each case agrees with that predicted using the argument of the dominant eigenvalue, and is approximately twice the mean age of reproduction. The word approximately is used partly because it is difficult to measure the period and partly because of uncertainty in how the mean age of
Figure 1

Small oscillations about the equilibrium of the populations.
reproduction should be defined (Leslie 1966).

When the argument of the survival function is not the number of eggs produced the relation between the mean age of spawning and the period may break down. An example of this is shown in Figure 1(d) which shows the fluctuations about an unstable equilibrium for a population with five year classes all of which contribute to density dependent mortality while only the last two produce eggs. This population shall be referred to as population B and its parameters are given in Appendix 1. In this case the period is only two years. Another difference between this case and the previous one is that the equilibrium is stable when there is no fishing mortality and becomes unstable as fishing mortality increases.

A major difference between the stable and unstable situations is that in the unstable case the oscillations cannot continue to grow as an upper limit to recruitment is set by the shape of the stock-recruit curve. However in the simulations I have carried out the period of the persistent oscillations appeared to be related to the argument of the eigenvalues whose modulus was greater than one. Figure 2 shows sections of the series generated by the unstable cases shown in Figure 1 a long time after the initial perturbation. In the first panel the fluctuations in population A appear to be stable, while the second panel shows the pattern of the fluctuations in population B changing from the two year periodicity of the small oscillations to a pattern with a dominant year class occurring every four years. In the first
Figure 2

Large fluctuations about unstable equilibrium populations.
example the period could be related to the argument of the
dominant eigenvalue which has a period of 12.3 years and in the
second case the period can be related to the second eigenvalue
with a period of 3.8 years. The figures suggest the fluctuations
are settling into limit cycles, however in the simulations
carried out none of the fluctuating populations ever settled
into a fixed pattern.

In a natural population the effect of density dependent
population processes would be modified by random or
unpredictable variation such as those caused by weather. In many
cases these would distort the patterns to such an extent as to
make them unrecognisable and this prompted Ricker (1954) to
remark that the only fishery which showed fluctuations that
resembled those that would be caused by a steep descending
stock-recruit relation were those shown by the Georges Bank
haddock *Melanogrammus aeglefinus* (Linnaeus). Ricker was only
concerned with a special case of the stock-recruit relation I am
considering, and when the more general properties are considered
it can be seen that other fisheries do show fluctuations that
could be attributed to the effect of the stock-recruit curve.

A good example is provided by simulation of the dynamics of
sockeye salmon of the Adams and Skeena rivers (Larkin and
McDonald 1968, Larkin 1971) which reproduced the cyclic
dominance with a period of four or five years that is
characteristic of these stocks. The model used in these
investigations was more complicated than the forms I am
considering but Larkin (1971) made the point that a similar
result could be obtained using a model which in my notation can be written as $N(1,t+1) = U(t) \cdot f[V(t)]$. In fact Figure 2(b) shows a pattern of cyclic dominance with a 4 year period generated by such a model. It is interesting that the simple assumption of density dependent mortality that is a function of the numbers in earlier year classes than those spawning is sufficient to account for the cyclic dominance in salmon populations. Various mechanisms have been suggested as causes of this type of mortality, the most likely of which seems to be natural predation (Ward and Larkin 1964).

Another possible example is provided by the blue pike *stizostedion vitreum glaucum* (Hubbs) population of Lake Erie which showed a persistent pattern of oscillations over the period 1915-1960. Regier et al. (1969) suggested that this was due to the effect of predation on the young of the year by older fish coupled with the effects of an extensive fishery, which is the same type of situation as that which produced the cyclic dominance shown in Figure 2(b).

However with the exception of these few cases which show a clear pattern in their fluctuations it is likely to be difficult to detect the effects of fluctuations about an unstable equilibrium. Figure 3 shows the fluctuations for the populations A and B when they are modified by a random variable. In both the unstable cases the original pattern is visible, however in the stable population (Figure 3b) it is not possible to detect a eight year cycle by eye. This periodicity can be however detected by spectral analysis of the
Figure 3

Fluctuations about equilibrium populations modified by a random variable.
data and an example of the results of this is shown in Figure 4. Each spectrum is taken from a 100 year sequence of the data shown in Figure 3, and in each case the dominant frequency is clearly shown. However, in practice it is unusual to get a series of data as long as these and usually one must be content with yield data rather than year class strength. Furthermore in any long series of data the inherent patterns are likely to be obscured by trends in the pattern of the development of a fishery or by environmental changes.
Figure 4

Spectra of series of recruits generated by populations modified by random variables.

The spectral density is in units of 

\( \text{(Recruits/1000)}^2 \).
The Model Applied To Yellowfin Tuna

The yellowfin fishery in the eastern Pacific Ocean was chosen as an example for several reasons; there are catch and effort data available from the year 1934 onwards, there has been a considerable amount of work done on the biology of this fish, information is available on the relative fecundity, mortality rates, growth rates, and age composition of the stocks. Additionally the parameters for both the logistic model (Schaefer 1957, Schaefer 1961, IATTC 1971) and the Beverton and Holt model (Hennemuth 1961b) have been estimated, and thus the results of using my model may be compared with the results from these models.

There are of course some problems associated with the data, the most serious of these being the question of whether the fishery can be treated as one which operates on a single stock. Since 1934 there has been an increase in the area exploited by the fishing fleet, and in the late 1950's there was a major change in the fishing method from bait fishing to purse seining. As well as confusing the measurement of fishing effort, this change accelerated the offshore spread as the larger purse seiners have a greater range than the baitboats. An account of these changes is given in a series of reports, (Martin 1962, Alverson 1963, Calkins and Chatwin 1967, 1971). The Inter-American Tropical Tuna Commission (IATTC) has used an informal division of the exploited area (IATTC 1971) that is shown in Figure 5. Up to 1962 the fishery operated entirely within area A1, and after 1962 the fleet started exploiting the remaining
Figure 5

The eastern tropical Pacific Ocean showing the CYRA and the subdivisions A1 and A2.

The shaded area is the historic area A1 and the remainder of the CYRA is area A2.
EASTERN PACIFIC YELLOWFIN TUNA
REGULATORY AREA

Area defined according to the recommendation of the Inter-American Tropical Tuna Commission, Quito, Ecuador, May 16-18, 1962
portion (A2) of the Commission's yellowfin regulatory area (CYRA). Since 1966 the fishery inside the CYRA has been regulated by a closed season which is imposed after a quota has been filled. In recent years the fishing season has been shorter and this has encouraged boats to fish area A3 outside the CYRA.

It is not known whether the enlarged fishing area contains one homogeneous or several discrete stocks, though the evidence from tagging, morphometric, and genetic studies (Joseph et al. 1964, Pink and Bayliff 1970) suggests there is some but not complete mixing of fish from different areas. More recently the migration of tagged yellowfin from coastal regions to outside the CYRA has been observed (IATTC 1971). On the other hand Schaefer (1967b) argues that the close relationship between change in effort and catch per unit of effort for the fishery in the CYRA suggests the yellowfin in the CYRA belong to a unit stock independent of the fish west of the CYRA. Further, the average weights of yellowfin from the three areas was 49.2, 53.7, and 58.6 lbs in 1969, and 30.6, 45.6, and 67.9 in 1970. (IATTC 1971). These differences appear to be caused by differing proportions of fish of different ages, suggesting that total mortality decreased with distance from shore, and hence that the stocks in the different areas were independent.

Yellowfin from the eastern Pacific Ocean have not yet been successfully aged using hard parts (Suzuki 1971), and hence most estimates involving ageing of the fish, (for example growth

1In 1971 the season was closed on 9 April. Vessels that are in port at the time of closure are allowed to make one more unregulated trip after unloading.
rates and age composition of the stocks) are based on the method of modal progression, i.e. the recognition of year classes in length frequency data (Hennemuth 1961a). This of course will result in some errors of classification.

Spawning activity is largely confined to the first three quarters of the year (Orange 1961, Kume and Schaefer 1966, Kume and Joseph 1969). Kume and Joseph suggest spawning is most intense during the second quarter, and I shall follow them and assign age zero to be on the first of April. Hennemuth (1961a) assigns age 0 in August, and so my ages are approximately four months greater than Hennemuth's ages.

Growth

Hennemuth (1961a) using length data collected from baitboats during the period 1954-1958 estimated the parameters for the von Bertalanfyy growth formula, and after converting from length to weight obtained

\[ w(t) = 218 \cdot [1 - \exp(-0.6(t-0.85))]^3 \text{ lbs} \]  

(5)

where \( t \) is measured in years from August.

This relation describes the data well for fish older than 1.5 years but underestimates the average weight of younger fish in the catches (see Hennemuth 1961a Figure 30). This of course may be due to the selection by the fishing method of the faster growing young fish, but whatever the reason this would to some extent bias yield per recruit calculations based on equation
Thus for ages of 5, 6 and 7 quarters I have used the mean of succeeding mid quarter average weights given in Table 5 of Davidoff (1969). For younger fish I have assumed a uniform growth rate from 0.01 lbs at the end of the first quarter. Table 1 gives the weights at the beginning of each quarter and the corresponding exponential growth rates during the quarter. This growth rate agrees with the rates estimated by Davidoff (1963) using data collected from baitboats and purse seiners during the period 1951-1961, and Kume and Joseph (1969) using data collected from the Japanese long line fishery during the period 1964-1967. A considerably lower growth rate for tagged fish was found by Schaefer et al. (1961). This could be due to the effect of tagging on growth, or because of the effect on the size selective fishery of the modal progression estimates.

