
Guidelines for Harvesting Species of Different Lifespans

Project R. 4823

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FINAL REPORT

R. 4823 Guidelines for harvesting species of different life spans

1. Objective of the project

The objective of this project was to develop simple guidelines, underpinned by rigorous mathematical analysis, for the harvesting of fish species with different lifespans.

2. Work carried out

A computer program implementing an extremely flexible, fully age-structured simulation model of the dynamics of exploited fish stocks has been developed. The mathematical structure of the model of the dynamics of exploited fish populations is similar to that described by Beverton and Holt. The key biological parameters are the rate of natural mortality (M), the growth rate of the species (K) and the size at which sexual maturity is reached. The primary variables that can be manipulated to adjust yield levels are the size at which exploitation begins and the fishing mortality rate imposed by harvesting.

Population regulation via density dependence is allowed for in the model through incorporation of a non-linear relationship between the spawning stock biomass and the subsequent recruitment of juvenile fish to the population. Of the several frequently used stock-recruitment relationships in fisheries models, most attention has been given here to the Beverton and Holt version, which has the twin advantages of having a simple mathematical form, and of being relatively conservative in the degree of density dependence it attributes to the population. Results have also been obtained, however, for the Ricker form of the stock-recruitment relationship, which allows for higher degrees of density dependent regulation. Stochastic variability in recruitment is also allowed in the model.

The computer program was used to examine the way the maximum sustainable yield of a fish stock, measured as a proportion of its unexploited biomass, varied as a function of the key biological parameters, and of the size at which exploitation first commences (the size at first capture). In particular, simple guidelines for harvesting were sought by examining the relationship between yield-biomass ratios and the natural mortality rate, and the relationship between the fishing mortality rate producing maximum yield and the natural mortality rate. The results obtained have been documented in two scientific papers¹, one which was presented to the British Ecological Society Symposium on Large Scale Ecology and Conservation Biology, and the other to the Royal Society discussion meeting on Generalizing Across Marine and Terrestrial Ecology. Reprints of the papers are appended to this report.

MRAG has entered into a formal agreement with the International Center for Living Aquatic Resources Management (ICLARM) to be a collaborator in the FISHBASE project, which they are conducting jointly with FAO. As part of that agreement, access has been obtained to a development version of a very extensive database of estimates of biological parameters for a wide range of fish species. Access has also been obtained to a comprehensive set of stock-recruitment data for over 100 fish stocks. These two data sources have been used to develop tables of estimates of yield-biomass ratios and fishing mortality rates for key fish species.

¹ Kirkwood, G.P., Beddington, J.R. and J.A. Rossouw. 1994. Harvesting species of different lifespans. pp199-227 in Edwards, P.J., May, R. and Webb, N.R. (Eds) "Large Scale Ecology and Conservation Biology". Blackwell Scientific Publications.

Beddington, J.R. and M. Basson. 1994. The limits to exploitation on land and sea. Phil. Trans. Roy. Soc. Lond. B. 343: 87-92

3. Results

Background

The idea that long-lived, slow-growing species have less potential to provide a sustainable yield than short-lived, fast-growing species was encapsulated in a simple formula in 1971 by Gulland. He related the potential yield of a species to its natural mortality rate in the equation

$$Y = \frac{1}{2} M B_0,$$

where M is the natural mortality rate and B_0 is the virgin population biomass of exploitable fish (i.e. those fish of length greater than or equal to the (potential) length at first capture). While the title of this study refers to lifespan, we have followed Gulland's example and have concentrated exclusively on relating yield to the natural mortality rate. Although the lifespan of any individual fish is well defined, this is not so for a population. It is clear, however, that lifespan is inversely related to the natural mortality rate. Indeed, if lifespan is taken as the average age at death in a population, then if the natural mortality rate is constant, the lifespan so defined is the reciprocal of the natural mortality rate.

Subsequently, several authors have examined the Gulland formula, finding that the maximum sustainable yield was usually somewhat less than $\frac{1}{2}MB_0$, but that considerable variation about that value was possible. In none of these analyses, however, was full account taken of both the age-structure of the population and the relationship between spawning stock size and recruitment. The aim of this study was to examine the potential yield of species with different life histories and different stock-recruitment relationships across the whole range of life spans: from annual species, like squid, to the very long-lived, such as whales or the orange roughy. Following the Gulland line, yield was examined as a proportion of the virgin exploitable biomass, using the computer program developed as part of the project. Complementary results were obtained when yield is expressed as a proportion of total virgin biomass.

The bulk of the study concentrated on the case where there is no stochastic variation in recruitment. However, a solely deterministic analysis provides only a guide to the potential yield, and two further situations were considered where stochastic environmental variation is involved. The first examined the relationship between mean and variance of yield for different parameter combinations and the way this relates to the deterministic results. The second, more unusually, examined the ability of species of different life-spans to respond to and recover from catastrophic events.

Deterministic equilibrium analysis

Constant recruitment

The first important result obtained was that, in the case of constant recruitment, and across species for which the ratio M/K is constant, it has been shown analytically that the proportionality between the yield-biomass ratio and the natural mortality rate hypothesised by Gulland is correct.

Yield-biomass ratios when recruitment is constant have been calculated for M values in the range 0.05-3.0 yr^{-1} . This allows consideration of species with lifespans as disparate as whales and orange roughy at the low M end to annual species such as squid at the other end. Using the large set of estimates of M and K obtained from ICLARM's FISHBASE database, we found that typically M/K varies within the range 0.5 - 4.0 yr^{-1} .

Table 1 below lists the constants of proportionality in the relationship between the yield-biomass ratio and M , for a range of values of M/K and of the length at first capture measured as a proportion of the maximum length (l_c), for the case when the length at maturity is equal to the 60% of the maximum length. The results confirm previous findings that in many cases the constant of proportionality is less than the value of $\frac{1}{2}$ in the Gulland formula. For the parameter values examined, only for high values of M/K and high l_c was the constant $\frac{1}{2}$ or higher.

Table 1. Constants of proportionality in the relationship between the yield-biomass ratio and M when recruitment is constant, for different values of l_c and M/K .

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.30	0.25	0.22	0.22	0.22
0.4	0.35	0.32	0.32	0.36	0.41
0.6	0.45	0.44	0.52	0.60	0.66
0.8	0.63	0.69	0.77	0.82	0.85

The corresponding fishing mortality rates measured as a proportion of M are given in Table 2.

Table 2. Fishing mortality rates producing maximum yield as a proportion of M when recruitment is constant, for different values of l_c and M/K .

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	1.10	0.89	0.81	0.85	0.94
0.4	1.45	1.37	1.79	3.01	9.60
0.6	2.40	3.20	∞	∞	∞
0.8	10.20	∞	∞	∞	∞

Table 1 illustrates that the proportion of the exploitable biomass that can be taken sustainably increases considerably with length at first capture. It should be noted, however, that while the proportion of exploitable biomass that can be taken increases with l_c , the exploitable biomass itself decreases. When measured as a ratio of yield to total biomass, the corresponding constant of proportionality actually decreases. When M/K varies even over the wide range of 0.5-4.0, Table 1 shows that the constants of proportionality are rather similar for a given l_c .

Alternative stock-recruitment relationships

Given the direct proportionality found between the yield-biomass ratio and M when recruitment is constant, it was tempting to hypothesise that the same relationship might hold when recruitment varies as a function of the size of the spawning stock. Unfortunately, this turned out not to be true, but for many biologically likely parameter combinations the relationship was found to be very close to proportional for all practical purposes.

For the Beverton-Holt stock-recruitment relationship, the higher the degree of density dependence (measured as a parameter d taking values in the range 0 to 1; see appended papers), the less does recruitment decline as the spawning stock size is reduced below unexploited levels. In the limit with maximal density dependence, recruitment is constant regardless of spawning stock size. Results obtained indicate that the approximate constant of proportionality in the relation between yield-biomass ratio and M increases as the degree of density dependence increases.

This finding, of course, implies that for fish stocks that exhibit low degrees of density dependence, the Gulland formula is even more optimistic than was suggested above. Table 1 indicates that yield taken as a percentage of virgin exploitable biomass is more likely to be around $0.3M$ than the $0.5M$ that Gulland suggested. When more realistic levels of density dependence are considered, the percentage yield is further reduced, perhaps to between $0.1M$ and $0.2M$.

Inspection of the full set of empirical relationships obtained indicates that substantial departures from proportionality between yield-biomass ratios and M occur only for quite high values of M (e.g. $M > 1$) and primarily when the degree of density dependence is also small. This particular combination of parameters is biologically the most unlikely: normally one expects that low degrees of density dependence in a stock-recruitment relation will be associated with species that have long life-spans and therefore low mortality rates, and conversely that species with nearly constant recruitment even for small spawning stock biomasses will be short-lived and fast growing.

In view of these latter remarks, we attempted to derive an approximate empirical formula expressing the yield-biomass ratio as a function of M , l_c , d , and M/K , for the case where the length at maturity was 50% of the maximum length. After some trial and error, the best log-linear regression fit to estimated yield-biomass ratios corresponded to the formula

$$SY/ExB_0 = [1 - (1-d)^2] \exp(-1.33 + 0.64l_c - 0.31\frac{M}{K} + 0.80l_c\frac{M}{K})$$

This gave quite good predictions over the ranges of parameters examined for the chosen value of length at maturity. However, attempts to generalise this empirical formula further by treating yield-biomass ratios additionally as a function of the length at maturity did not succeed in identifying a sufficiently accurate and simple formula. Since the computer program quite easily allows calculation of yield-biomass ratios for any given set of parameters in any case, further attempts to develop a general formula were curtailed.

Age-dependent mortality

Most standard fisheries models make the assumption that the natural mortality rate does not vary with age, but there is some evidence that natural mortality rates can increase with age for older fish. In practice, however, it is usually difficult enough just to estimate a constant average natural mortality rate for a fish species, so predictions of yield will normally be based on an assumed constant M . We therefore investigated the extent to which allowing for M to increase with age will affect the results presented for constant M .

Our simulation studies indicated that an erroneous assumption of a constant M leads to a negative bias in the predicted yield-biomass ratios. That is not serious, however, because the direction of the bias and its relatively small size (the maximum bias is around 25% in the cases examined) indicates that an erroneous assumption of constant M is likely to result in a slightly conservative prediction of potential yield when in fact M actually increases with age.

The special case of very short-lived species

On the surface, the results described apply equally for all values of M . However, some difficulties arise in the definition of exploitable biomass when M is large, and the argument for treating at least some very short-lived species as special cases becomes unanswerable when one considers annual species like squid, which die immediately after spawning.

The difficulty that occurs is not that any of the calculations are incorrect, but rather that the values calculated for the unexploited population biomass no longer correspond to anything really measurable. This biomass as defined actually represents an average value throughout a year. When M is relatively small, the biomass is roughly constant throughout the year, and it is reasonable to treat an estimate of abundance in an unexploited population made at virtually any time throughout a year as an acceptable estimate of the average biomass. However, for annual species that die after spawning, not only do these biomasses vary considerably throughout the year for ages up to the age at maturity, but they are zero for the remainder of the year. In such circumstances, it is more realistic to examine ratios of yield to the biomass in an unexploited population at the start of what would be the fishing season for an exploited stock. Apart from being easily interpretable, this biomass has the additional virtue of being practically measurable, e.g. by pre-season surveys of abundance or retrospectively via within-season stock assessments.

Yield-biomass ratios were therefore examined for two dynamics models: the standard one as described earlier, and an alternative where M is infinite for all ages exceeding the age at maturity. Comparing the results across models when the exploitable biomass is measured at the start of the fishing season, the yield-biomass ratios are considerably higher when the fish die immediately after spawning, particularly for low values of l_c . In fact, when death occurs after spawning, for the smaller values of l_c the ratio of MSY to the exploitable biomass at the start of the season can be substantially greater than 1.0. This apparently

odd finding simply reflects the fact that fishing has started well before the population has reached its maximum biomass for the year.

Estimates of yield-biomass ratios and fishing mortality rates for selected species

Using estimates of biological and fishery-related parameters contained in the FISHBASE database, as well as estimates of stock-recruitment parameters obtained from other sources, preliminary estimates of yield-biomass ratios and fishing mortality rates have been obtained for 53 commercially exploited or exploitable marine fish species. Tables of these are included in the summary report appended. Clearly as the amount of information recorded on the database increases, this table can be extended.

The effect of stochastic recruitment

In their examination of the statistical properties of recruitment in some commercial fish species, several authors have found that the frequency distribution of annual recruitment was similar to that of a log-normal distribution. Accordingly, we investigated the probability distribution of annual yield when the annual recruitment is log-normally distributed with mean equal to that predicted by the deterministic Beverton-Holt stock-recruitment relationship.

For low values of M , the median annual yield-biomass ratio was found to be very close to the corresponding deterministic value, but as M increased, the median began to fall below the deterministic value. There was a strong tendency for increased skewness in the distribution of annual yield-biomass ratios as M increases.

A direct result of the increasing skewness with M is that, while in most cases the annual yield-biomass ratio will be much less than $\frac{1}{2}M$, in an important minority of cases it can exceed $\frac{1}{2}M$, sometimes substantially. This ability to gain benefits in terms of high yields during good years flows directly from the assumption that fishing mortality (or equivalently fishing effort) is the variable that is used to control the level of harvesting. If harvesting is controlled by pre-set annual catch quotas, this benefit will not be available, and unless the quotas are set conservatively there can be an important risk of stock collapse.