Mortality

Estimates of mortality of yellowfin have been published by Hennemuth (1961b), Schaefer et al. (1961), Fink (1965), Davidoff (1965), and Bayliff (1971). A summary of these estimates is given in Table 2. The estimates vary considerably and, although some of the variation can be explained in terms of events in the fishery, they do not provide good estimates of natural and fishing mortality. The estimates give no assurances that natural mortality has remained constant over the period 1953-1963. Figure 6 shows the catch curves for the year classes 1954-1964, using data given by Davidoff (1969). In the absence of good estimates of mortality I shall follow Schaefer (1967b) and investigate the consequences of assuming natural mortalities of
### Table 1

Estimated weight and exponential growth rate of yellowfin tuna.

<table>
<thead>
<tr>
<th>Qtr.</th>
<th>Weight lbs</th>
<th>Growth rate</th>
<th>Qtr</th>
<th>Weight lbs</th>
<th>Growth rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>2.7</td>
<td>0.675</td>
<td>19</td>
<td>149.8</td>
<td>0.055</td>
</tr>
<tr>
<td>6</td>
<td>5.3</td>
<td>0.524</td>
<td>20</td>
<td>158.3</td>
<td>0.047</td>
</tr>
<tr>
<td>7</td>
<td>9.0</td>
<td>0.348</td>
<td>21</td>
<td>165.8</td>
<td>0.040</td>
</tr>
<tr>
<td>8</td>
<td>12.7</td>
<td>0.597</td>
<td>22</td>
<td>172.5</td>
<td>0.030</td>
</tr>
<tr>
<td>9</td>
<td>23.0</td>
<td>0.433</td>
<td>23</td>
<td>178.5</td>
<td>0.029</td>
</tr>
<tr>
<td>10</td>
<td>35.5</td>
<td>0.329</td>
<td>23</td>
<td>183.6</td>
<td>0.025</td>
</tr>
<tr>
<td>11</td>
<td>49.4</td>
<td>0.257</td>
<td>25</td>
<td>188.2</td>
<td>0.021</td>
</tr>
<tr>
<td>12</td>
<td>63.8</td>
<td>0.205</td>
<td>26</td>
<td>192.2</td>
<td>0.018</td>
</tr>
<tr>
<td>13</td>
<td>78.3</td>
<td>0.166</td>
<td>27</td>
<td>195.6</td>
<td>0.015</td>
</tr>
<tr>
<td>14</td>
<td>92.3</td>
<td>0.135</td>
<td>28</td>
<td>198.7</td>
<td>0.013</td>
</tr>
<tr>
<td>15</td>
<td>105.7</td>
<td>0.112</td>
<td>29</td>
<td>201.3</td>
<td>0.011</td>
</tr>
<tr>
<td>16</td>
<td>118.2</td>
<td>0.093</td>
<td>30</td>
<td>203.6</td>
<td>0.010</td>
</tr>
<tr>
<td>17</td>
<td>129.8</td>
<td>0.078</td>
<td>31</td>
<td>205.5</td>
<td>0.008</td>
</tr>
<tr>
<td>18</td>
<td>140.3</td>
<td>0.065</td>
<td>32</td>
<td>207.2</td>
<td></td>
</tr>
</tbody>
</table>

### Table 2

Estimates of total mortality and fishing effort for yellowfin tuna.

<table>
<thead>
<tr>
<th>Year</th>
<th>(a)</th>
<th>(b)</th>
<th>(c)</th>
<th>(d)</th>
<th>Effort</th>
</tr>
</thead>
<tbody>
<tr>
<td>1953</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.55</td>
<td>36,356</td>
</tr>
<tr>
<td>1954</td>
<td>1.72</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>36,356</td>
</tr>
<tr>
<td>1955</td>
<td>1.72</td>
<td>-</td>
<td>-</td>
<td>2.26</td>
<td>17,198</td>
</tr>
<tr>
<td>1956</td>
<td>1.72</td>
<td>1.93</td>
<td>1.43</td>
<td>27,204</td>
<td></td>
</tr>
<tr>
<td>1957</td>
<td>1.72</td>
<td>1.20</td>
<td>1.54</td>
<td>26,768</td>
<td></td>
</tr>
<tr>
<td>1958</td>
<td>1.72</td>
<td>0.88</td>
<td>1.54</td>
<td>31,135</td>
<td></td>
</tr>
<tr>
<td>1959</td>
<td>-</td>
<td>1.28</td>
<td>0.77</td>
<td>1.43</td>
<td>28,271</td>
</tr>
<tr>
<td>1960</td>
<td>-</td>
<td>5.17</td>
<td>6.59</td>
<td>1.19</td>
<td>35,841</td>
</tr>
<tr>
<td>1961</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.64</td>
<td>41,646</td>
</tr>
</tbody>
</table>

(a) Hennemuth (1961b) average over all areas 1954-1958.
(b) Fink (1965) Baja California.
(c) Fink (1965) Northern Peru.
(d) Davidoff (1965) average over all areas.

The fishing effort is given in standard baitboat days.
Figure 6

Catch curves for the 1954-1964 yellowfin tuna year classes.
0.55, 0.8, and 1.05 with the corresponding catchability coefficients $0.48 \cdot 10^{-4}$, $0.38 \cdot 10^{-4}$, and $0.28 \cdot 10^{-4}$, per standard baitboat day. For the years 1961-1968 the total effort is available in terms of standard baitboat days as well as standard purse seine days, and thus it is possible to estimate the corresponding catchability coefficients for standard purse seine days. These coefficients were obtained by multiplying those for baitboats by the regression coefficient of baitboat effort on purse seine effort for the years 1961-1968. This gave catchability coefficients of $0.80 \cdot 10^{-4}$, $0.63 \cdot 10^{-4}$, and $0.46 \cdot 10^{-4}$ for purse seiners.

Hennemuth (1961a) gives the age of first capture as 20 months, which corresponds to my ninth quarter. However the data given by Davidoff (1969) in his Table 2 shows that most year classes become fully vulnerable in their eighth quarter (quarter five in his Table). This Table shows no clear difference in the age of first capture during the period when the fishery changed from baitboats to purse seiners, and consequently I am assuming that the change did not effect the age of first capture. In Davidoff's Table there are a considerable number of fish caught before the eighth quarter, this is partly the result of the extended spawning period, and consequent error in the age designation of the fish, and partly because recruitment to the fishery is not knife edged. Because the number of fish captured before their eighth quarter is small it is not worth estimating a selection curve and thus for both the baitboat and purse seine fisheries it is assumed that catchability is zero until the eighth quarter which corresponds to an age of first capture of
1.75 years.

Fecundity

Joseph (1963) estimated the relation between the weight of mature female fish and the number of maturing eggs as:

\[ \text{Eggs (millions)} = 0.106 + 0.046 \times \text{Weight (lbs)} \]

Orange (1961) states that at a length of 120cm (age 3) 50% of the fish are maturing, while fish larger than 140cm (age 4 and older) are all mature, and his Figure 6 suggests about 10% of fish of length 80cm (age 2) are mature. The average fecundity for each age group can be calculated using this information as is shown in Table 3. The frequency of spawning is not known, though it is likely that female yellowfin spawn at least twice a year (Schaefer et al. 1963). However, providing the frequency does not change with age it will be absorbed in the constants \( c \) and \( k \) in equation 6(a) below.

The model

The yield per recruit can be estimated from my model by dividing the equilibrium yield by the equilibrium number of recruits. This is shown in Figure 7 together with the yield per recruit for the Beverton and Holt model using 0.8 as the natural mortality. The two models give very similar results and I shall use my estimates when I refer to yield per recruit below. Figure 8 shows the yield, effort, and estimated yield per recruit for
Table 3

Average weight and fecundity of female yellowfin tuna in the third quarter.

<table>
<thead>
<tr>
<th>Age groups</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weight lbs</td>
<td>23.0</td>
<td>79.3</td>
<td>129.8</td>
<td>165.3</td>
<td>188.2</td>
<td>201.3</td>
<td>208.7</td>
</tr>
<tr>
<td>Eggs/mature female x10*</td>
<td>1.17</td>
<td>3.71</td>
<td>6.08</td>
<td>7.73</td>
<td>8.76</td>
<td>9.37</td>
<td>9.71</td>
</tr>
<tr>
<td>% Mature</td>
<td>10%</td>
<td>50%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>Relative Fecundity</td>
<td>0.12</td>
<td>1.85</td>
<td>6.08</td>
<td>7.73</td>
<td>8.76</td>
<td>9.37</td>
<td>9.71</td>
</tr>
</tbody>
</table>
Figure 7

Yield per recruit in the yellowfin tuna fishery.
Figure 8

Yield and estimated yield per recruit in the yellowfin tuna fishery, 1932-1968.

Yield

Yield per recruit
the years 1934-1968. It is clear that a considerable amount of compensation has taken place during the period, i.e. yield has been increasing while yield per recruit has been constant or slightly decreasing. This suggests that recruitment has been increasing to compensate for the fall in yield per recruit. Much the same effect is seen when the values 0.55 and 1.05 are used for natural mortality, and thus it is appropriate to use the Ricker stock-recruit relation in the model. The model is then;

\[ N(1,t) = c \cdot \sum [h(i) \cdot N(i,t-1)] \cdot \exp\{-k \cdot \sum [h(i) \cdot N(i,t-1)]\} \] (6a)

\[ N(j,t) = \exp\{-Z(j)\} \cdot N(j-1,t-1) \quad j=2,3,\ldots,t. \] (6b)

And the annual yield is given by

\[ C = \sum [F(i) \cdot N(i,t) \cdot (1-\exp\{-Z(i)\})/Z(i)] \quad \text{(numbers)} \] (7a)

\[ Y = \sum [F(i) \cdot N(i,t) \cdot w(i) \cdot (1-\exp\{B(i)\})/B(i)] \quad \text{(weight)} \] (7b)

where the fishing mortality \( F(i) \) is the product of the catchability \( q(i) \) and the effort \( X \), \( Z(i) = M(i) + F(i) \), and \( B(i) = G(i) - F(i) - M(i) \).
Estimation of the parameters $c$ and $k$

The unknown parameters $c$ and $k$ in equation (2a) can be estimated by minimizing the function

$$\mathbb{E}\{ (Y(i) - [A_i(c,k,X,N^0)]^2) \}.$$ 

Where $A_i(c,k,X,N^0)$ is the value of the annual yield given by the model in year $i$, with population $N^0$ at the beginning of the first year, and $X$ the vector giving the fishing effort for each year. $N^0$ is unknown and could be treated as a set of parameters to be estimated. However as the exploitation rate in the early years of the fishery was quite low, it probably did not affect the population much and so I have assumed that $N^0$ is the equilibrium population with the fishing effort for 1934.

The model was fitted using catch and effort data shown in Table 4 for the two sets of years 1934-1960 and 1934-1968. Both sets were tried to see if there is a difference which could be related to the change in fishing method from bait fishing to purse seining and the subsequent rapid increase of the area exploited in recent years. In addition the fitting was tried for each of the three sets of mortality data. The best result was obtained using $M = 1.05$, and in this case the estimates of $c$ and $k$ were $2.34\times10^{-5}$ and $1.23\times10^{-13}$ for the years 1934-1960, and $3.35\times10^{-5}$ and $1.69\times10^{-13}$ for the years 1934-1968. Figure 9 shows the corresponding stock-recruit relations, and the residual sum of squares about the regression and mean for each case are shown below.
Table 4

Catch of yellowfin tuna and fishing effort in the Commission's yellowfin regulatory area 1934-1968.

<table>
<thead>
<tr>
<th>Year</th>
<th>Catch</th>
<th>Effort</th>
</tr>
</thead>
<tbody>
<tr>
<td>1934</td>
<td>60,913</td>
<td>5,879</td>
</tr>
<tr>
<td>1935</td>
<td>72,294</td>
<td>6,295</td>
</tr>
<tr>
<td>1936</td>
<td>78,353</td>
<td>6,771</td>
</tr>
<tr>
<td>1937</td>
<td>91,522</td>
<td>8,233</td>
</tr>
<tr>
<td>1938</td>
<td>78,288</td>
<td>6,830</td>
</tr>
<tr>
<td>1939</td>
<td>110,418</td>
<td>10,488</td>
</tr>
<tr>
<td>1940</td>
<td>114,590</td>
<td>10,801</td>
</tr>
<tr>
<td>1941</td>
<td>76,841</td>
<td>9,584</td>
</tr>
<tr>
<td>1942</td>
<td>41,965</td>
<td>5,961</td>
</tr>
<tr>
<td>1943</td>
<td>50,058</td>
<td>5,930</td>
</tr>
<tr>
<td>1944</td>
<td>64,869</td>
<td>6,475</td>
</tr>
<tr>
<td>1945</td>
<td>89,194</td>
<td>9,377</td>
</tr>
<tr>
<td>1946</td>
<td>129,701</td>
<td>13,958</td>
</tr>
<tr>
<td>1947</td>
<td>160,151</td>
<td>20,383</td>
</tr>
<tr>
<td>1948</td>
<td>206,993</td>
<td>24,781</td>
</tr>
<tr>
<td>1949</td>
<td>200,070</td>
<td>23,923</td>
</tr>
<tr>
<td>1950</td>
<td>224,810</td>
<td>31,856</td>
</tr>
<tr>
<td>1951</td>
<td>186,015</td>
<td>18,403</td>
</tr>
<tr>
<td>1952</td>
<td>195,277</td>
<td>34,834</td>
</tr>
<tr>
<td>1953</td>
<td>140,042</td>
<td>36,356</td>
</tr>
<tr>
<td>1954</td>
<td>140,033</td>
<td>26,228</td>
</tr>
<tr>
<td>1955</td>
<td>140,865</td>
<td>17,198</td>
</tr>
<tr>
<td>1956</td>
<td>177,026</td>
<td>27,204</td>
</tr>
<tr>
<td>1957</td>
<td>163,020</td>
<td>26,768</td>
</tr>
<tr>
<td>1958</td>
<td>148,450</td>
<td>31,135</td>
</tr>
<tr>
<td>1959</td>
<td>140,484</td>
<td>28,271</td>
</tr>
<tr>
<td>1960</td>
<td>244,331</td>
<td>35,841</td>
</tr>
<tr>
<td>1961</td>
<td>230,886</td>
<td>41,646</td>
</tr>
<tr>
<td>1962</td>
<td>174,063</td>
<td>42,248</td>
</tr>
<tr>
<td>1963</td>
<td>145,469</td>
<td>33,303</td>
</tr>
<tr>
<td>1964</td>
<td>203,882</td>
<td>42,090</td>
</tr>
<tr>
<td>1965</td>
<td>180,086</td>
<td>43,228</td>
</tr>
<tr>
<td>1966</td>
<td>182,294</td>
<td>40,393</td>
</tr>
<tr>
<td>1967</td>
<td>178,944</td>
<td>33,814</td>
</tr>
<tr>
<td>1968</td>
<td>225,000</td>
<td>39,199</td>
</tr>
</tbody>
</table>

The catch is in thousands of lbs and the effort is in standard baitboat days.
Figure 9

Stock-recruit relations generated by fitting the model to data for 1932-1960 and for 1934-1968.
### Fit to the years 1934-1960

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>d.f.</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>About regression</td>
<td>1.79$\cdot 10^{16}$</td>
<td>7.18$\cdot 10^{14}$</td>
<td>25</td>
<td></td>
</tr>
<tr>
<td>About mean</td>
<td>8.37$\cdot 10^{16}$</td>
<td>32.2$\cdot 10^{14}$</td>
<td>26</td>
<td>0.22</td>
</tr>
</tbody>
</table>

### Fit to the years 1934-1968

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>d.f.</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>About regression</td>
<td>2.85$\cdot 10^{16}$</td>
<td>8.63$\cdot 10^{14}$</td>
<td>33</td>
<td></td>
</tr>
<tr>
<td>About mean</td>
<td>11.2$\cdot 10^{16}$</td>
<td>32.9$\cdot 10^{14}$</td>
<td>34</td>
<td>0.26</td>
</tr>
</tbody>
</table>

Contours for the residual sum of squares surface for the model fitted to the data for 1934-1960 are shown in Figure 10, the surface is a ridge with steeply sloping sides indicating that the estimates of $c$ and $k$ are strongly correlated. This means that the maximum height of the stock-recruit curve, given by $x = \frac{c}{ke}$, is more critical to the goodness of the fit than is the location of the maximum, given by $U = \frac{1}{k}$. Figure 11 shows the annual yields with the best fit of the model using each of the data sets.

Both the mean square about the regression, and the ratio of mean square about the regression to mean square about the mean indicate the fit of the model to the restricted data set is better than the fit to the full set of data. These differences are not very large and because of the structure of the model it is not practical to try to apply a statistical test to them.
Figure 10

The surface of the residual sum of squares for the model with the data for area A1.

The contours for \((19, 20, 30, 50, 100) \times 10^{15}\) lbs² are shown.
Figure 11

Yield of yellowfin tuna from the CYRA.

Expected values using the fit to the data for 1934-1960

Expected values using the fit to the data for 1934-1968

Data ▼
However the marked drop in the prediction of yield after 1960 by the model fitted to the data for 1934-1960 is an indication that the stock being exploited increased after 1960, suggesting that fish in the area that was exploited after 1960 are to some extent part of stocks separate from those exploited before 1960. I shall refer to the model as the model for A1 or the model for the CYRA depending on whether the parameters used with it are those obtained from the data for 1934-1960, or from the data for 1934-1968.

If year class size is not much altered by variations in natural mortality the residuals about the regression would be correlated, i.e. the effect of a small or large year class should persist for two or three years, and this should cause runs of observations greater than or less than the expected values to be longer than if the residuals were distributed independently. For the model for A1 there are 4 runs of observations above the expected values and 4 runs below, the longest run being the 9 above for the years 1939-1947. The one sample runs test (Siegel 1956) shows that this is a significant departure at the 5% level from what would be expected with a null hypothesis of independently distributed residuals. The mean length of the runs is just over 3 years and this is also consistent with the hypothesis that the residuals are mainly due to the effect of variations in the relative year class strength. Much the same effects are shown by the model for the CYRA. These correlations may of course be caused solely by the structure of the model rather being present in the data. However, the comparison with the general productivity model which is discussed
below makes this seem unlikely.

Figure 12 shows the equilibrium yield predicted by the model for area A1 compared to that of the logistic model (IATTC 1963) fitted to the data for the years 1934-1961. The two models agree well for values of effort less than 24,000 days which is the region most of the data is from. The difference between the models for larger values of effort provides a reminder of the dangers of extrapolating outside the range of the data. It is also interesting to compare the results from the model for A1 with those obtained by Pella and Tomlinson (1969). They fitted their general productivity model to the data for the years 1934-1967 and found they could explain 83% of the variation about the mean of the data (R in their notation and 1.- the value of the ratio given above). As they estimated four parameters from the data it not surprising that this is better than the 74% I obtained for the years 1934-1968 with two estimated parameters. As well as explaining about the same amount of the variance the fit of the two models is surprisingly similar in view of the differences between them. The years that each model overestimated the data are shown below.

|---------------------|---------|---------|---------|------|

Thus all but 6 of the 33 residuals agree in sign and this is a significant departure from what would be expected if the two sets of residuals were independent. In addition Pella and Tomlinson's residuals show the same serial correlation as those
Figure 12

Comparison of equilibrium yields for the logistic and age structure models.
Thousands of Baitboat Days

Yield in Millions of LBS

Logistic Model

Model for Area A1
for the model for A1. These similarities support the contention that the structure shown by the residuals is inherent in the data, and is not the result of fitting an age structure model.