Recovery from a stock collapse

We also examined the ability of a population to recover from a catastrophic mortality episode. Specifically, we examined a case in which a population is initially in equilibrium, being harvested at the fishing mortality rate that produces the deterministic MSY. Just before the start of the spawning season in the first year, it is assumed that the entire spawning stock dies, so that there is no recruitment at all at the beginning of the second year. Subsequently, the population is allowed to recover, if it can. During the recovery period, fishing continues at the same rate.

For each case where M was sufficiently low that the age at maturity is greater than one year, the spawning stock biomasses recovered (eventually) despite continued exploitation. The key to the recovery was that the unfished age-classes in longer-lived species provided a buffer against such catastrophic events. In contrast, under the conditions simulated any species with M sufficiently high that the age at maturity is less than one year will by definition be completely extinguished by the catastrophe hypothesised. This may seem an extremely unlikely scenario, but all that is required to bring about conditions nearly matching those simulated is for the species to have a critical spawning biomass below which recruitment is severely diminished. Then a bout of overfishing, for example, could well result in an almost complete stock collapse.

It follows that in this sense, longer-lived species can show a greater resilience than short-lived ones. Further, the greater the number of unfished age-classes, the greater the amount of buffering. Thus extremely long-lived fish species, such as orange roughy, have the ability to withstand occasional major catastrophic events, despite the very low sustainable yields they provide.

Summary conclusions

The primary conclusion that may be drawn is that although there is a clear approximately proportional relationship between sustainable yield and natural mortality, the constant of proportionality is smaller than had originally been proposed by Gulland. Even in the case where recruitment remains constant regardless of how small the mature stock size is, yield taken as a percentage of virgin exploitable biomass is more likely to be around $0.3M$, rather than the $0.5M$ that Gulland suggested. When more realistic levels of density dependence are considered, the percentage yield is further reduced, perhaps to between $0.1M$

and $0.2M$.

When looked at specifically in terms of lifespans, the non-linear relationship between M and lifespan implies that for longer-lived species, the sustainable yields are both low and almost independent of lifespan. An exception to this ground rule is the behaviour of very short lived species. In these species, the details of the life cycle dominate their response to exploitation, such that on sensible and measurable definitions of exploitable biomass, the stock may be capable of producing sustainable yields well in excess of the biomass measured at the start of the fishing season.

Tables of yield-biomass ratios and fishing mortality rates have been calculated for a wide range of values of the key biological and fishery-related parameters. These are included in the attached outline of results. These tables will allow estimation (by interpolation if necessary) of yield-biomass ratios and fishing mortality rates for most species, given values of the appropriate parameters. In addition, however, a table of estimates of yield-biomass ratios and fishing mortality rates for 53 selected commercially exploited marine fish species has also been calculated, using information contained in the FISHBASE database and other sources. This has been included in the attached outline of results.

The deterministic results are a useful guide to expectations in the real world, particularly for relatively long-lived species. The investigation of stochasticity in recruitment and its implications for the expected variation in yield complements other findings that a management policy of constant effort with a target level of fishing mortality can produce substantial benefits in terms of high yields when recruitment is high. The strength of this effect with increasing mortality (reduced lifespan) is particularly marked.

While very short-lived species can provide high yields, the brief examination of the effect of catastrophic events on their dynamics indicates that longer-lived species retain a resilience to catastrophes that is not available to the short-lived species, which can be particularly vulnerable to a combination of high exploitation and occasional environmental events that devastate the spawning stock.

A more detailed description of results obtained immediately follows this final project report. Published scientific papers arising from this research are also appended.

4. Implications of the results for achieving the objectives

As the results outlined above indicate, this project has been very successful in achieving its objectives. Analysis of a detailed rigorous mathematical model for the dynamics of fish stocks, incorporating both age-structure and density dependence in the form of a stock-recruitment relationship, has revealed simple and practical guidelines for calculating the maximum sustainable yield available from a stock in terms of the virgin exploitable biomass and the natural mortality rate. Similar guidelines are also available for the fishing mortality rate producing maximum yield as a proportion of the natural mortality rate. The computer program developed for this project also allows explicit calculation of yield-biomass ratios given estimates of key biological and technical parameters. This has been used in conjunction with fisheries databases such as FISHBASE and comparable compilations of estimated stock-recruitment relationships to obtain estimates of yield-biomass ratios for a number of important fish stocks.

5. Priority tasks for follow up

The results obtained in this project set the scene for more detailed investigations of individual species and groups of species, both in terms of extending the range of species for which individual estimates of yield-biomass ratios and fishing mortality rates have been calculated, and in terms of examining the way in which the key parameters that determine yields vary. In this latter context, the dependence found by Pauly between natural mortality, growth in size, and mean water temperature for a wide range of fish stocks affords the possibility of further assessment of the potential yields of species in marine ecosystems of different types.

The final report details estimates of yield-biomass ratios for important fish species for which the current version of the FISHBASE database contains estimates of the key parameters. This database is still under development by ICLARM and FAO and it is anticipated that over time the range of species for which key parameter estimates are available will expand greatly. Also, the computer software packages LFDA and CEDDA developed by MRAG under another Fisheries Management Science project allow independent estimation of several of the key biological parameters used in the calculation of yield-biomass ratio. It therefore seems desirable that any subsequent adaptive phase for this project should include development of appropriate computer software with accompanying manuals for the direct calculation of yield-biomass ratios.

OUTLINE OF RESULTS OBTAINED

1. Introduction

The idea that long-lived, slow-growing species have less potential to provide a sustainable yield than short-lived, fast-growing species was first encapsulated in a simple formula by Gulland (1971). This formula directly related the potential yield of a species to its natural mortality rate in the equation

$$Y = \frac{1}{2} M B_0,$$

where M is the natural mortality rate and B_0 is the virgin exploitable population biomass.

Gulland's argument was a simple mix of a theoretical consideration, that the level at which maximum sustainable yield can be obtained occurs at $\frac{1}{2}$ the unexploited level in a simple logistic model, and an observation from experience of fisheries world-wide that indicated that the maximum yield appeared to occur when the level of fishing mortality was roughly equal to that of natural mortality.

While the title of this study refers to lifespan, we have followed Gulland's example and have concentrated exclusively on relating yield to the natural mortality rate. While the lifespan of any individual fish is well defined, this is not so for a population. It is clear, however, that lifespan is inversely related to M . Indeed, if lifespan is taken as the average age at death in a population, then if M is constant, the lifespan so defined is the reciprocal of M .

In the context of generalised stock production models, of which the logistic model is one simple example, the Gulland formula was re-examined by Shepherd (1982). He found that the maximum sustainable yield was usually somewhat less than $\frac{1}{2}MB_0$, but variation by a factor of three either way about that value was possible. However, Shepherd's analysis did not take age-structure into account.

Beddington and Cooke (1983) examined the Gulland formula using a more detailed age-structured model. In their analysis, they distinguished between the yield as a proportion of the exploitable biomass (defined as the biomass above the age or length at which exploitation starts) and the total biomass. Clearly, this distinction is particularly significant in cases where exploitation starts at a relatively advanced age. Results were presented for a range of life-spans of typical commercially exploited fish. They found the Gulland formula tended to be optimistic, with the potential yield being somewhat lower than it predicted. Their analysis was further restricted by a decision to examine recruitment in a simple way. It was assumed constant above a threshold adult biomass.

The aim of this project was to examine in a general way the potential yield of species with different life histories and different stock-recruitment relationships across the whole range of life spans: from annual species, like squid, to the very long-lived, such as whales or the orange roughy.

Following the Gulland line, yield was examined as a proportion of the unexploited biomass. There are really two interrelated levels of yield viewed in this way: that as a proportion of the total biomass and that as a proportion of the exploitable biomass. The former is perhaps the more ecologically interesting, in that it sets a limit to the yield that particular species in an ecosystem can provide. The latter lies more in the domain of the fishery manager, who is interested in the limits of commercial exploitation, and has the ability to adjust the age or length at which exploitation commences. Because this latter context is more natural for the intended users of the guidelines developed, most attention was placed on determining potential yield as a proportion of virgin exploitable biomass

In our examination of the deterministic case, which takes up the bulk of this report, we demonstrate that the potential yield measured as a proportion of the virgin biomass is indeed approximately proportional to the natural mortality rate, at least for biologically feasible combinations of parameters. The constants

of proportionality are functions of the key parameters of growth, mortality (life span) and the density dependent response as focused in the variation in recruitment with mature stock size. We also briefly examine the extent to which the presence of age-dependence in natural mortality might affect the predictions.

Clearly, a solely deterministic analysis provides only a guide to the potential yield. Two situations were examined where environmental variation is involved. The first follows Beddington and May (1977) by examining the relationship between mean and variance of yield for different parameter combinations and the way this relates to the deterministic results. The second, more unusually, examines the ability of species of different life-spans to respond to and recover from catastrophic events.

2. Methods

In this section, we first briefly outline the essentials of the models used to describe the population dynamics of an exploited fish population. Readers interested in the detailed mathematical formulation are referred to Kirkwood *et al* (1994), a copy of which is appended. Here, we will simply attempt to highlight the main elements in the models and the role played by the key biological and fishery parameters. We then draw on information contained in the FISHBASE database being developed jointly by ICLARM and FAO to identify likely ranges of values for these key parameters.

2.1 Population dynamics model

Dynamics of a single cohort

The dynamics of the fish population are assumed to be described by an age-structured model in continuous time. The model is formulated as a set of equations that, by and large, follow the mathematical structure of the dynamics of exploited fish populations described in Beverton and Holt (1957) and used by Beddington and Cooke (1983). The key biological parameters are the rate of natural mortality, the growth rate of the species and the size at which sexual maturity is reached. The primary variables that can be manipulated to adjust yield levels are the size at which exploitation begins and the mortality rate imposed by harvesting.

Consider first with the dynamics of a single cohort of fish, which initially consists of R fish born at age zero.

Let t_c = the age at first exploitation of fish in the cohort;
 L_c = the length at first exploitation;
 t_m = the age at sexual maturity;
 L_m = the length at sexual maturity;
 M = the instantaneous rate of natural mortality ;
 F = the instantaneous rate of fishing mortality;
 $N(t)$ = the number of fish of age t years; and
 $w(t)$ = the weight of fish of age t years;

The dynamics of the cohort are described by the following equations:

$$\begin{aligned} N(0) &= R, \\ N(t) &= R \exp(-Mt) && \text{for } 0 < t \leq t_c, \\ &= R \exp(-Mt - F(t-t_c)) && \text{for } t \geq t_c. \end{aligned}$$

These equations assume that R fish recruit to the cohort at age zero. As they grow, their numbers diminish through the action of a constant exponential rate of natural mortality M until age t_c . From age t_c onwards, fishing also occurs at a constant exponential rate F . This latter assumption is equivalent to assuming that the selectivity of the fishing gear is constant on all fish aged t_c and older. Adjustments would have to be made if a highly selective gear is being used, or if fish migrate from the fishing grounds at a later stage of their life.

In an unfished cohort ($F=0$), the total biomass over its lifespan is

$$TB_0 = \int_0^{\infty} R \exp(-Mt)w(t)dt.$$

This expression can be thought of as the sum over all ages of the surviving numbers at age t times the weight at age t . The exploitable biomass is given by an equivalent expression, except that now the "sum" is taken only over all ages greater than or equal to the age at first capture:

$$ExB_0 = \int_{t_c}^{\infty} R \exp(-Mt)w(t)dt.$$

In common with standard fisheries practice, we assume that growth can be modelled by the von Bertalanffy (1938) growth curve, with the weight $w(t)$ at age t given by

$$w(t) = W_{\infty} (1 - \exp(-K(t-t_0)))^3,$$

where W_{∞} is the asymptotic weight, K is the growth rate and t_0 is the nominal age at which length is zero. Lengths and ages are related via

$$l(t) = L_{\infty} (1 - \exp(-K(t-t_0))),$$

however as it is more convenient to deal with lengths as proportions of the asymptotic length L_{∞} , from now on we will use lower case letters to refer to the length at first exploitation $l_c = L_c/L_{\infty}$ and the length at sexual maturity $l_m = L_m/L_{\infty}$ measured relative to L_{∞} .

Figure 1 illustrates for nominal values of the natural mortality and growth parameters the relationship between numbers, individual weight and biomass at age in a cohort of fish. Figure 2 presents essentially similar information about the biomass, except now it portrays the distribution of population biomass with length of fish as a proportion of the asymptotic maximum length. Also shown on Figure 2 are the critical components of the population: the total biomass, the exploitable biomass (of those fish with lengths greater than or equal to the length at first capture) and the spawning stock biomass (of those fish with lengths greater than or equal to the length at maturity).

With these preliminaries, Kirkwood *et al* (1994) then detailed how the equilibrium yield from a fish population can be calculated. For the case where the annual recruitment (R in the equation above) is constant, the dynamics of a cohort are exactly the same as those of the population at any one time.