The hypothesis that the stocks in area A1 should be treated separately from those in the other areas can be tested using the predictions of yield by the model for A1, using effort data for A1 from 1962-1970. The mean squared difference between the predicted and observed yields in A1 in that time period was $7.67 \times 10^{14}$, which is in good agreement with the mean squared differences obtained from the regressions above. The mean square of the residuals between the prediction of yield by the model for A1 using the data for all of the CYRA for the years 1962-1968 and the actual yields was $35.1 \times 10^{14}$, indicating that the hypothesis gives a better explanation of the data than is obtained under the assumption that the fish in areas A1 and A2 can be treated as if they belonged to a single stock.

The experimental fishing programme

To test the accuracy of the sustained yield predicted by their model the Commission undertook an experimental fishing programme in 1969. This programme consisted of increasing the quota to $240 \times 10^6$ lbs which was a little more than the estimate of maximum sustained yield (IATTC 1971). The quota was to remain in effect until the catch per unit effort fell to 3 short tons per standard purse seine day. The catch per unit effort expected on the basis of the Commission's model (IATTC 1972) is shown below, with the observed catch per unit effort and yield.
<table>
<thead>
<tr>
<th>Year</th>
<th>Catch per unit effort expected</th>
<th>Catch per unit effort observed</th>
<th>Yield (10^6 lbs) all CYRA</th>
<th>Yield (10^6 lbs) A1 only</th>
</tr>
</thead>
<tbody>
<tr>
<td>1968</td>
<td>-</td>
<td>6.1</td>
<td>229</td>
<td>167</td>
</tr>
<tr>
<td>1969</td>
<td>5.1</td>
<td>6.0</td>
<td>253</td>
<td>114</td>
</tr>
<tr>
<td>1970</td>
<td>4.0</td>
<td>6.0</td>
<td>282</td>
<td>160</td>
</tr>
<tr>
<td>1971</td>
<td>3.0</td>
<td>4.1</td>
<td>228</td>
<td>120</td>
</tr>
</tbody>
</table>

Though the catch per unit of effort has declined over the period 1968-1972, the decline has been less than was expected on the basis of the Commission's model. This discrepancy becomes even larger when the effect of the high levels of mercury found in some tuna on fishing strategy is considered. Because of higher mercury content of older fish, fishermen have been avoiding schools of large fish, and thus the catch per unit of effort in 1971 may underestimate the abundance compared to the abundance estimates for earlier years (IATTC 1972). Additionally, 1971 was an exceptionally good year for skipjack tuna *Katsuwonus pelamis* (Linnaeus). This caused a shift in effort from yellowfin to skipjack, which had the effect of reducing the catch per unit of effort for yellowfin (IATTC 1972).

The discrepancy may be accounted for using the assumption of separate stocks. The maximum sustainable yield predicted by the model for A1 using gear P is 167 \times 10^6 lbs with a corresponding catch per unit effort of 5.8 tons per day. As the catch for area A1 has not been greater than the maximum sustained yield for the years 1968-1970, and as the catch per unit effort for A2 appears to be independent of effort and greater than 6 tons per day, I would expect catch per unit effort...
to have remained at the 1968-1970 level. Thus, unless the effects of the mercury levels and skipjack abundance on fishing strategy can be shown to have caused the drop in catch per unit of effort observed in 1971 and 1972, the results of the experimental fishing programme suggest that the true stock structure is between the extremes of no mixing and complete mixing, this contention is supported by the results of recent tagging experiments (IATTC 1972).

The fitting of the model does not give any indication of how partial mixing of stocks may be occurring. Two possible situations that might be considered are that the two areas contain stocks that mix in some years, or that there is some mixing of fish from the two areas each year. Because the division into areas is based on historical patterns of the fishery caused mainly by the type of boat and fishing method used, rather than on the biology of the fish it is to be expected that this division is not the most appropriate for the fishery. Tagging experiments and observations of genetical differences should in future provide information that can be used as a rational basis for the division of the CYRA into subareas containing separate or near separate stocks.

The outer areas

Figure 13 shows the catch per unit effort against effort in area A2 for the years 1962-1970. There is no sign of a relation between the two quantities and there is no point in attempting to fit the model to this data. The same conclusion applies to
Figure 13

Catch per unit of effort and effort for area A2, 1962-1970.
area A3 for which there is only three years data. The lack of a relationship indicates that the impact of the fishery on the stocks in this area is not yet great enough to affect the catch and effort statistics. Thus increased fishing effort in these areas may be expected to provide a proportionally increased yield.

The dynamics of the model for A1

The model for A1 is stable for all values of fishing mortality and thus the model does not predict the existence of large fluctuations in year class strength, and in this it agrees with observations (Davidoff 1969). The period corresponding to the dominant eigenvalue was nearly 10 years when there was no fishing and just greater than 4 years for the highest value of fishing mortality of about 1.2. Thus if the small oscillations predicted by the model do occur they will contribute to the spectrum in the range of 0.1 to 0.25 cycles per year. In fact there is a minor peak in this region of the spectrum which is shown in Figure 14. However, this peak is small compared to the peak associated with frequencies lower than 0.1 cycles per year which reflects the trends in the development of the fishery. Thus the peak at medium frequencies cannot be taken as strong evidence supporting the descriptive ability of the model.
Figure 14

The spectra for the yellowfin catch data from area A1.

The spectral density is in units of (yield in lbs/10^8)^2.
Harvest strategies for yellowfin tuna

In this section I will explore the consequences of using different harvest strategies with the model for the yellowfin fishery in area A1. The effect of a fishery on a fish population is determined by two factors. The first is the gear selectivity which determines how the gear will affect fish of different sizes, and secondly the fishing effort which will determine how much mortality is applied. I shall use a vector (called the gear) to represent the gear selectivity of a particular fishing gear, and multiply this vector by a scalar (fishing effort) to get the age specific quarterly instantaneous mortality. The purse seine fishery which has an age of first capture of about 1.75 years (7 quarters) can be represented by a gear, say gear P, that has zeros in the first seven positions and units in the remaining positions. The strategy that is usually examined first is that which gives the maximum sustained yield.\(^1\) However it has been realised for some time that the maximum sustained yield is not necessarily the best biological or economic policy (Dickie 1962), and it is of interest to examine other policies that may have advantages that compensate for their smaller yield. The definition of what it is that makes a yield optimum is outside the range of this study and so I shall confine my attention to maximizing yields subject to various constraints.

\(^1\)IATTC operates under the direction of an international convention which requires that the stocks be held at a level that will allow the maximum sustained yield to be taken from them.
Sustained annual yields

The maximum sustained yield policy for the model was found by searching the values of sustained yield for different values of fishing mortality for each quarter of the life of the fish. The search was subject to the constraint that the instantaneous fishing mortality rate was not allowed to exceed 5.0 in any quarter. The best policy found was one with fishing mortality zero for the first eleven quarters of the fish's life, 0.1 for the twelfth, and 5.0 for the remaining quarters. This policy gives a yield of $246\times10^6$ lbs, which is considerably better than the maximum of about $165\times10^6$ lbs that can be achieved with the age of first capture fixed as it is now.

Because a fishing mortality of 5.0 applied for one quarter will reduce a cohort to less than one percent of its initial size this policy is not much different from one in which a fishing mortality of 5.0 is applied in the thirteenth quarter and on subsequent anniversaries, and in fact the yield for this policy is $245\times10^6$ lbs. The difference in yield between the policies is insignificant, and the second policy is to be preferred because it requires less effort as fishing is only carried out in one quarter of the year. I shall call the gear corresponding to the last policy gear A, and this has the value of 1. in positions 13, 17, ..., 29 and zeros in the other positions.

Calkins (1965) has outlined the difficulties involved in increasing the age of first capture by increasing the minimum size limit. He shows that because of the mixture of sizes and
sometimes species within schools, a minimum size larger than the current minimum size is not feasible with the present method of fishing. However it is possible to change the average size of first capture by opening the fishing season at some time other than the beginning of the year. Figure 15 shows the yield for gear A, together with the yields for a set of gears operated in other quarters. These gears form three logical groups;

(1) Those that first capture fish in their fourth year, (A).
(2) Those that first capture fish in their third year (B,C,D,and E).
(3) Those which takes fish which are still in their second year, (F).

The only cause of differences within a group is the difference in yield per recruit. This is because the effect of mortality on a year class at the end of a year is independent of what time of the year the mortality occurred.

The age composition for the maximum equilibrium yield for the gears A, C, and P is shown below. If the strengths of incoming year classes were distributed as an independent random variable the coefficient of variation of annual yields would be somewhat less than the coefficient of variation of year class strength. The square of the ratio of the latter coefficient to the former is equal to the sum of the squares of the proportions of each year class in the catch (see Appendix 2) and the square root of this quantity is shown under the heading S.
Figure 15

The sustained yields for quarterly gears.
Prior to 1966 the average of the catch per standard day's fishing for the first quarter was about 10-20% higher than the average over the whole year (Joseph 1970). This suggests that catchability may be lower in the later part of the year, and this would be a good reason not to try harvesting only in this part of the year. However when the fishery is spread over the year the model predicts a drop of about the same size in catch per standard days fishing as a result of a decline in biomass of the stock and thus it is not necessary to postulate a drop in catchability.

Another way of changing the age of first capture is to use a different fishing method. An example of this is the Japanese longline fishery in the eastern Pacific. The age of first capture for this fishery is a little more than a year greater than that of the surface fishery. The incoming year classes are first exploited in the second or third quarter of the year (Kume and Joseph 1969) and thus this fishery very nearly corresponds to the gear that gives the maximum sustained yield.
Optimisation over a span of years

In this case we require that the yield be optimum over some period possibly with some constraint on the state of the stocks after that period. If the aim is maximization of yield with no constraint then it is clear that the stocks would be destroyed at the end of the period. Figure 16 shows the best strategies found for maximizing yields over periods of five and ten years using gear P. As usual the strategies were constrained so that fishing mortality was less than 5.0 per quarter. These policies gave yields of $1.21 \times 10^7$ and $2.20 \times 10^7$ lbs with annual averages of $2.42 \times 10^6$ and $2.20 \times 10^6$ lbs, both of which are better than any sustained annual yield that can be achieved with gear P.