Figure 1 Population numbers, individual weight and population biomass by age class for an unexploited cohort of fish

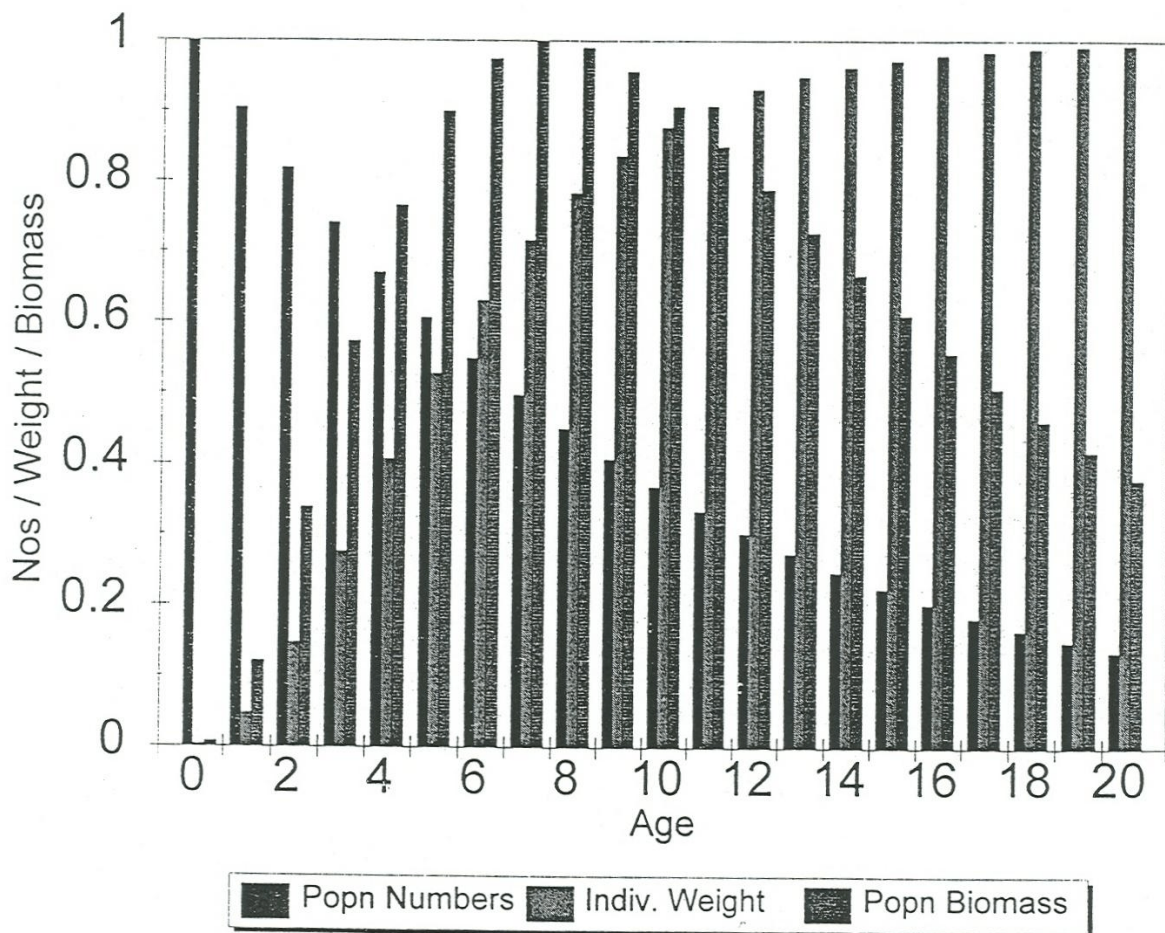
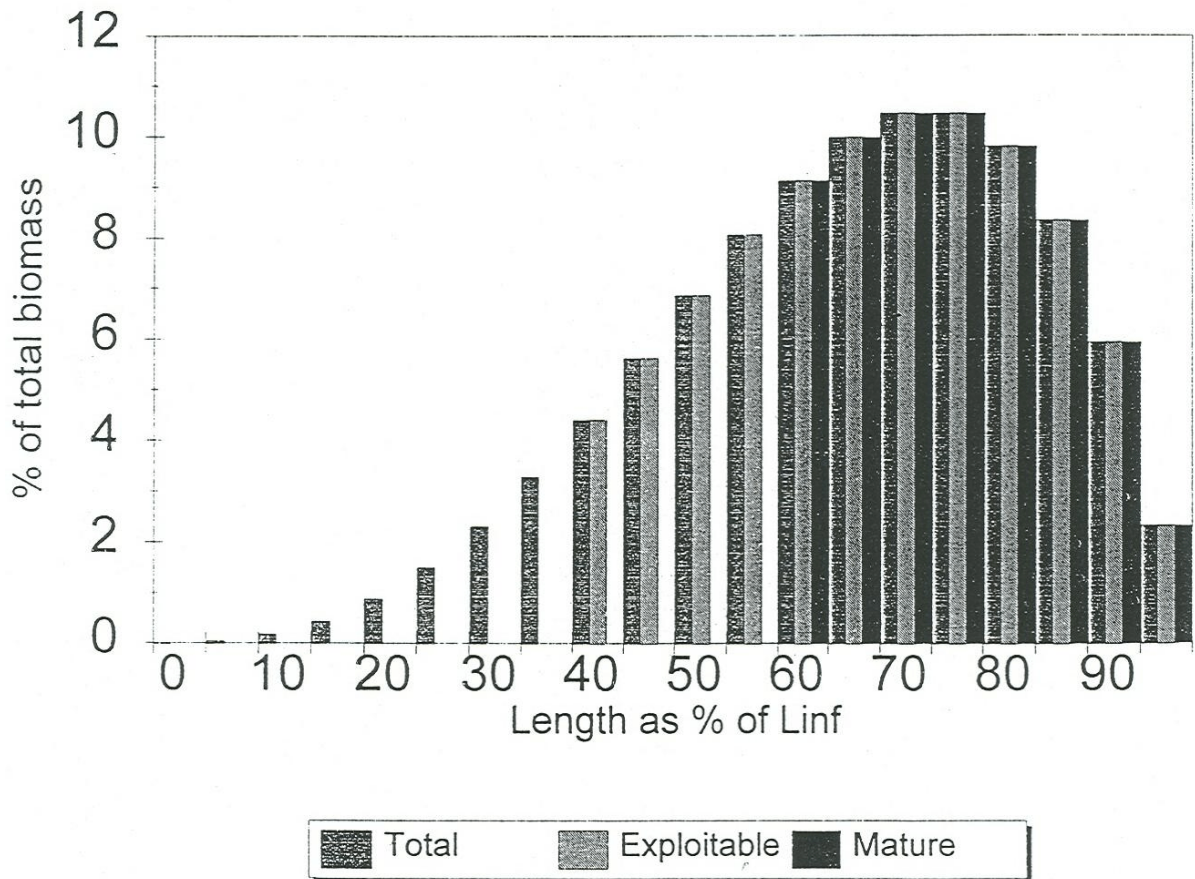


Figure 2 Population biomass by length class for an unexploited cohort of fish. Different shadings distinguish length classes contributing to the total population biomass, the exploitable population biomass and the mature population biomass.



Allowing for a stock-recruitment relationship

In the model as described so far, all parameters have been assumed to be constant; they are neither age-dependent nor density-dependent. We shall examine later what happens if the natural mortality rate varies with age. For most fish populations, it is believed that by far the majority of density-dependent effects occur during the egg and larval stages of their life history. In consequence, most fisheries models incorporate all density dependence into a non-linear relationship between the spawning stock biomass and the subsequent recruitment of juvenile fish to the population. For convenience, we suppress the egg and larval stages, and assume various relationships between the average sexually mature stock biomass during the spawning season of a year and the subsequent recruitment of fish nominally aged zero at the beginning of the following year.

There are various possible stock-recruitment relationships that display different degrees of density dependence. The two most frequently used stock-recruitment relationships in fisheries were proposed by Beverton and Holt (1957) and by Ricker (1954). Of these, the humped form proposed by Ricker (1954) incorporates the greatest degree of density dependence, and thus in a sense represents an extreme. Here, we have concentrated primarily on the Beverton and Holt (1957) form, which has the twin advantages of having a very simple mathematical form and of being relatively conservative in the degree of density dependence it attributes to the population. Some results are also given when a Ricker-type stock-recruitment relationship is assumed. In fact, for convenience and flexibility, we have actually used in the calculations the Shepherd (1982) functional form of stock-recruitment relationship rather than the Ricker form. The two can be made to be almost indistinguishable by suitable choices of parameters.

Figure 3 illustrates the types of stock-recruitment relationship that have been examined. Each has been constrained so that they imply the same unexploited equilibrium stock size. The lower straight line joining the origin to the unexploited equilibrium is the so-called "replacement" line, indicating the level of recruitment for any given spawning stock biomass SSB that is just sufficient to replace that biomass. This represents a case where there is no density dependence at all in the stock-recruitment relationship; such a population would inevitably collapse if exploited. The Beverton-Holt stock-recruitment relationship is an asymptotic relationship that has the property that recruitment always increases with spawning stock biomass. The straight line parallel to the x-axis represents the case of constant recruitment. It is actually a limiting form of the Beverton-Holt relationship. Note that an assumption of constant recruitment is actually equivalent to assuming a considerable degree of density dependence. The last curve, representing a Ricker-type relationship, has the humped form indicating that the numbers of recruits can actually be at a maximum at levels of spawning stock biomass less than the unexploited level. This is equivalent to assuming a very high degree of density dependence.

Figure 4 illustrates the parameterization we have used for the Beverton and Holt stock-recruitment relationship. Different relationships are indexed by a parameter d that takes values in the range 0 to 1, where a value of zero corresponds to no density dependence (i.e. the replacement line) and a value of 1 corresponds to constant recruitment. Finally, the set of stock-recruitment relationships actually used in the subsequent calculations are shown in Figure 5. These correspond to values of d of 0.25, 0.5, 0.75 and 1, and to a humped Ricker stock-recruitment relationship indexed by the ratio R_m/R_0 of the maximum number of recruits at any stock size to the number of recruits in the unexploited population.

Figure 3 Different possible types of stock-recruitment relationships, each having the same unexploited equilibrium population size.

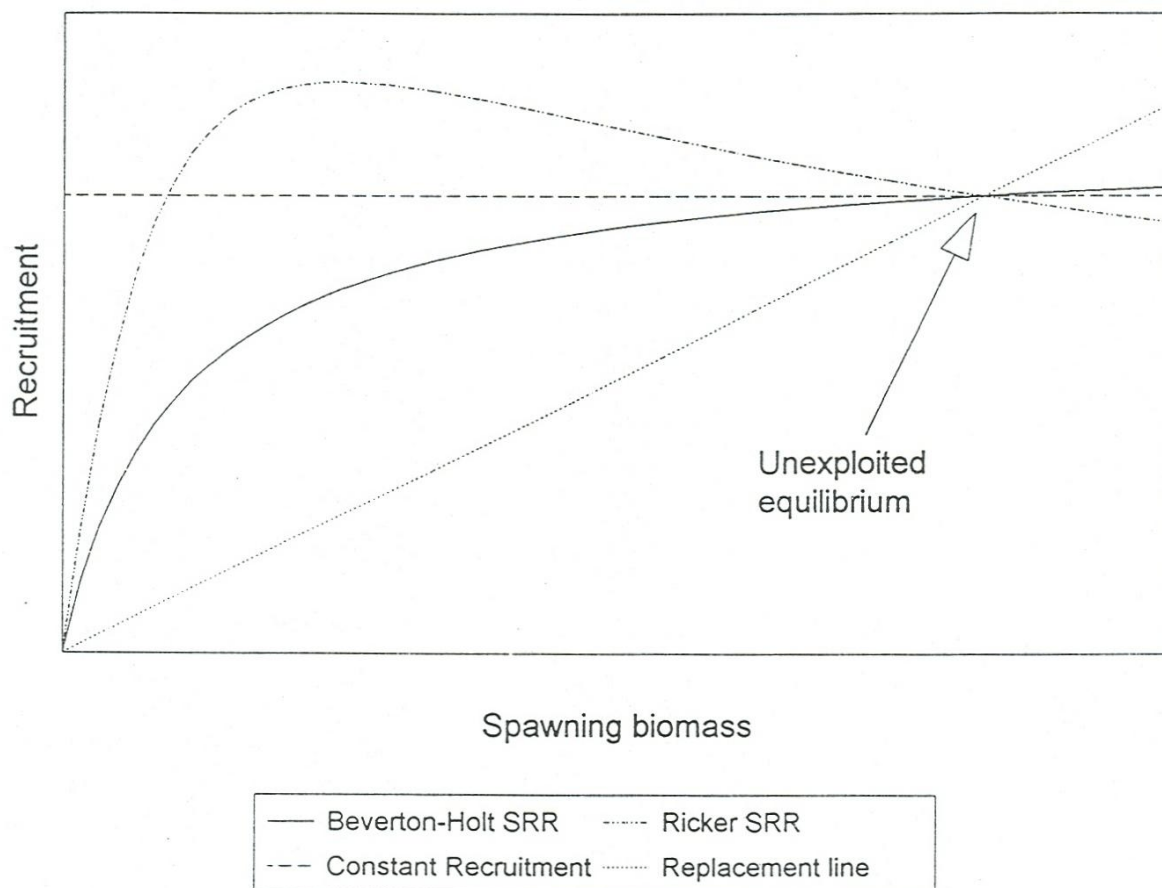


Figure 4 Parametrization used for the Beverton-Holt stock-recruitment relationship.

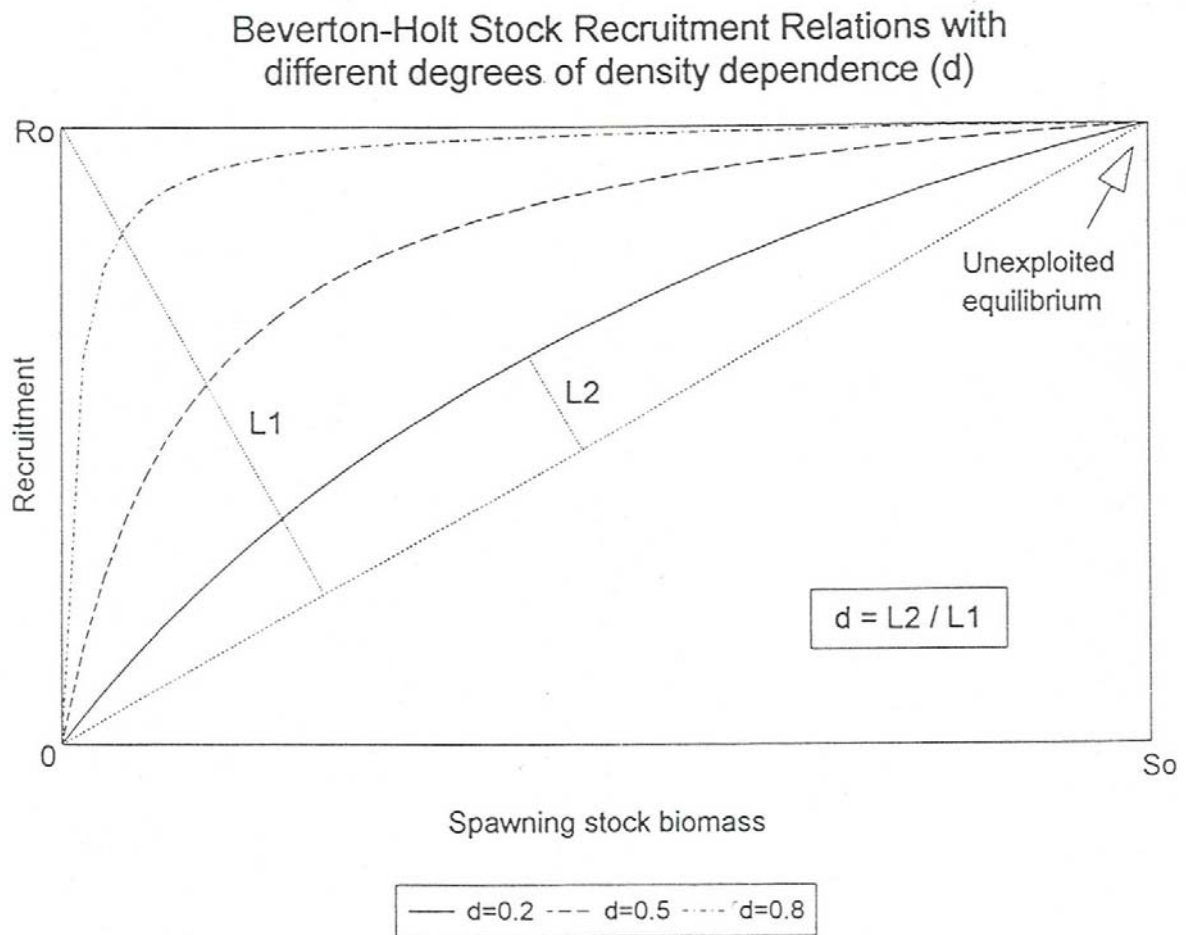
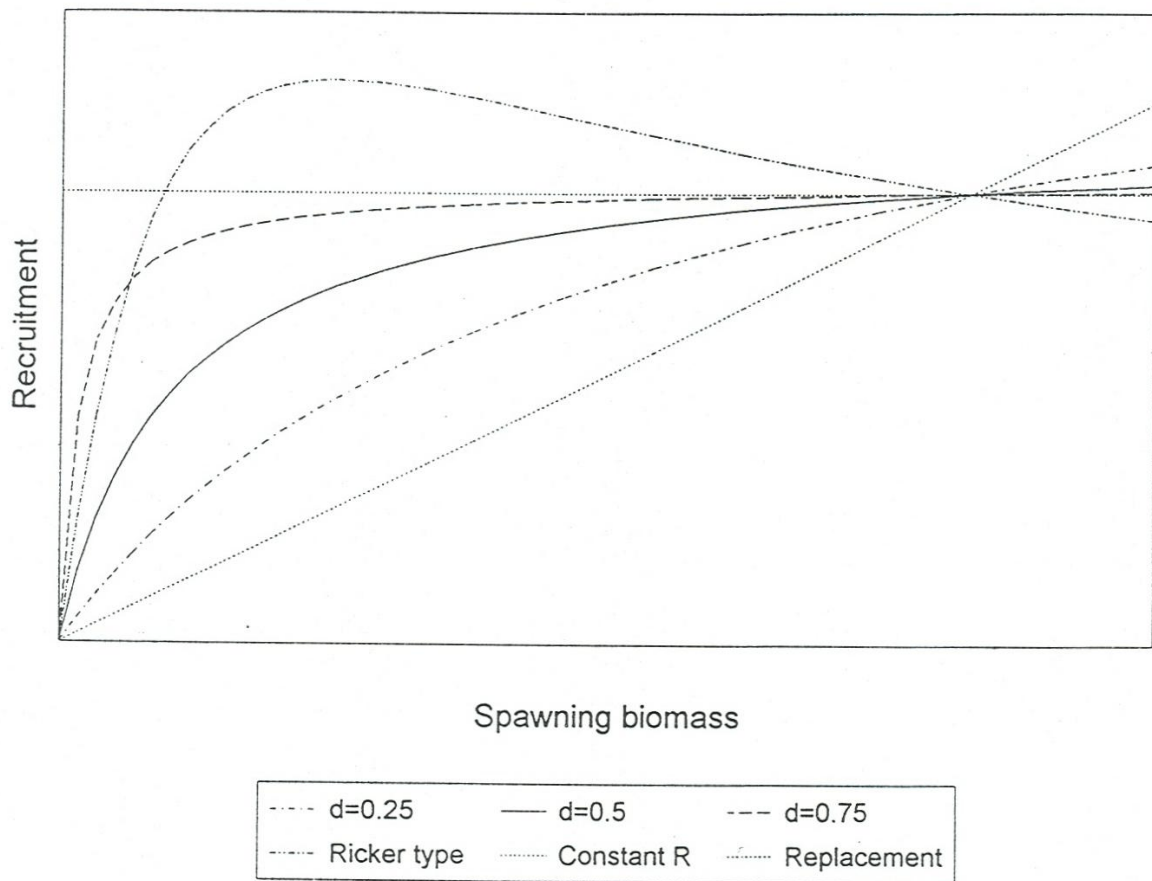


Figure 5 Stock-recruitment relationships used in the calculations of yield-biomass ratios, corresponding to $d=0.25, 0.5, 0.75$ and 1.0 (constant recruitment), and to the Ricker-type relationship with $R_m/R_0 = 1.2$.



Calculation of sustainable yields and biomasses

A flexible computer program implementing the population dynamics model has been developed and used to develop the results presented in the following sections. At its core are routines that first calculate the unexploited equilibrium population numbers and biomasses at age (or length), given specified values of the biological and fishery parameters. In the deterministic case, these routines then search for the fishing mortality rate that produces the maximum sustainable yield and calculate the equilibrium total and exploitable population biomass that corresponds to that level of fishing mortality. This is repeated for a range of values of the natural mortality rate, allowing the relationship between the yield-biomass ratios (MSY/ExB_0 and MSY/TB_0) and the natural mortality rate M to be determined. As outlined later, in most cases this turns out to be exactly or approximately linear across species for which M/K is constant. The approximate constant of proportionality between the yield-biomass ratio and M is then calculated as the value of the yield-biomass ratio when $M=1$.

2.2 Typical values of parameters

As already indicated, the principal biological parameters that characterise the dynamics of the fish stock in the model we have used are the rate of natural mortality M , the growth rate K , the length at sexual maturity L_m and the density dependence parameter d of the Beverton and Holt stock-recruitment relationship. There is also one important fishery-controlled parameter, the length at first capture L_c . Being a fishery-specific parameter, the length at first capture L_c can take a wide range of values, however there are natural inter-relationships between the various biological parameters that can be taken advantage of to reduce the dimensionality of the problem.

The most important of these is the negative correlation between values of the natural mortality rate M and the growth rate K . This is sufficiently strong that the ratio M/K takes only a restricted range of values. As part of this project, MRAG has entered into a cooperative agreement with ICLARM on the development of an extensive database of biological and fishery parameters for finfish species world-wide. This database, called FISHBASE, is being jointly developed by ICLARM and FAO, and it contains, *inter alia*, recorded estimates of M , K , L_∞ and L_m for a large number of species. Through the cooperative agreement between MRAG and ICLARM, we have been able to gain access to a development version of FISHBASE and thus access to a wide range of estimates of the biological parameters.

Figure 6 illustrates the frequency distribution of estimates of M/K for commercially exploited marine fish species extracted from FISHBASE. As can be seen, the vast majority of values fall in the range 0.5 - 4.0, with a modal value in the range 1.0 - 1.5. Results in the following sections have been calculated for values of M/K of 0.5, 1.0, 2.0, 3.0 and 4.0.

Figure 7 illustrates the frequency distribution of estimates of L_m for commercially exploited marine fish species also extracted from FISHBASE. The majority of these estimates fall in the range 0.4 - 0.9, with a mode between 0.5 and 0.7. Results presented in the tables in the following sections are given for $L_m = 0.4, 0.6$ and 0.8 . Values of L_c used were 0.2, 0.4, 0.6 and 0.8, thus in most cases encompassing values lower than and higher than the selected values of L_m .

Results have been calculated for values of the natural mortality rate, M , of $0.05-3.0 \text{ yr}^{-1}$. This allows consideration of marine species with lifespans as disparate as whales and orange roughy at the low M end to annual species such as squid at the other end.

Figure 6 Frequency distribution of estimates of M/K for commercially exploited marine fish species extracted from FISHBASE.

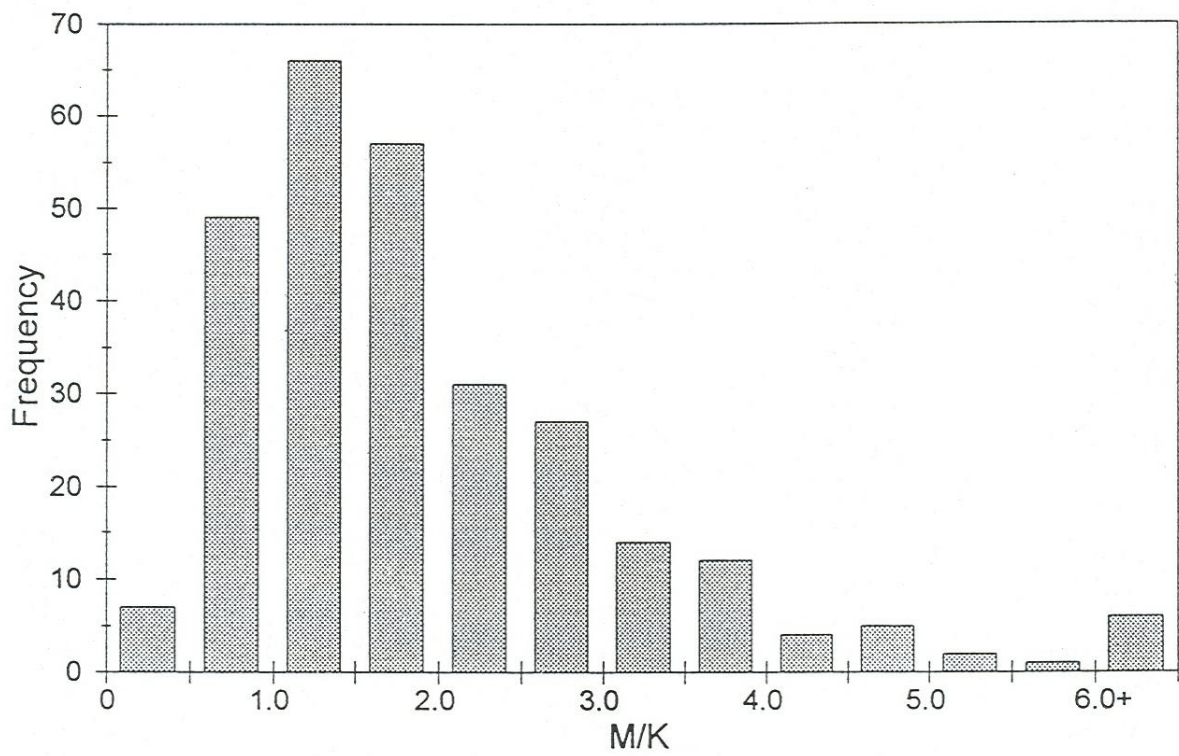
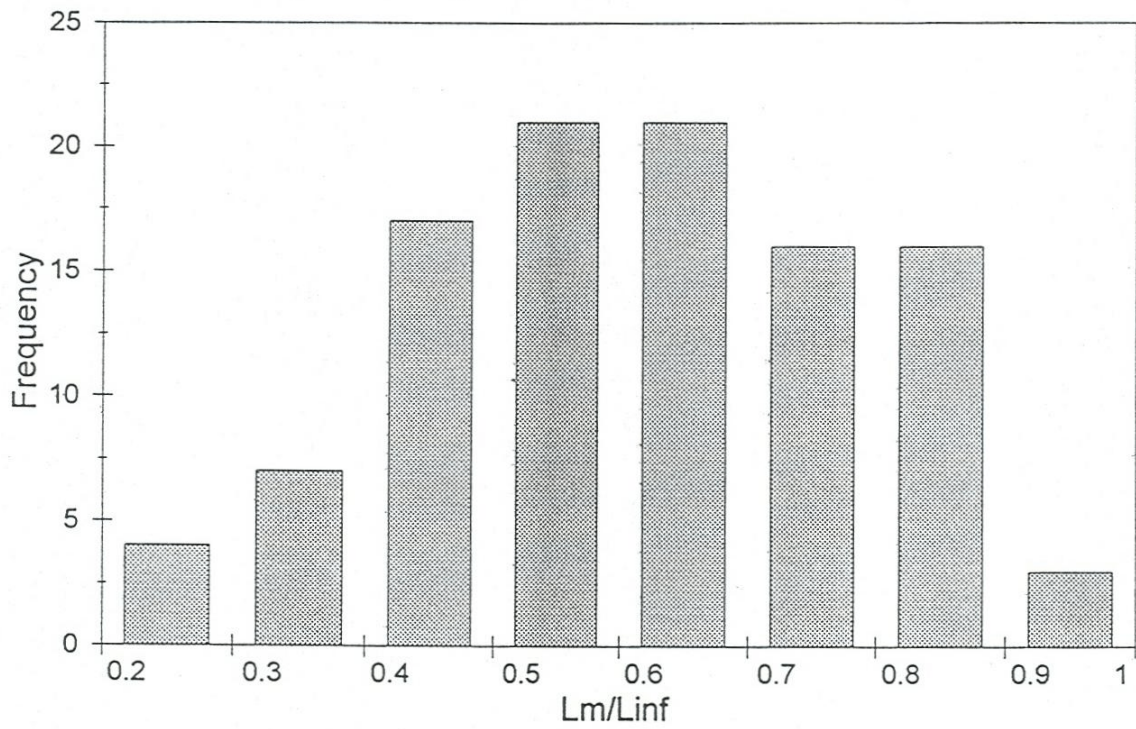


Figure 7 Frequency distribution of estimates of L_m/L_∞ for commercially exploited marine fish species extracted from FISHBASE.