This type of harvesting is similar to the pulse harvesting that is used by some trawling fleets which inflict a high mortality on fish in an area in a relatively short time span (and then leave the area). A major problem with this type of harvesting is that it is possible that a stock would not recover after being severely depressed. This could be the result of competitive exclusion which is probably at least a factor in the loss of the sardine fisheries of California, Japan, and South Africa, or simply through a failure of the depressed stock to reproduce successfully, as may be happening to the haddock stocks of Georges Bank (Grosslein and Hennemuth 1972).

However if these problems do not occur the model indicates that good year classes would be formed two years after the cessation of harvesting, and that the biomass would have recovered to its virgin state five years after the cessation of
Figure 16

The yield for policies of maximizing the total yield over periods of 5 and 10 years.

The numbers below the histograms are the values of quarterly instantaneous fishing mortality in hundredths.
harvesting. In addition, by this time four good year classes would have formed and so after resting five years the pattern could be repeated. Thus the long term average annual yields for these policies are $121 \times 10^6$ lbs and $145 \times 10^6$ over periods of ten and fifteen years respectively.

Periodic harvesting

Walters (1969) has suggested that when there is no way of increasing the age of first capture above some critical age a periodic policy may provide the maximum long term yield. To check if this is the case when gear P is being used I looked at the consequences of harvesting for one year and then leaving the stock untouched for periods of one, two, and three years. Figure 17 shows the long term average yield obtained with each of the three patterns. The catch composition at the fishing mortality that gave the maximum yield for each pattern is shown below.

<table>
<thead>
<tr>
<th>Year of life</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>S</th>
</tr>
</thead>
<tbody>
<tr>
<td>One year closure</td>
<td>0.10</td>
<td>0.52</td>
<td>0.27</td>
<td>0.08</td>
<td>0.02</td>
<td>0.60</td>
</tr>
<tr>
<td>Two year closure</td>
<td>0.10</td>
<td>0.42</td>
<td>0.35</td>
<td>0.10</td>
<td>0.02</td>
<td>0.57</td>
</tr>
<tr>
<td>Three year closure</td>
<td>0.11</td>
<td>0.39</td>
<td>0.30</td>
<td>0.16</td>
<td>0.03</td>
<td>0.53</td>
</tr>
</tbody>
</table>

Maximum average annual yields were $164 \times 10^6$, $151 \times 10^6$, and $128 \times 10^6$ lbs for the policies of one, two, and three year closure. Closure for one year gives a yield and catch composition much like those for gear P while the policies of closure for two or three years have lower average annual yields. The lower yields are compensated for a little by the fact that
Figure 17

The average yield for periodic harvesting with one, two, and three years between harvesting years.
FISHING MORTALITY IN HARVESTING YEARS

YIELD IN MILLIONS OF LBS

1 YEAR DELAY
3 YEAR DELAY WITH MIXING OF STOCKS
2 YEAR DELAY
3 YEAR DELAY

FISHING MORTALITY IN HARVESTING YEARS

0.5 1.0 1.5 2.0 2.5 3.0

10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 200
the yield is spread more evenly over the year classes with a
subsequent decline in variability of yield.

This kind of strategy shares with the previous type the
problem of what to do with the fleet in the years when there is
no fishing. One possibility if there is a group of more or less
independent stocks is to fish them in turn. If for example there
are three independent stocks we could fish each for one year and
then leave it for two years, while fishing in the other areas.
In this case we would get a sustained yield three times as large
as the average yield of one of the areas. If on the other hand
there is some transfer of fish between stocks, then a fishing
effort applied in one area will produce fishing mortality in the
other areas. Thus if we had three stocks identical to those in
A1 but whose members interchange so a fishing effort in one area
produces 60% of its fishing mortality in that area and 20% in
each of the other areas, then the pattern of fishing mortality
in any area is 0.6F, 0.2F, 0.2F instead of F, 0, 0. The effect
of this is of course to produce a policy whose effect is midway
between the sustained policy and the on-off policies. The yield
for this policy is shown in Figure 17.

The relations between sustained or average yield and effort
shown in Figures 12, 14, and 16 are typical of domed yield
curves. They have the property that each increase in effort gets
a smaller return in increased yield. Consequently, if the cost
of harvesting is substantial compared to the value of the
harvest the most economical strategy is to harvest at some rate
less than that for the maximum sustained yield. The reduction of
the marginal return is illustrated by the fact that the strategies of using gear P, C, and P with a 2 year pause, with a harvesting rate of 67% of that which gives the maximum yield would give respectively yields of 88%, 83%, and 90% of the maximum in each case.

Random variation in recruitment

To get some idea of the effect of random variation in recruitment, simulations of various policies were tried with a version of the model which had the recruits for each year multiplied by a random variable that was uniformly distributed between 0.5 and 1.5. The table below shows the results of 100 year simulations with the gears P, C, and A at the fishing mortality which gave the maximum yield. A 25 year yield sequence for each gear is shown in Figure 18.

<table>
<thead>
<tr>
<th></th>
<th>gear P</th>
<th>gear C</th>
<th>gear A</th>
</tr>
</thead>
<tbody>
<tr>
<td>Expected yield</td>
<td>166</td>
<td>193</td>
<td>245</td>
</tr>
<tr>
<td>Mean yield</td>
<td>162</td>
<td>182</td>
<td>229</td>
</tr>
<tr>
<td>Sample standard deviation</td>
<td>31</td>
<td>40</td>
<td>67</td>
</tr>
<tr>
<td>Coefficient of variation</td>
<td>0.19</td>
<td>0.22</td>
<td>0.29</td>
</tr>
</tbody>
</table>

The sample means are all significantly less than the values expected on the basis of the deterministic model, and this effect increases as the maximum yield increases. The standard deviation of the yield from gear P was less than that from gear C, which in turn was less than the standard deviation of the
Figure 18

Harvest sequences from simulations of the yellowfin tuna population with random variation in recruitment.
yield from gear A. The expected values for the coefficient of variation assuming that the year class strengths are independently distributed were 0.17, 0.21, and 0.29 which are quite close to the results of the simulation.

Summary

There are several factors that must be born in mind when deciding what is an optimum strategy for fishing, and some of these factors can be studied with the aid of the model. The first thing that is usually considered is the total yield and the cost of getting it. The nature of the purse seine fishery for yellowfin suggests that the cost of harvesting will not rise as fast as the value of the yield, and thus at first sight the maximum yield would seem to be the ideal target.

However there are several problems associated with maximizing the yield. Firstly it seems that it may be necessary to change to another fishing method which would almost certainly increase the cost of harvesting. Secondly there is a general trend of increasing variability of annual yields as yield increases which would make the larger yields less attractive. Finally, strategies with large total yields involve the capture of older fish which may cause market problems because of the high levels of mercury in these fish.

The annual yield from the present fishing method can be increased slightly by changing the time for the unregulated fishery from the beginning of the year to the third or fourth quarter. This change would not increase the proportion of old
fish in the catch, and would only slightly increase the variability of the yield.
Harp Seals

The fishery for the harp seal on the east coast of Canada provides an example of the use of the model with a linear stock recruit relation. This simply is Leslie's model or the method of life tables, and is included in this thesis as it illustrates the usefulness of age structure data in estimating the dynamics of this population.

The linear model is used in this case because it would not be expected that density dependent effects would be important while the population remained close to its present low size. Because harp seals are long lived and have a slow rate of population increase the population will not grow very rapidly even if the harvest is stopped entirely. Also it is unlikely that the population will be much depressed by over harvesting in future years.

Life history

The life history of the harp seal is important in relation to the harvest and is outlined in the following summary which is taken mainly from Sergeant (1963).

Adult harp seals start migrating from Arctic waters in November and move down the coast of Labrador reaching the north of the Gulf of St Lawrence by January. They remain in open water until the ice begins to form in the latter part of February, when the females form whelping groups on the ice. There are two major whelping grounds, known as the Gulf and Front, the first
being in the Gulf of St Lawrence and the latter being in the open sea to the east of Newfoundland. Initially the pups are covered with the white hair which makes their pelts so attractive to the industry. This begins to loosen after a week and the pups moult at two weeks. At this time they begin to enter the water and are deserted by their mothers. The adults breed in late March and shortly afterwards the seals move onto the ice to moult. Moulting patches begin to form about the 10th of April and at this time they are composed mainly of adult males and bedlamers (immature seals with a range of ages from 1 to about 5 years) which have just arrived from the north. Adult females start joining the groups at about the 20th of April and are fully represented in about a week. Following the moult the seals follow the edge of the breaking ice and return to the Arctic.

It is not clear to what extent animals from the two herds intermingle, though recent studies indicate that while there may be some homing to the Gulf or Front there is not a sharp division between the two herds (Sergeant 1971). In this study it is assumed that the two herds form a single breeding population.

One of the most important consequences of the harp seal behaviour is that because hunting is carried out at a time when the seals are congregated in a few easily located dense groups of the catch per unit of effort does not give a reliable indication of population size. Another important consequence is the effect of the closing date of the hunt on the sex ratio of the kill. Because adult females do not join the moulting groups
until late April they can be protected by closing the season before they arrive.

Seal hunting

Though some seals are killed by landsmen on the coasts of Canada and Greenland the major part of the kill is taken from whelping and moulting patches by sealers operating from Canadian and Norwegian ships. Statistics for the harvest are given in the ICNAF Statistical Bulletin. From these figures I have estimated the number of females killed every year (see Appendix 1). Over the last ten years the sealers operating from ships have taken an average of 230,000 pups, and 50,000 older seals. A small part of this kill (approximately 8000 pups, 1000 bedlamers, and 1000 adults) is taken by Eskimos, from Canada and Greenland and I have assumed that this will remain constant in future years. Thus this kill will appear in all my population projections.

The model and parameters.

There is no information as to whether harp seals are monogamous (C.O.S.S. 1972), and so the model is in effect a model of the dynamics of the female population, expressed in terms of a 1:1 sex ratio. If only a few males are required for breeding all the estimates of kills may be increased by the number of surplus males that can be captured.
The model is

\[ N(1,t+1) = \sum_{i} [H(i) \cdot S(i) \cdot N(i,t)] \]

\[ N(i+1,t+1) = S(i) \cdot N(i,t) \quad i = 1, 2, \ldots, 30. \]

Where \( N(i,t) \) is the number of seals beginning their \( i \)th year of life in year \( t \), \( H(i) \) and \( S(i) \) are the age specific pregnancy and survival rates.

To use the model for predictive purposes it is necessary to have estimates of birth rates, mortality and the population size and structure in at least one year.

Pregnancy rates can be taken from data given by Sergeant (1971) in his Table 1. These rates were rounded and divided by 2 to give the following rates which are relative to a population with a sex ratio of 1:1.

<table>
<thead>
<tr>
<th>Age</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9 and over</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pregnancy rates</td>
<td>.01</td>
<td>.11</td>
<td>.31</td>
<td>.42</td>
<td>.42</td>
<td>.45</td>
</tr>
</tbody>
</table>

This data is based on observations on seals collected in the Gulf during the years 1966-1969, and gives a slightly lower reproductive rate than had been observed in earlier years.

The mortality rate for adult seals was estimated by Ricker (MS.) who found a total annual mortality of 15%. This reflected conditions 10-20 years ago when the hunting mortality for adults was about 7%. Ulltang (MS.) using more recent samples found a
total mortality of 12%. Hunting mortality had declined to about 5% for the animals in Ulltang's sample and so both estimates give a figure of about 8% for natural mortality, which is the figure used here.

Estimates of the size of the breeding population are available from several sources of data. The most direct estimates obtained are those from aerial surveys of both whelping and moulting seals. Results of these surveys are discussed by Sergeant (1966, 1971) and a summary of the results is

<table>
<thead>
<tr>
<th>Year</th>
<th>Adults</th>
<th>Pups</th>
</tr>
</thead>
<tbody>
<tr>
<td>1950</td>
<td>730,000</td>
<td>440,000</td>
</tr>
<tr>
<td>1959</td>
<td>370,000</td>
<td>240,000</td>
</tr>
<tr>
<td>1970</td>
<td>180,000</td>
<td></td>
</tr>
</tbody>
</table>

Because it is difficult to find all the seals in photographs these estimates tend to be on the low side but they do indicate a large drop in population during the twenty year period.

It is possible to get a minimum estimate of pup production in any year simply by taking the sum of the members of that year class that are harvested. This procedure was used by Oritsland (1971) to get a minimum estimate of 292,000 pups for the 1967 year class.

Another estimate can be made using a method based on the variation of the age composition of samples of seals. This method was suggested by Sergeant (1971) and modified by Ricker
(MS.). Assuming that the samples represent the population the ratio \( K(i) \) of age 1 to adult seals in samples is be given by

\[
K(i) = \frac{Q \cdot \{ M(i) - C(i) \}}{M(i)}
\]

where \( M(i) \) and \( C(i) \) are the pup production and kill in year \( i \) and \( Q \) is a constant. By further assuming that the pup production in years \( i \) and \( j \) was the same and equal to \( M \), Ricker showed that

\[
M = \frac{\{ K(i) \cdot C(j) - K(j) \cdot C(i) \}}{\{ K(i) - K(j) \}}
\]

In fact if the pup production in the years \( i \) and \( j \) is not same the estimate of \( M \) given above by the formula above would lie between \( M(i) \) and \( M(j) \) since \( M(i) > M(j) \), implies that \( M(i) > M > M(j) \). For

\[
M(i) = \frac{\{ M(i) / M(j) \} \cdot K(i) \cdot C(j) - K(j) \cdot C(i) \}}{\{ K(i) - K(j) \}} > M
\]

and thus \( M \) gives an estimate between \( M(i) \) and \( M(j) \). Ricker obtained a mean estimate of 273 thousand pups in 1968 using a comparison of the 1968 year class with those of 1966, 1967, 1969 and 1970. The data used are shown in Table 5, and it can be seen that the pup kill in 1968 was unusually low giving high values of \( K \) for that year class. Ricker suggested that because this year provided the greatest contrast with the other years, comparisons using it would give the most reliable results. However it can also be argued that because this year is unlike the rest, the assumptions about the ratios are less likely to be
Table 5

Numbers of age one year and adult seals in samples at St Anthony and the Front.

<table>
<thead>
<tr>
<th>Year</th>
<th>Pup kill</th>
<th>St Anthony</th>
<th></th>
<th></th>
<th>Front</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Class</td>
<td>age 1 adults</td>
<td>ratio</td>
<td>age 1 adults</td>
<td>ratio</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1966</td>
<td>257</td>
<td>18</td>
<td>261</td>
<td>0.069</td>
<td>176</td>
<td>377</td>
<td>0.467</td>
</tr>
<tr>
<td>1967</td>
<td>280</td>
<td>7</td>
<td>165</td>
<td>0.042</td>
<td>84</td>
<td>332</td>
<td>0.253</td>
</tr>
<tr>
<td>1968</td>
<td>158</td>
<td>87</td>
<td>68</td>
<td>1.279</td>
<td>62</td>
<td>33</td>
<td>1.879</td>
</tr>
<tr>
<td>1969</td>
<td>235</td>
<td>41</td>
<td>434</td>
<td>0.094</td>
<td>105</td>
<td>186</td>
<td>0.565</td>
</tr>
<tr>
<td>1970</td>
<td>226</td>
<td>39</td>
<td>285</td>
<td>0.137</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 6

Estimates of pup production using Sergeant's method.

<table>
<thead>
<tr>
<th></th>
<th>St Anthony</th>
<th></th>
<th></th>
<th></th>
<th>Front</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1966</td>
<td>289</td>
<td>317</td>
<td>263</td>
<td>317</td>
<td></td>
<td>1966</td>
<td>362</td>
<td>290</td>
</tr>
<tr>
<td>1967</td>
<td>304</td>
<td>317</td>
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<td></td>
<td>1967</td>
<td>317</td>
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<td>234</td>
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<td></td>
<td>1968</td>
<td>268</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1969</td>
<td>255</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Each estimate is based on comparisons between the data for the years heading the row and column containing the estimate.
true in this year. This suspicion is strengthened by looking at the ratios of the values of $K$ for the Front and St Anthony samples. This ratio which should be constant has the values 6.8, 6.0, 1.5, 6.0 for the years 1966 to 1969. The estimates of $M$ based on all the available comparisons are shown in Table 6, which illustrates that if the 1968 comparisons are ignored the mean estimates would be considerably larger.

Using this information an ICNAF assessment subcommittee (ICNAF 1971) estimated pup production as 400,000, 350,000, and 300,000 in the years 1960, 1965, and 1970. These estimates were compared with population simulations starting from arbitrary stable populations in 1938. The harvest for each year is given in Table 7 as the number of pups, bedlamers, and adults killed. For each year of the simulation the kill of bedlamers and adults is taken from the year classes according to their relative strength. The results of the simulation that was chosen as the best estimate of the population history are shown in Table 8.

Harvest policies

Even with the assumption of a linear stock recruit relation in the model there is a wide choice of possible harvest strategies. For example it is possible to find sustained harvests with different stock structures. Leslie (1945) showed that a sustained harvest consisting of age classes in the same frequency as they appear in the population could be obtained using a harvest rate of $1-1/\lambda$ where $\lambda$ is the dominant eigenvalue of the life table matrix. In general an equilibrium harvest can
<table>
<thead>
<tr>
<th>Year</th>
<th>Pups</th>
<th>Bedlamers</th>
<th>Adults</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1938</td>
<td>221</td>
<td>34</td>
<td>7</td>
<td>262</td>
</tr>
<tr>
<td>1939</td>
<td>102</td>
<td>19</td>
<td>17</td>
<td>139</td>
</tr>
<tr>
<td>1940</td>
<td>132</td>
<td>32</td>
<td>13</td>
<td>177</td>
</tr>
<tr>
<td>1941</td>
<td>17</td>
<td>35</td>
<td>8</td>
<td>60</td>
</tr>
<tr>
<td>1942</td>
<td>2</td>
<td>20</td>
<td>5</td>
<td>26</td>
</tr>
<tr>
<td>1943</td>
<td>6</td>
<td>3</td>
<td>2</td>
<td>11</td>
</tr>
<tr>
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<td>6</td>
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<td>24</td>
</tr>
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<td>1945</td>
<td>10</td>
<td>21</td>
<td>4</td>
<td>34</td>
</tr>
<tr>
<td>1946</td>
<td>73</td>
<td>18</td>
<td>9</td>
<td>100</td>
</tr>
<tr>
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<td>47</td>
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</tr>
<tr>
<td>1948</td>
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<td>45</td>
<td>39</td>
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</tr>
<tr>
<td>1949</td>
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<td>28</td>
<td>33</td>
<td>288</td>
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<td>276</td>
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<tr>
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<td>66</td>
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<td>292</td>
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<td>27</td>
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<td>57</td>
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<td>1956</td>
<td>341</td>
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<td>35</td>
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<td>1957</td>
<td>165</td>
<td>20</td>
<td>58</td>
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<td>51</td>
<td>316</td>
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<td>1960</td>
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<td>30</td>
<td>75</td>
<td>275</td>
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<tr>
<td>1961</td>
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<td>7</td>
<td>11</td>
<td>197</td>
</tr>
<tr>
<td>1962</td>
<td>214</td>
<td>35</td>
<td>63</td>
<td>313</td>
</tr>
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<td>278</td>
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<td>41</td>
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</tr>
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<td>1965</td>
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<td>17</td>
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<td>236</td>
</tr>
<tr>
<td>1966</td>
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<td>23</td>
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<tr>
<td>1971</td>
<td>210</td>
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Table 8
Estimated harp seal population history, 1938-1971.