Considerable work has been undertaken recently aimed at trying to collate and characterise stock-recruitment relationships. Most notable amongst these has been the work of Mace and Sissenwine (1993), Mace (1994) and Myers *et al* (1994). These references contain estimated stock-recruitment relationships for a number of exploited fish stocks, though they tend unsurprisingly to be mostly for stocks taken in temperate waters in developed countries. It is still a little early to attempt to identify characteristic values of the parameter d we have used to index the stock-recruitment relationships, so we have used values for d of 0.25, 0.5, 0.75 and 1.0, as well as a typical humped Ricker-type stock-recruitment relationship. These stock-recruitment relationships are those illustrated in Figure 5.

The tables produced in the next section for the cited values of biological parameters are intended to allow readers to determine (if necessary by interpolation) the approximate maximum yield-biomass ratio and corresponding fishing mortality rate for most combinations of estimates of biological parameters for a fish stock.

3. Sustainable yields for constant recruitment

In this section, we present the relationships found between the deterministic equilibrium maximum sustainable yield (MSY) and the size of the exploitable biomass in a population prior to the commencement of exploitation (ExB_0). The first case considered was that in which recruitment is constant and independent of the size of the spawning stock. This simplest case was examined by Beddington and Cooke (1983), and it is the only one for which any analytic progress can be made. Where recruitment varies according to a stock-recruitment relationship, no analytic results are available, and purely numerical methods must be used.

As described in Kirkwood *et al* (1994), algebraic manipulation of the mathematical expression for the ratio MSY/ExB_0 reveals that MSY/ExB_0 is directly proportional to M , provided M/K and l_c are kept constant. Also, the fishing mortality rate F_{MSY} that produces the maximum sustainable yield is proportional to M for given values of l_c and M/K . The proportionality between the yield-biomass ratio and the natural mortality rate proposed by Gulland therefore is correct.

At first sight, this finding appears to contradict the results obtained by Beddington and Cooke (1983), whose figures suggest that the relationship between yield-biomass ratios and M is neither proportional nor linear. The difference lies in the requirements that M/K be constant, and that yield-biomass ratios be viewed as a function of l_c , rather than of t_c . The requirement that M/K be constant is not at all restrictive; it simply indicates that the constant of proportionality in the relationship will vary with both the value of M/K and that of l_c . Precisely the same arguments apply to the relationship between M and the ratio of MSY to unexploited total biomass (TB_0), although the constants of proportionality are different, of course. Whether in practice it is more convenient to concentrate on exploitable or total biomasses depends on which of these two quantities is easier to estimate.

Table 1a. Constants of proportionality in the relationship between the ratio MSY/ExB_0 and M when recruitment is constant, for different values of l_c and M/K .

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.30	0.25	0.22	0.22	0.22
0.4	0.35	0.32	0.32	0.36	0.41
0.6	0.45	0.44	0.52	0.60	0.66
0.8	0.63	0.69	0.77	0.82	0.85

Table 1a lists the constants of proportionality in the relationship using exploitable biomass for a range of values of l_c and M/K . Note that in the case when recruitment is constant, it is unnecessary to consider different values of l_m . Table 1a confirms the results obtained by Beddington and Cooke (1983) that in many cases the constant of proportionality is less than the value of $\frac{1}{2}$ in the Gulland formula. For the parameter values examined, only for high values of M/K and high l_c is the constant $\frac{1}{2}$ or higher. The constant increases monotonically with l_c for constant M/K , but shows a minimum at intermediate values of M/K for each l_c .

Table 1b. Constants of proportionality in the relationship between the ratio MSY/TB_0 and M when recruitment is constant, for different values of l_c and M/K .

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.30	0.25	0.22	0.21	0.22
0.4	0.35	0.31	0.30	0.30	0.29
0.6	0.43	0.39	0.35	0.28	0.19
0.8	0.51	0.41	0.21	0.08	0.03

When the ratios are calculated in terms of total biomass, Table 1b shows that very similar constants of proportionality to those shown in Table 1a are obtained for low values of l_c and/or M/K . However, now the constants generally take their lowest values when both l_c and M/K are high. That the greatest differences between the two sets of results appear for high values of l_c and M/K is of course to be expected, given the differences in the definitions of total and exploitable biomass.

In reality, the differences in the constants of proportionality when both M/K and l_c are high may not be as great as suggested in these tables. The differences arise in part because the ratio between the fishing mortality rate at MSY (F_{MSY}) and M increases as M/K and l_c increase. Pauly and Soriano (1986) have shown that if allowance is made for recruitment to the fishery to occur gradually over a range of lengths, rather than instantaneously on reaching length l_c as assumed here, then the F_{MSY} in the constant recruitment case is lower, as is the maximum yield. This point will be pursued further elsewhere, and for the rest of this report we will retain the assumption of knife-edged selection.

Table 2 gives values of F_{MSY} measured as a proportion of M for the same sets of values of M/K and l_c .

Table 2. Values of F_{MSY}/M for different values of l_c and M/K .

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	1.10	0.89	0.81	0.85	0.94
0.4	1.45	1.37	1.79	3.01	9.60
0.6	2.40	3.20	∞	∞	∞
0.8	10.20	∞	∞	∞	∞

For smaller values of l_c and M/K , it is interesting to note that F_{MSY} is indeed approximately equal to M , as Gulland hypothesised. However, as l_c and M/K increase, so does the value of F_{MSY} . An infinite fishing mortality rate (of course impossible to achieve in practice) corresponds to catching all fish immediately they reach the appropriate length at first capture. Essentially, infinite fishing mortality becomes optimal when for given values of M/K the length at first capture is greater than the length at which population biomass is maximized (see Figure 2).

4. Allowing for a stock-recruitment relationship

4.1 Nature of relationship between yield-biomass ratio and M

Given the direct proportionality found between MSY/ExB_0 and M when recruitment is constant, it is tempting to hypothesise that the same relationship might hold when recruitment varies as a function of the size of the spawning stock. This is not true, but for many biologically likely parameter combinations the relationship turns out to be very close to proportional. As in the preceding section, we will concentrate primarily on investigating the relationships between MSY/ExB_0 and M . However, we now also need consider different values of I_m . We first examine the extent of non-linearity in the relationship between yield-biomass ratios and M .

The typical result of allowing recruitment to vary with spawning stock size is seen in Figure 8. There, the empirical relationship between MSY/ExB_0 and M is shown for differing degrees of density dependence in the stock-recruitment relationship, in a typical case where $I_c=0.4$, $I_m=0.6$, and $M/K=1$. Two features are obvious. Firstly, the overall impression is that the relationship is very close to linear. Note that the apparent "waviness" of the lines is an artefact of the time-step used in the numerical calculations. The second feature is that the approximate slope of the lines increases as the degree of density dependence in the stock-recruitment relationship increases. This is, of course, as it should be: as the degree of density dependence increases, the population can withstand relatively greater reductions in spawning stock biomass corresponding to larger fishing mortalities, and thus support greater sustainable yields.

Figure 9 shows typical relationships between MSY/ExB_0 and M when I_c varies, with M/K set at 1.0, I_m set at 0.6 and d set to 0.75. The relative proportion of the exploitable biomass that can be taken sustainably increases with length at first capture. Note, however, that while the proportion of exploitable biomass that can be taken increases with I_c , the exploitable biomass itself decreases.

Typical relationships between MSY/ExB_0 and M when M/K varies are shown in Figure 10. Somewhat surprisingly, even over a range of M/K of 0.5-4.0 the relative proportions of exploitable biomass that can be taken sustainably are rather similar. Figure 11 shows the effect of varying I_m for the case where $M/K=1.0$, and I_c is set equal to I_m .

Figure 12 breaks the illusion that the departure from proportionality in the relationship between yield-biomass ratios and M is always at most minor. This figure illustrates a case where the degree of density dependence is low ($d=0.25$), and where $I_m=0.4$ and $I_c=0.6$. For high values of M , the apparent slope of the line can increase substantially. The other unusual feature of Figure 12 is the pronounced hump in the uppermost lines for M values above around 0.75. This is not an artefact. Rather, it is a real feature arising from the unusual combination of a high M/K , a length at first capture that exceeds the length at maturity, and a relatively small degree of density dependence in the stock-recruitment relation. For these values of M , it becomes important whether fishing during a year commences before or after the start of the spawning period and whether or not in terms of yield it is worth leaving some spawning stock to survive and spawn an extra year.

Inspection of the full set of empirical relationships obtained indicates that substantial departures from proportionality occur only for quite high values of M and primarily when the degree of density dependence is small. A full investigation of the way in which species occupy different regions of parameter space is beyond the scope of this report. However, this particular area of parameter space is biologically the most unlikely: normally one expects that low degrees of density dependence in a stock-recruitment relation will be associated with species that have long life-spans and therefore low mortality rates, and conversely that species with nearly constant recruitment even for small spawning stock biomasses will be short-lived and fast growing.

Figure 8 Relationships between MSY/ExB_0 and M for different degrees of density dependence in the stock-recruitment relationship, when $I_c=0.4$, $I_m=0.6$, and $M/K=1$.

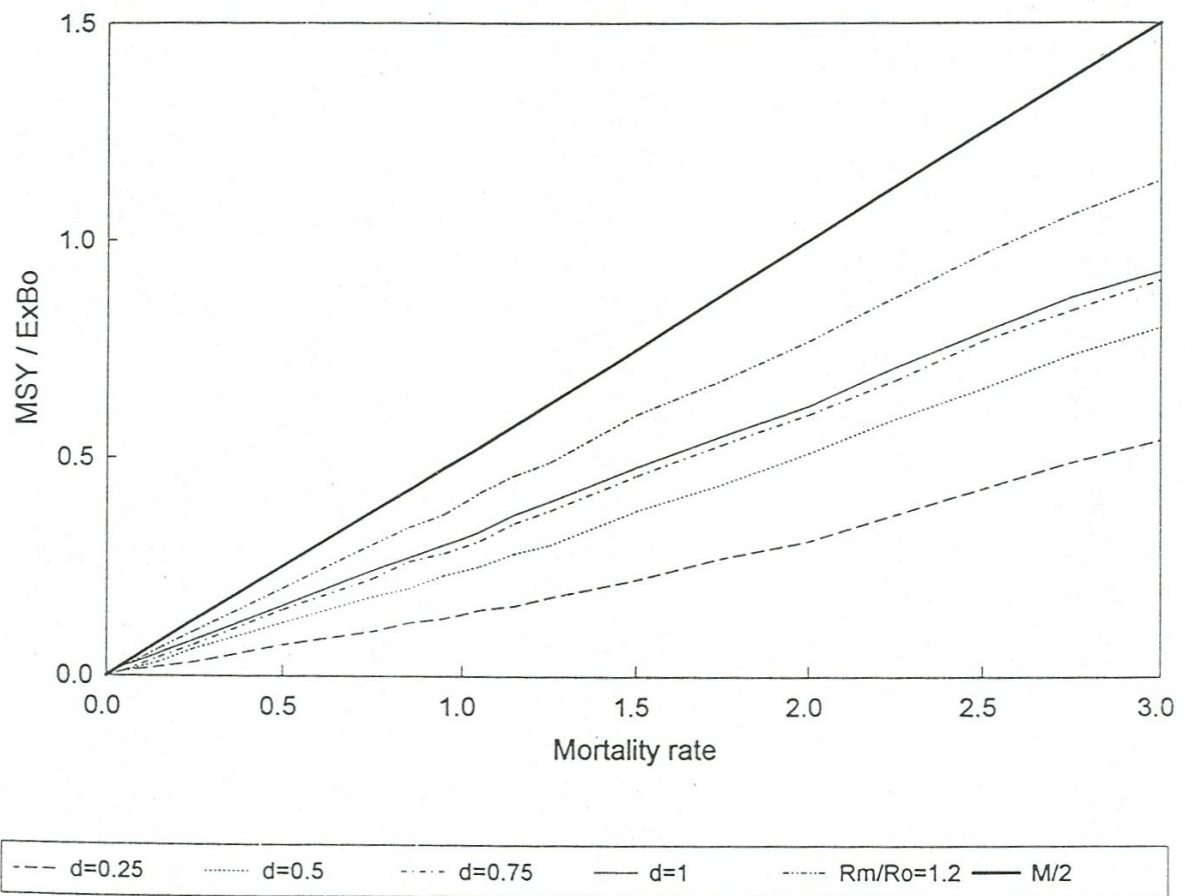


Figure 9 Relationships between MSY/ExB_0 and M for different values of l_c , when $d=0.75$, $l_m=0.6$, and $M/K=1$.