<table>
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<tr>
<th>Year</th>
<th>0-1</th>
<th>1-2</th>
<th>2-3</th>
<th>3-4</th>
<th>4-5</th>
<th>5-6</th>
<th>adults</th>
<th>total</th>
</tr>
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<tbody>
<tr>
<td>1938</td>
<td>337</td>
<td>105</td>
<td>97</td>
<td>89</td>
<td>82</td>
<td>75</td>
<td>749</td>
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<td>332</td>
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<td>89</td>
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<td>76</td>
<td>70</td>
<td>738</td>
<td>1493</td>
</tr>
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<td>1940</td>
<td>322</td>
<td>212</td>
<td>94</td>
<td>79</td>
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<td>1559</td>
</tr>
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<td>694</td>
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</tr>
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<td>150</td>
<td>158</td>
<td>81</td>
<td>68</td>
<td>676</td>
<td>1690</td>
</tr>
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<td>1943</td>
<td>300</td>
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<td>244</td>
<td>134</td>
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<td>61</td>
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<td>1822</td>
</tr>
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<td>223</td>
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<td>112</td>
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<td>202</td>
<td>185</td>
<td>88</td>
<td>117</td>
<td>955</td>
<td>2221</td>
</tr>
<tr>
<td>1956</td>
<td>409</td>
<td>160</td>
<td>221</td>
<td>180</td>
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<td>79</td>
<td>925</td>
<td>2139</td>
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be taken by using harvest rates $c(i)$ such that the reproductive potential is equal to 1, i.e.

$$\sum \{ H(i) \cdot Q(i) \} = 1$$

Where $Q(i) = S(1) \cdot [1-c(1)] \cdot S(2) \cdot [1-c(2)] \cdots S(i) \cdot [1-c(i)]$

Thus a sustained harvest of pups only can be taken by setting $c(1)=1-1/E$ and $c(i)=0$ for $i>1$, where $E$ is the reproductive potential with no hunting mortality. With the parameters I have used the dominant eigenvalue is 2.03 which gives a sustained harvest from all age groups of 51% of the population. The value of $E$ is 2.95 which gives a sustained harvest of pups only, of 66% of the pup production. These sustained rates of harvest only apply to situations where the stable age distribution has already been reached, and of course this is not the case with this stock. In fact this population is now declining, and because it takes six years before pups join the breeding population reducing the harvest of pups will not alter the pup production until after 1977. The estimated pup production for the years 1972-1977 is

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<th>Year</th>
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The estimate of maximum sustained yield of pups only starting from the estimate of the present stock structure was found by trial and error to be 164 thousand pups (plus the
Eskimo kill of 8,000 pups and 2,000 older seals). Another policy that could be tried is that of allowing kill of 20 thousand adults and bedlamers in addition to the Eskimo kill. In this case the sustained yield is only 126 thousand pups and thus the difference of 38 thousand pups is traded off against 20 thousand older seals.

A simple way of assessing the effect on the population of killing female seals of different ages is to look at the expected number of pups that would be produced in the remainder of the seal's life, which is shown in Figure 19. This figure shows that from the point of view of maximizing reproduction the least desirable age groups to harvest are the 6 year olds, and that the best age groups to harvest are the very old ones and the pups. To maximize profit the value of seals of different ages would have to be considered, and in addition the expected future pup production would have to be discounted.

Sensitivity of the model as applied to harp seals

If a model of this type is to be used for management purposes it is important to know the sensitivity of its output to changes in parameters. Furthermore, it is important to be able to make observations which can be compared with predictions of the model to test its performance. For these observations to be useful they must provide a critical test of the model, i.e. the observations must be sensitive to changes in the parameters. Two possible sets of observations are the sizes of age groups, and the ratios of sizes of age groups. Ratios of the
Expected number of pups to be born to female seals of different ages.
Expected number of pups to be born.
numbers in age groups have the advantage of being easier to measure than actual numbers, but they are not as sensitive to changes in parameters as the actual numbers are.

I tested the sensitivity of the model using three sets of survival and pregnancy rates as well as a variety of initial population sizes. The sets of parameters were:

1. The estimates given above.

2. A set with a mortality rate of 6% and pregnancy rates increased by 10%.

3. A set with a mortality rate of 10% and pregnancy rates decreased by 10%.

The sustained yields of pups only with these three sets of parameters were respectively 66%, 78%, and 49% of pup production. Figures 20(a)-(d) show the model's predictions of strengths of the year classes 1967, 1969, 1970, and 1971 relative to the 1968 year class, as a function of the 1970 pup production for the three sets of parameters. The ratios shown are those predicted by the model for the year 1972. The ratio for other years will vary slightly because of variations in the harvest of bedlamers taken from different age groups. Figure 21 (a)-(d) shows the predictions of numbers in 1972 for the different parameters as a function of the 1970 pup production.

Neither the numbers nor ratios of numbers in 1972 are very sensitive to the differences between the parameters, but they are both fairly sensitive to changes in population size as measured by the 1970 year class strength. Figure 22 shows the pup production projections for each of the parameter sets with a
Figure 20


Parameter set 1
Parameter set 2
Parameter set 3

(A) Ratio of 1967 to 1968 year class.
(B) Ratio of 1969 to 1968 year class.
(C) Ratio of 1970 to 1968 year class.
(D) Ratio of 1971 to 1968 year class.
Figure 21


Parameter set 1
Parameter set 2        - - - -
Parameter set 3        ---

(A) 1968 year class.
(B) 1969 year class.
(C) 1970 year class.
(D) 1971 year class.
Figure 22

Projected pup production using the three parameter sets.

The kills for the year 1972 onwards are 126,000 pups and 20,000 older seals in addition to the Eskimo kill of 10,000 seals.
1970 year class strength of about 300,000, and a harvest of 134,000 pups plus 22,000 older seals after 1971. Although these projections are substantially different after about 10 or 15 years, it would be difficult if not impossible to choose between them before 1976, by which time the pup production until 1982 is determined. Thus an error in assessing the state of the population at this stage will be hard to detect, and could lead to severe damage to the stocks.

In view of the possible error in the estimates of the state of the stocks it is essential that the best possible observations be made over the next few years to ensure that the population is not further depressed by over-harvesting. Table 9 shows the projections of numbers in the youngest age groups for the years 1972-1980 for each of the three parameter sets. In each case the 1970 pup production was approximately 300,000 and the annual harvest for the years 1972 onwards was 134,000 pups and 22,000 older seals. There are large differences between the three projections, but as noted above, direct observations of the population size may not be accurate enough to distinguish between these three possibilities. It is however easier to detect relative differences between numbers in age groups which can be exhibited as catch curves. The catch curves for the years 1976 and 1980 for the three projections are shown in Figure 23. There is very little difference between the predictions of catch curves in 1972 for the three sets of parameters, but Figure 23 shows the differences become more marked with time and that by 1980 there are large differences between the three curves.
Table 9


**Numbers In Thousands**

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Figure 23

The three sets of parameters are of course only a small sample from the possible range of the types of errors that may have been made in estimating the stock condition. However, regardless of the type of error made the catch curves will provide an indication of whether recruitment to the population is decreasing, constant, or increasing. This is because trends in recruitment will alter the apparent mortality rate that is shown by the catch curve. If recruitment is increasing the differences between numbers in successive age groups shown by the curve will be greater than that caused by mortality alone, and the apparent mortality will be higher than it would be if there were no trend in recruitment. The opposite effect occurs when recruitment is declining.

Using Figure 23 as a guide it can be seen that for the harvest schedule used above we could say the population was being over harvested if the average slope of the observed catch curve was less than 0.04 in 1976 or less than 0.11 in 1980.

Unless methods of obtaining direct estimates of population size are improved in the next few years it would be best to concentrate on obtaining accurate catch curves to be used as indicators of trends in recruitment.

Density dependent effects

It is of interest to speculate about harvest policies that might have been applied at the initiation of the fishery that could have ensured a larger sustained harvest. According to
Chafe (1923) between 500,000 and 700,000 pups were killed annually in the 1840's. Bearing in mind the lower efficiency of hunting at that time a figure of one million would seem to be a reasonable estimate for the pup production in the unharvested population. Because of the large range of population size it is now necessary to consider the effect of population size on the parameters. A reasonable simple assumption is that population size has a linear effect on pregnancy rates and no effect on survival. Then the reproductive potential $E$ will be a linear function of pup production and we can write

$$E = a - b \cdot n$$

where $E$ is the reproductive potential when the population has a pup production of $n$. The corresponding sustained harvest of pups is then

$$C = n \cdot (E - 1) / E$$

The constants $a$ and $b$ can be evaluated using the assumption that $E = 1$ when the pup production is one million and that $E = 2.95$ when the production is 300,000. This gives values of $a$ and $b$ of 3.78 and 2.78 and a sustained harvest of $n \cdot (1 - n) / (1.36 - n)$. The maximum sustained harvest is thus 320,000 pups which is taken from a population with a pup production of 660,000, more than twice as large as the present population.