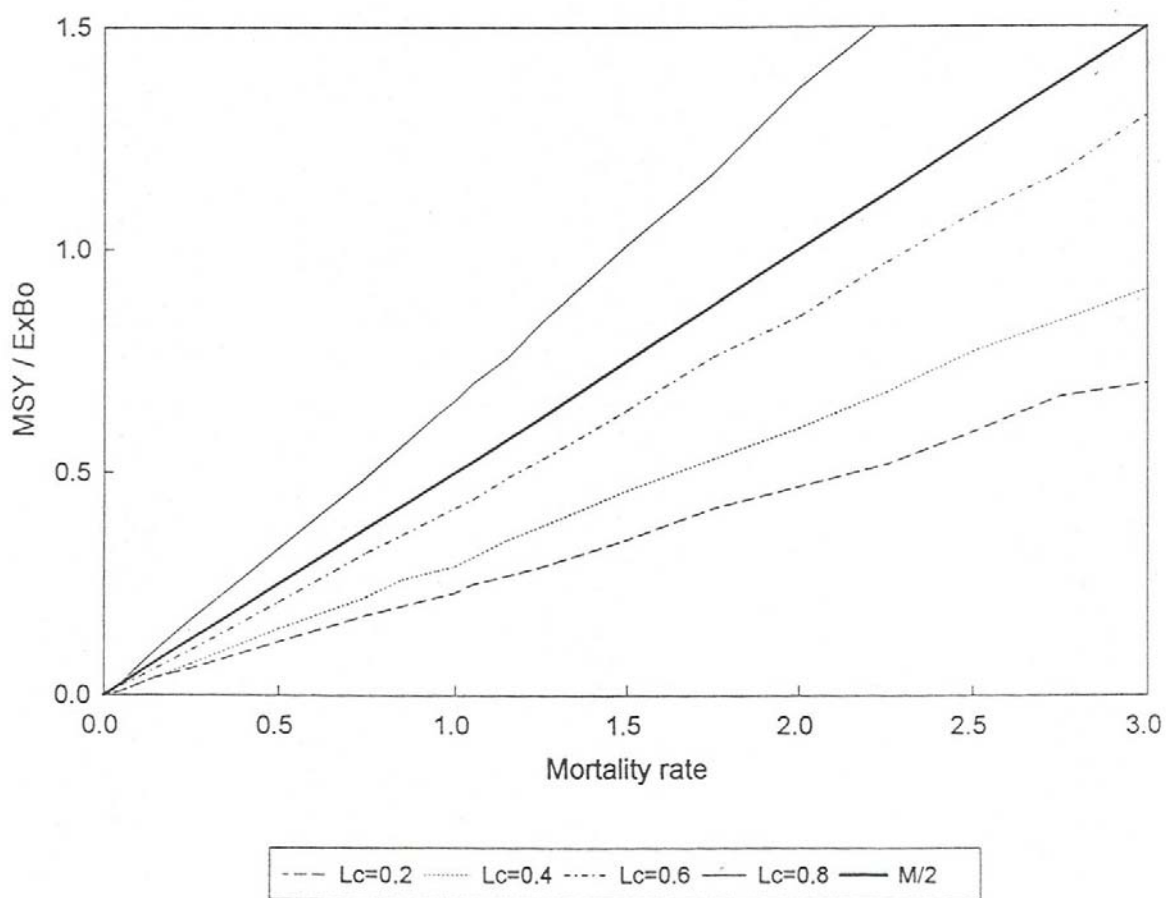


Figure 10 Relationships between MSY/ExB_0 and M for different values of M/K , when $l_c=0.4$, $l_m=0.6$, and $d=0.75$.

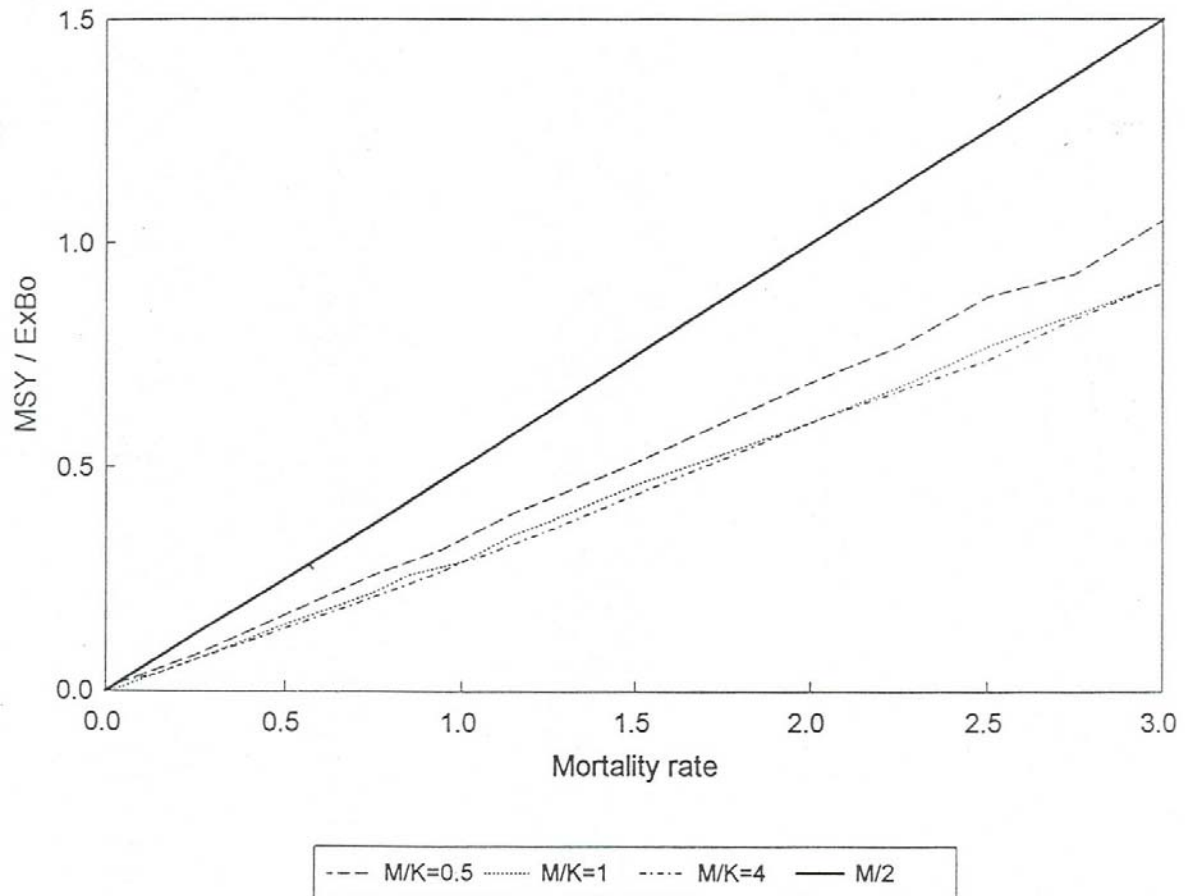


Figure 11 Relationships between MSY/ExB_0 and M for different values of l_m , when $l_c=0.4$, $l_m=0.6$, and $d=0.75$.

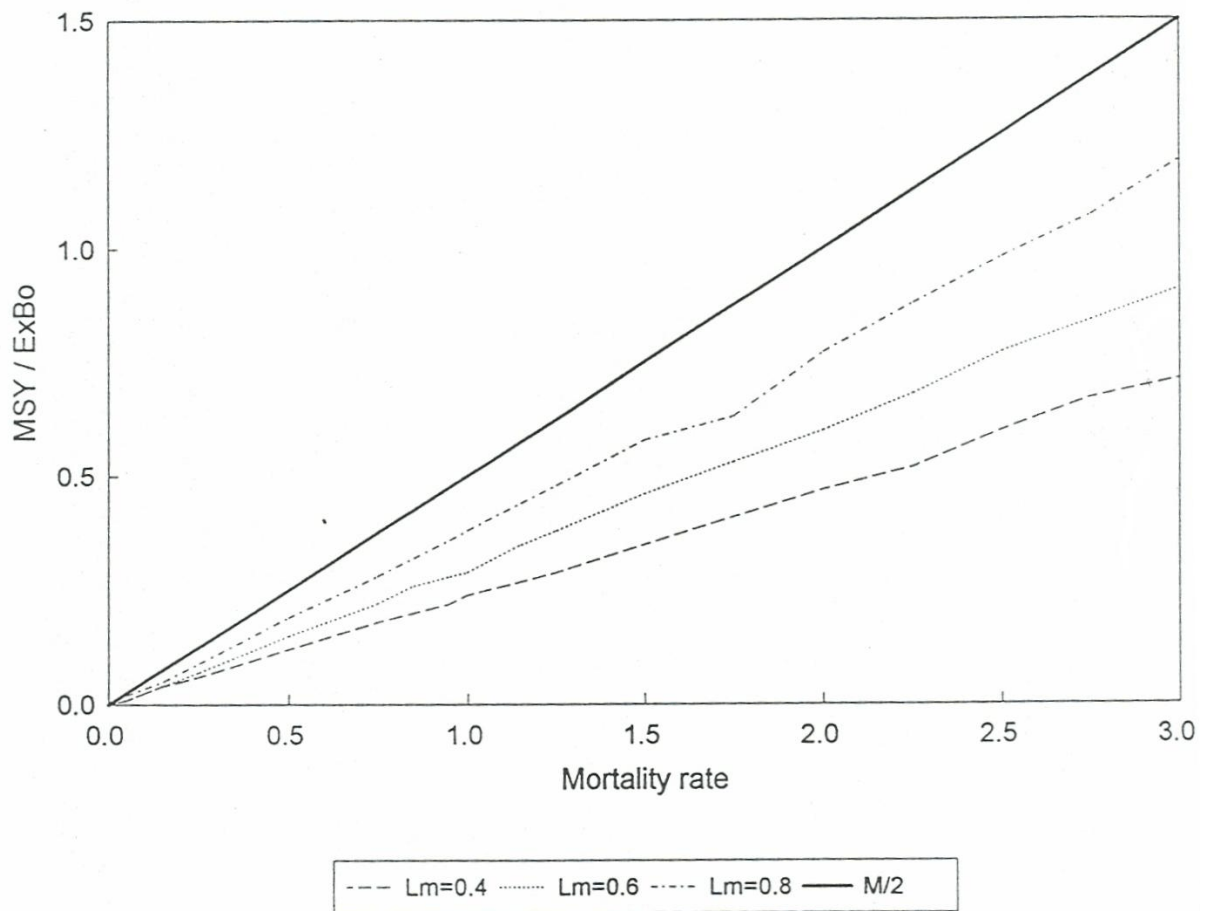
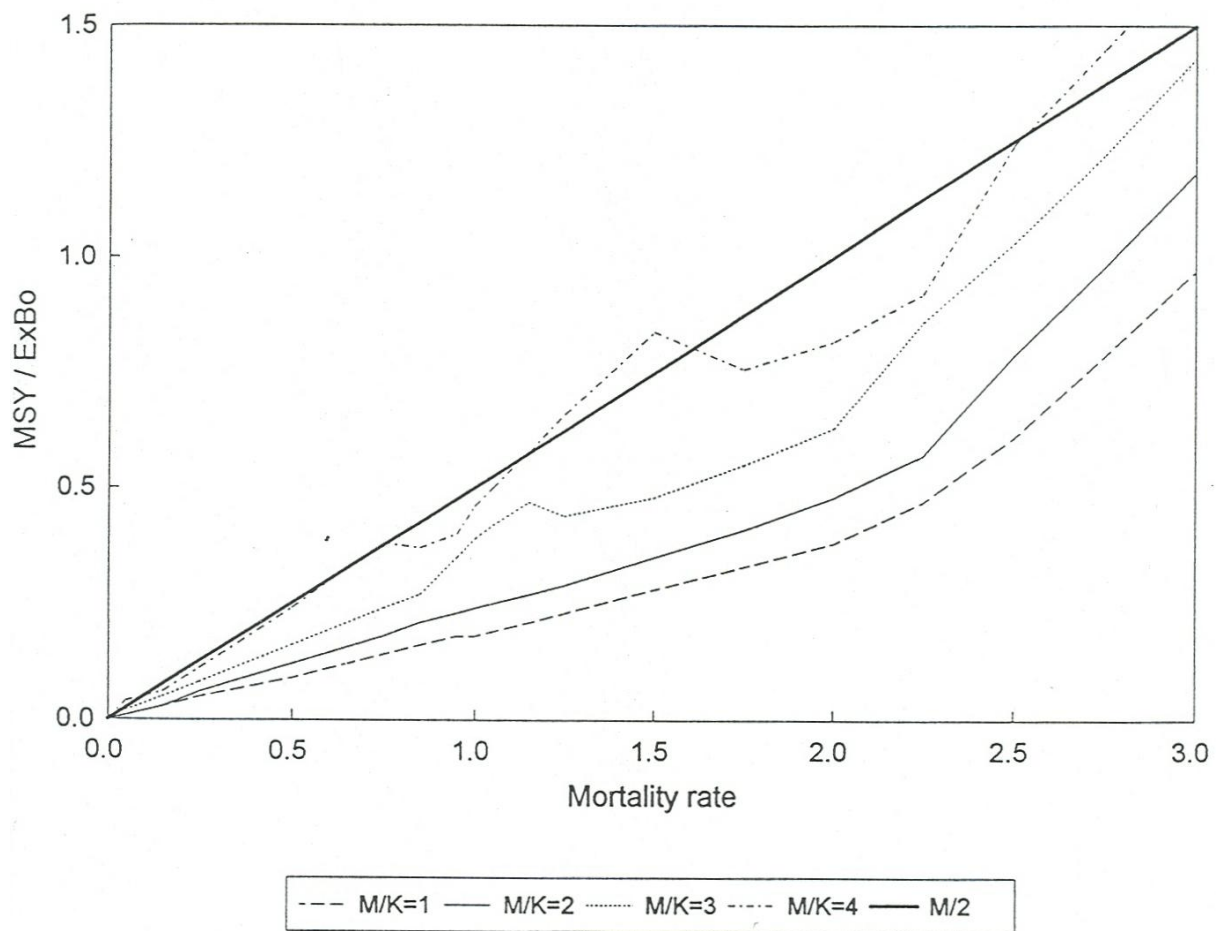


Figure 12 Relationships between MSY/ExB_0 and M for different values of M/K , when $I_c=0.6$, $I_m=0.4$, and $d=0.25$.