If the stock size $U$ is measured in terms of the number of pups needed to maintain the stock then
\[ n = E \cdot U \]

which can be combined with the relation between \( E \) and \( n \) giving

\[ \frac{n}{U} = a - b \cdot n \]

or \[ n = a \cdot U / (1 + b \cdot U) \]

Thus the assumption of a linear decline in fecundity leads to the Beverton and Holt type of stock recruit relation which is shown in Figure 24. The sustained yield of pups at any stock size is the difference between the stock recruit curve and the replacement line.

Of course other assumptions could have been made about the nature of the effects of population size on the life history parameters and these would lead to different stock recruit curves. However, as any curve is constrained to pass through the three points 0, A, and B it is unlikely that radically different conclusions would result if a different curve was used. For comparison the Ricker curve that passes through the three points is also shown on Figure 24. This curve has a parameter of 1.2 and gives a maximum sustained yield of 420,000 pups at a pup production of 820,000 pups.
Figure 24

Stock-recruit curves for harp seals.
The dynamics of the model for harp seals

With a stock recruit relation of the type \( n = U \cdot f(U) \) such as those shown in Figure 24 it is unlikely that the model would be unstable. With the two cases shown the model is stable for all values of fishing mortality, as the Beverton and Holt curve always gives a stable population and a Ricker curve must have a parameter greater than 2 to make the model unstable. A stock-recruit curve of this type would have to have a much more pronounced dome and steeper right hand limb than the Ricker curve in Figure 24 if it were to produce an unstable equilibrium in this population. Even if this is the case for this population such an instability would only occur at low fishing mortalities and thus is of little importance in the present situation.

On the other hand if the stock-recruit relation were of the more general type \( n = U \cdot f(V) \) then it is possible to get fluctuations with a high harvest rate. For example if density dependent mortality occurs as a result of interactions between adult and immature seals at the winter feeding grounds (Sergeant 1971), high hunting mortalities could lead to fluctuations in year class strength.
Discussion

In this study the properties and uses of a class of population models that are useful in fisheries management has been examined. These models which are referred to as dynamic age structured models are essentially a life table modified by a stock recruit relation. The recruitment is made up of the product of the number of eggs produced by the population and a survival term which is a function of the stock "density", which was defined to be a linear combination of the numbers of fish of various ages. Because of the assumption that the natural mortality of older fish is constant this density dependent survival regulates the model population. A wide range of survival functions has been suggested in the literature for this role, but unless there is some knowledge of the mechanisms involved it is probably best to restrict the choice of function used to one which leads to one of the Leslie, Beverton and Holt, or Ricker stock-recruit relations.

One of the most important benefits that can be got from using these models is that it is possible to use them to investigate the effects of a much wider range of harvest strategies than can be investigated with either the yield per recruit or surplus production models. This wider range includes the important possibilities of harvesting only a portion of the age classes present and policies which fluctuate in time.

Another major benefit is associated with the age structure of the model, i.e. harvest policies may be designed to ensure as many age groups as possible make a significant contribution to
the population which will minimize the effect of fortuitous fluctuations in year class strength on yield or recruitment. Furthermore with an age structured model full use can be made of year class strength data that is routinely collected for many fisheries. This data can be used as data for the model or as a test of the performance of the model.

The use of this type of model is appropriate when the relative year class size is more or less fixed, apart from changes caused by fishing mortality, soon after it is produced. This requirement is satisfied if variation in the number of fish recruited is larger than the variation in year class size due to variations in the natural mortality, and if there are no strong interactions between year classes once recruited. The approach is of course applicable to other animals than fish as is suggested by the choice of a seal population as an example. In fact it could be used as a management model for any population that exhibits age structure with the required properties. On the other hand the approach is of course of no use for those tropical fish populations in which which reproduce throughout the year, and thus do not have separate age groups.

The dynamic nature of the model makes it suitable for use in conjunction with an experimental approach to harvesting, in which harvest policies are thought of as experimental designs. The object of the experiment is to understand the dynamics of the population as a necessary step in optimizing the yield. The most obvious way of experimenting is to explore policies that are like the one which is thought to be the best. This is really
refining the estimates of the parameters over a small region which is thought to contain the optimum policy, and is what the IATTC is doing with their experimental fishing programme. An alternative approach which is likely to be a more useful way of getting information when not much is known of the stocks is to violently stress the population with the intention of learning its behaviour under a wide range of situations. This would be a much faster method of finding out about the dynamics of the population and of testing the model than is the method of examining the effect of small changes in fishing policies.

The major shortcoming of this type of model is its complexity, and the consequent difficulty in examining the behaviour of the model. Associated with this is the need for more parameters than are required for the logistic or yield per recruit models.

One of the principal features of the model is the idea of the population regulation by a stock-recruit relation. Although this concept is well entrenched in fisheries literature no really convincing mechanisms causing this type of density dependence have been found. This is probably due to the major interest of fisheries workers being in management, as opposed to the interest of workers in other fields such as small mammal populations in how, or whether populations are regulated. Because of this it is necessary that research be carried out to test whether the assumption of the existence of a stock-recruit relation is helpful in giving a reasonable description of the population.
One of the most interesting possibilities for future development of age structured models is their application to harvesting in multiple species fisheries. Multispecies forms of the model will of course more complex than single species forms, however the principal difficulty is likely to lie in establishing the form of the interaction between populations, which seems even more difficult than it is to measure the effect of density dependent mortality. Thus it is to be expected that the multispecies forms of the model will only be developed in situations where it is reasonable at least to postulate a strong interaction between populations.

Finally it has for a long time been accepted that the use of mathematical models is essential for the rational management of fisheries, and progress in this field is thus associated with the development of models which are realistic in the sense that their behaviour mimicks that of the population as faithfully as possible. The dynamic age structured models studied in this thesis seem to be the most promising type of fisheries management model available at present and its use will encourage and assist the development of optimal management practices.


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Appendix 1

Although the equations (1) given on page 8 define the model some extra information describing their implementation is given here to make it possible to duplicate the computations. In addition the parameters used for the populations A and B used in the third chapter are given.

The basic scheme of the model is shown below for the case of an annual spawner.

These computations were carried out in double precision arithmetic on the IBM /360 computer operated by the UBC computing centre. The pseudo-random deviates were generated by a uniform random number generator that is described in the document "UBC RANDOM December 1970", which is distributed by the computing centre. A copy of the program is available from the author.
The populations A and B

These populations were constructed to have an equilibrium population with 1000 recruits with no fishing mortality and a instantaneous annual natural mortality of 0.2.

The stock recruit relation for population A is
\[ n = c \cdot U \cdot \exp(-k \cdot U) \]
with \( c = 4.022 \), and \( k = 0.000295 \). The fertility schedule was 1, 2, 4, 8, 12, 14, for ages 3 upwards.

The stock recruit relation for population B was
\[ n = c \cdot U \cdot \exp[-k \cdot \sum N(i)] \]
with \( c = 3.017 \), and \( k = 0.001004 \). The fertility schedule was 10 and 12 for ages 4 and 5 respectively.

The random variation in the population was simulated by multiplying by a pseudo-random number uniformly distributed between 0.1 and 1.9.

Appendix 2

The annual yield from the model can be written as
\[ Y(t+r) = k \cdot \sum p(j) \cdot N(1, t+j) \]

where \( Y(t) \) and \( N(1, t) \) are the yield and recruitment in year \( t \), \( p(j) \) is the proportion of the yield made up of fish of age \( j \), and \( k \) is a constant chosen so \( \sum p(j) = 1.0 \).
If \( N(1,t) \) is a sequence of independent random variables with variance \( s^2_N \) then the variance of \( Y(t) \) is
\[
\sigma^2_Y = k^2 \cdot \sum p(j)^2 \cdot s^2_N
\]
and if \( N \) is the expected value of \( N(1,t) \) the square of the coefficient of variation of \( Y(t) \) is
\[
\frac{s^2_Y}{k^2 \cdot N^2} = \frac{s^2}{\sum N^2} \leq \frac{s^2}{N^2}
\]
thus if the recruitment is a sequence of independent random variables the coefficient of variation of yield is less than the coefficient of variation of the recruitment.

When a non trivial stock recruit relation is used in the model the recruitment in successive years is no longer independent and so the expression above is only approximate.

Appendix 3

Treatment of the harp seal harvest statistics.

The harvest statistics for harp seals for the years 1938-1970 were taken from the ICNAF statistical bulletins for 1969 and 1970, and estimates of the 1971 harvest were given to me by Dr. H. D. Fisher (personal communication). The statistics are
divided into several categories which can be combined to produce
the following statistics.
(a) Pup kill.
(b) Seals one year and older. Denmark, Norway and the
U.S.S.R.
(c) Bedlamers Canada.
(d) Adult seals Canada.
(e) Total kill.

I have assumed that the group (b) was made up of 20%
bedlamers and 80% adults in the years 1938 to 1966, and 50%
bedlamers and 50% adults in the years 1967 to 1971. This change
in the age composition is the result of changes in hunting
practice (Dr. W. E. Ricker personal communication).

Differences between the total kill and the sum of the
individual figures for pups, bedlamers, and adults were made up
by adjusting the figures for bedlamers and adults according to
the formulae below

\[ O' = O \cdot \frac{T-P}{B+O} \]

\[ B' = B \cdot \frac{T-P}{B+O} \]

where \( T \) is the total kill, \( B \) is the kill of bedlamers, \( P \) is the
pup kill, and primes denote adjusted figures.

Estimates of females in each category were then made using
the following proportions of females.

Pups 50\%
Bedlamers 50%
Adults 40% 1938-1966
  15% 1967-1969
  34% 1970-1971

The reason for the changing sex ratios in the harvest is variation in the closing date of the hunt, which was introduced in 1967. As mentioned above the effect of an early closing date is to reduce the number of females in the adult harvest. The estimates of the proportion of females in the kill is taken from Oritsland (1971).