4.2 Nature of relationship between F_{MSY} and M

We also examined the relationships between F_{MSY} and M for differing values of the biological and fishery parameters. As with the yield-biomass ratios, in a wide range of cases, this relationship also turned out to be one of approximate proportionality. The relationships are illustrated in Figures 13-16 for the same parameter combinations used in Figures 8-11.

Substantial departures from proportionality occur for the same combinations of parameters identified for yield-biomass ratios: high M , low density dependence and either high M/K or for l_c larger than l_m . In those cases, F_{MSY} tends to become infinite.

Figure 13 Relationships between F_{MSY} and M for different degrees of density dependence in the stock-recruitment relationship, when $l_c=0.4$, $l_m=0.6$, and $M/K=1$.

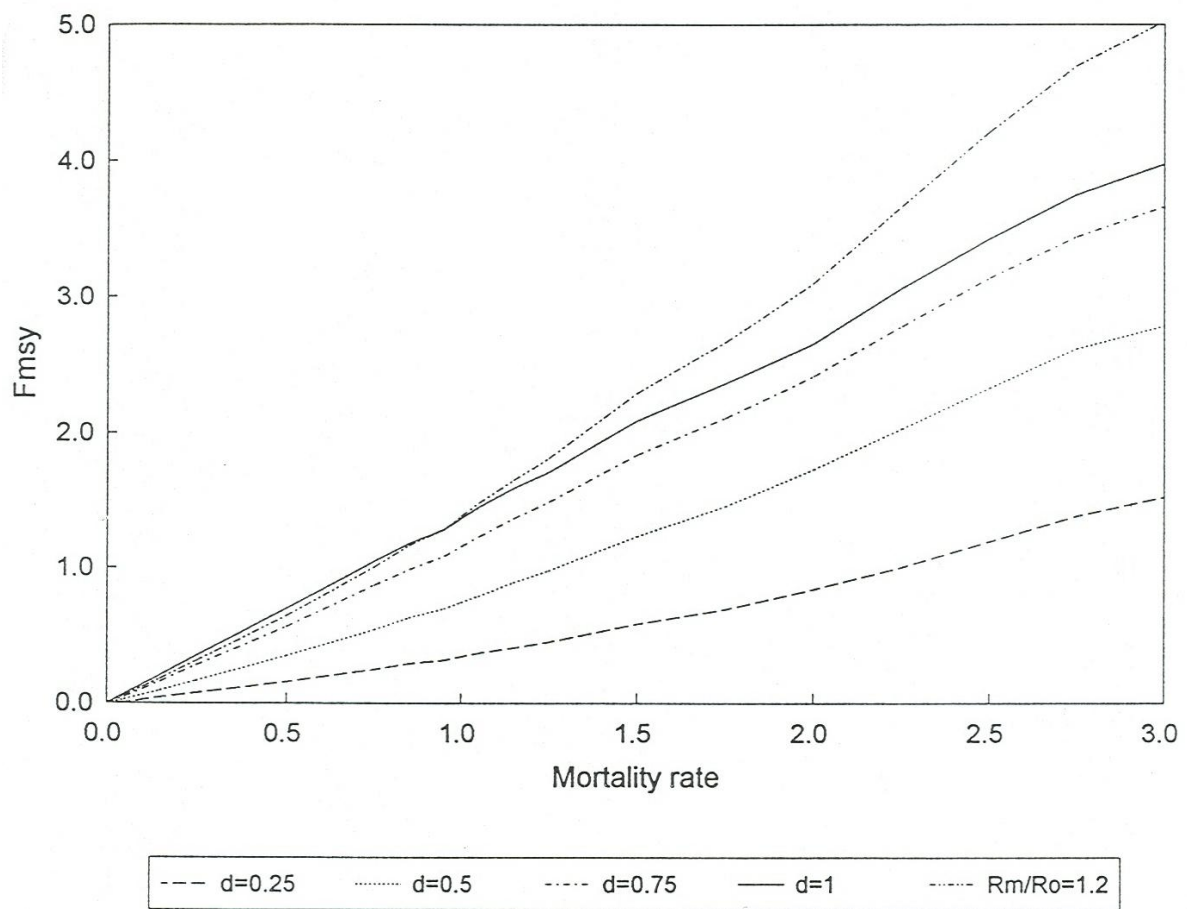


Figure 14 Relationships between F_{MSY} and M for different values of l_c , when $d=0.75$, $l_m=0.6$, and $M/K=1$.

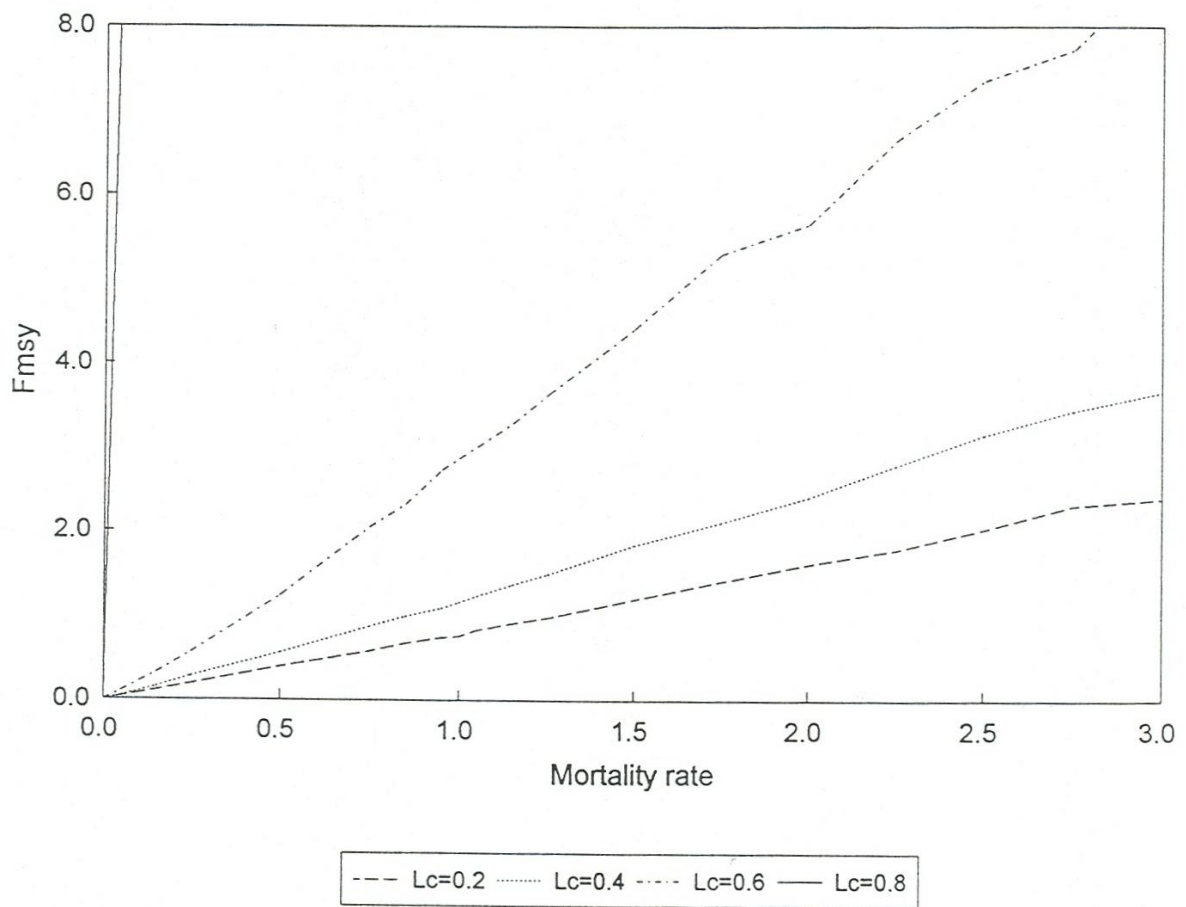


Figure 15 Relationships between F_{MSY} and M for different values of M/K , when $l_c=0.4$, $l_m=0.6$, and $d=0.75$.

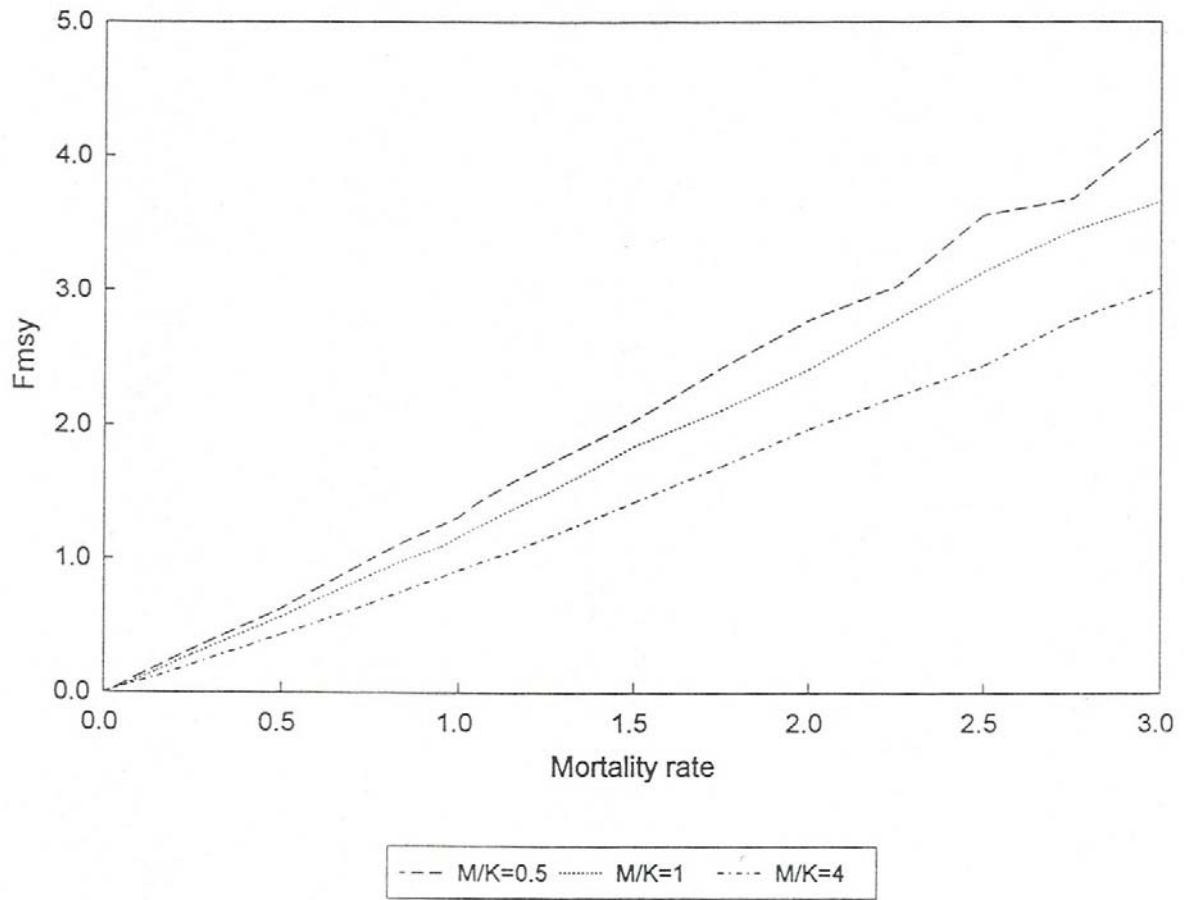
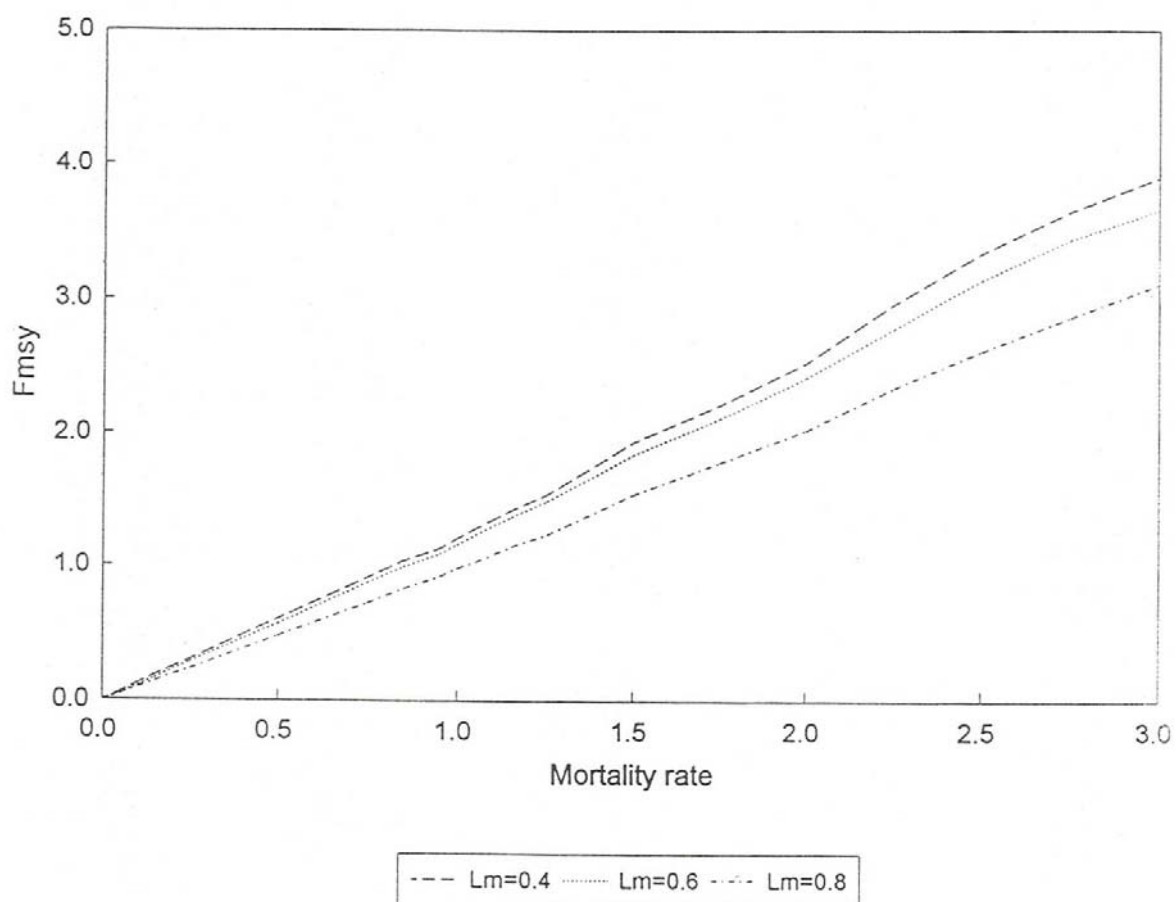


Figure 16 Relationships between F_{MSY} and M for different values of l_m , when $l_c=0.4$, $l_m=0.6$, and $d=0.75$.



4.3 *Approximate constants of proportionality between yield-biomass ratios and M and between F_{MSY} and M*

As indicated in the methods section, given the close-to-linear relationship observed in most cases between the yield-biomass ratios and M , we have taken as an estimate of the approximate constant of proportionality the value of the yield-biomass ratio when $M=1$. The following tables give values of this constant of proportionality and of F_{MSY}/M for the full set of values of the biological and fishery parameters investigated.

Table 4.1 Constants of proportionality in the relationship between the yield-biomass ratio and M , for different values of l_c , M/K and l_m , when $d=0.25$.

(a) $l_m = 0.4$

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.14	0.12	0.10	0.09	0.09
0.4	0.15	0.14	0.14	0.15	0.17
0.6	0.18	0.18	0.24	0.39	0.46
0.8	0.23	0.42	0.67	0.78	0.84

(b) $l_m = 0.6$

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.14	0.11	0.09	0.08	0.07
0.4	0.16	0.13	0.12	0.11	0.10
0.6	0.20	0.17	0.21	0.23	0.25
0.8	0.26	0.29	0.61	0.76	0.80

(c) $l_m = 0.8$

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.14	0.10	0.07	0.05	0.04
0.4	0.15	0.12	0.08	0.07	0.05
0.6	0.18	0.15	0.11	0.09	0.08
0.8	0.28	0.28	0.31	0.33	0.34

Table 4.2 Tables of F_{MSY}/M , for different values of l_c , M/K and l_m , when $d=0.25$.

(a) $l_m = 0.4$

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.33	0.28	0.24	0.22	0.20
0.4	0.37	0.35	0.38	0.42	0.48
0.6	0.45	0.49	0.82	∞	∞
0.8	0.65	∞	∞	∞	∞

(b) $l_m = 0.6$

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.35	0.25	0.20	0.16	0.14
0.4	0.41	0.30	0.28	0.24	0.21
0.6	0.53	0.42	0.66	0.78	0.90
0.8	0.77	1.06	∞	∞	∞

(c) $l_m = 0.8$

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.33	0.23	0.14	0.11	0.08
0.4	0.38	0.27	0.18	0.13	0.11
0.6	0.47	0.36	0.25	0.19	0.16
0.8	0.95	1.02	1.23	1.41	1.54

Table 4.3 Constants of proportionality in the relationship between the yield-biomass ratio and M , for different values of I_c , M/K and I_m , when $d=0.5$.

(a) $I_m = 0.4$

I_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.23	0.19	0.17	0.16	0.16
0.4	0.27	0.24	0.25	0.27	0.30
0.6	0.32	0.32	0.40	0.56	0.62
0.8	0.43	0.63	0.75	0.81	0.85

(b) $I_m = 0.6$

I_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.24	0.18	0.16	0.14	0.13
0.4	0.28	0.22	0.22	0.20	0.19
0.6	0.35	0.30	0.39	0.44	0.49
0.8	0.47	0.53	0.74	0.81	0.84

(c) $I_m = 0.8$

I_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.23	0.18	0.13	0.11	0.09
0.4	0.27	0.21	0.17	0.14	0.12
0.6	0.32	0.28	0.23	0.20	0.17
0.8	0.51	0.53	0.58	0.61	0.64

Table 4.4 Tables of F_{MSY}/M , for different values of l_c , M/K and l_m , when $d=0.50$.

(a) $l_m = 0.4$

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.68	0.57	0.49	0.46	0.44
0.4	0.82	0.79	0.91	1.17	1.62
0.6	1.07	1.24	2.63	∞	∞
0.8	1.74	∞	∞	∞	∞

(b) $l_m = 0.6$

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.72	0.51	0.42	0.35	0.30
0.4	0.89	0.64	0.63	0.54	0.47
0.6	1.38	1.00	2.82	4.29	5.11
0.8	2.94	6.38	∞	∞	∞

(c) $l_m = 0.8$

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.68	0.47	0.31	0.23	0.19
0.4	0.81	0.58	0.39	0.30	0.24
0.6	1.09	0.82	0.57	0.44	0.36
0.8	3.86	4.91	6.06	6.59	6.86

Table 4.5 Constants of proportionality in the relationship between the yield-biomass ratio and M , for different values of l_c , M/K and l_m , when $d=0.75$.

(a) $l_m = 0.4$

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.29	0.24	0.21	0.20	0.20
0.4	0.33	0.30	0.31	0.34	0.39
0.6	0.41	0.41	0.49	0.60	0.66
0.8	0.57	0.68	0.77	0.82	0.85

(b) $l_m = 0.6$

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.29	0.23	0.20	0.19	0.18
0.4	0.34	0.29	0.29	0.29	0.29
0.6	0.43	0.40	0.49	0.56	0.61
0.8	0.60	0.66	0.77	0.82	0.85

(c) $l_m = 0.8$

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.29	0.23	0.19	0.17	0.15
0.4	0.33	0.28	0.25	0.23	0.21
0.6	0.41	0.38	0.35	0.32	0.29
0.8	0.61	0.64	0.71	0.75	0.78

Table 4.6 Tables of F_{MSY}/M , for different values of l_c , M/K and l_m , when $d=0.75$.

(a) $l_m = 0.4$

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.99	0.81	0.71	0.71	0.72
0.4	1.28	1.21	1.54	2.42	4.74
0.6	1.94	2.42	7.09	∞	∞
0.8	4.31	∞	∞	∞	∞

(b) $l_m = 0.6$

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	1.01	0.76	0.66	0.59	0.53
0.4	1.31	1.06	1.12	1.02	0.91
0.6	2.18	1.97	7.27	10.99	12.95
0.8	10.03	∞	∞	∞	∞

(c) $l_m = 0.8$

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.98	0.73	0.53	0.42	0.35
0.4	1.24	0.98	0.72	0.55	0.45
0.6	1.85	1.53	1.10	0.84	0.69
0.8	7.02	11.38	14.88	16.29	16.94

Table 4.7 Constants of proportionality in the relationship between the yield-biomass ratio and M , for different values of l_c , M/K , when $d=1$.

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.30	0.25	0.22	0.22	0.22
0.4	0.35	0.32	0.32	0.36	0.41
0.6	0.45	0.44	0.52	0.60	0.66
0.8	0.63	0.69	0.77	0.82	0.85

Table 4.8 Tables of F_{MSY} / M , for different values of l_c , M/K , when $d=1$.

l_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	1.10	0.89	0.81	0.85	0.94
0.4	1.45	1.37	1.79	3.01	9.60
0.6	2.40	3.20	∞	∞	∞
0.8	10.20	∞	∞	∞	∞

Table 4.9 Constants of proportionality in the relationship between the yield-biomass ratio and M , for different values of I_c , M/K and I_m , with a Ricker-type stock-recruitment relationship.

(a) $I_m = 0.4$

I_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.38	0.31	0.27	0.27	0.28
0.4	0.44	0.39	0.40	0.45	0.51
0.6	0.56	0.55	0.65	0.67	0.73
0.8	0.77	0.77	0.81	0.84	0.86

(b) $I_m = 0.6$

I_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.38	0.31	0.27	0.26	0.25
0.4	0.44	0.39	0.39	0.39	0.39
0.6	0.55	0.54	0.64	0.74	0.81
0.8	0.78	0.85	0.83	0.85	0.87

(c) $I_m = 0.8$

I_c	M/K				
	0.5	1.0	2.0	3.0	4.0
0.2	0.38	0.31	0.25	0.22	0.20
0.4	0.44	0.39	0.33	0.30	0.27
0.6	0.55	0.51	0.46	0.42	0.38
0.8	0.79	0.85	0.94	1.00	1.04

Table 4.10 Tables of F_{MSY}/M , for different values of l_c , M/K and l_m , with a Ricker-type stock-recruitment relationship.

(a) $l_m = 0.4$

		M/K				
l_c		0.5	1.0	2.0	3.0	4.0
0.2		1.16	0.96	0.85	0.82	0.77
0.4		1.49	1.46	1.96	3.36	8.25
0.6		2.24	3.05	∞	∞	∞
0.8		4.67	∞	∞	∞	∞

(b) $l_m = 0.6$

		M/K				
l_c		0.5	1.0	2.0	3.0	4.0
0.2		1.20	0.86	0.73	0.59	0.50
0.4		1.58	1.16	1.17	0.95	0.81
0.6		2.66	2.12	13.43	17.43	19.71
0.8		10.44	∞	∞	∞	∞

(c) $l_m = 0.8$

		M/K				
l_c		0.5	1.0	2.0	3.0	4.0
0.2		1.15	0.80	0.51	0.38	0.30
0.4		1.45	1.01	0.65	0.48	0.38
0.6		2.14	1.51	0.97	0.72	0.57
0.8		15.88	19.93	22.97	24.42	25.29

4.4 An empirical formula

As described in Kirkwood *et al* (1994), we attempted to derive an approximate empirical formula expressing the yield-biomass ratio as a function of M , l_c , d , and M/K for the case when $l_m=0.5$. This was done using a log-linear regression in which the dependent variable was the calculated value of MSY/ExB_0 when $M=1$, for values of l_c in the range 0.3-0.6, d in the range 0.2-1.0, and M/K in the range 0.5-4.0. After some trial and error, the best fit obtained corresponded to the formula

$$ISY/ExB_0 = [1 - (1-d)^2] \exp(-1.33 + 0.64l_c - 0.31\frac{M}{K} + 0.80l_c\frac{M}{K})$$

This gave good predictions for the cited ranges of parameters. The value of R^2 obtained in the regression was 0.93. For only 16 of the 124 "observations" did the percentage prediction error exceed 10% and this only occurred for high values of M/K or low d . The maximum percentage prediction error was 23%. While we would not recommend immediate use of this formula at this stage, the good predictions obtained suggest strongly that practically useful predictions of yield in a wide variety of situations could be obtained using a relatively simple empirical relationship.

Attempts to generalise this empirical formula further by treating yield-biomass ratios additionally as a function of the length at maturity did not succeed in identifying a sufficiently accurate and simple formula. Since the computer program quite easily allows calculation of yield-biomass ratios for any given set of parameters in any case, further attempts to develop a general formula were curtailed.

5. Effect of age-dependent natural mortality

One of the criticisms made of simple fisheries models is that they make the assumption that the natural mortality rate does not vary with age. For the early stages in the life history of a fish species, the evidence is absolutely unequivocal that there are extreme variations in natural mortality with age. However, most models of exploited fish stocks, and certainly the ones considered here, have been formulated for late juvenile and adult fish, for which an assumption of an approximately constant natural mortality rate may be more tenable. Even so, there is also evidence that natural mortality rates can increase with age for older fish; e.g. see Beverton and Holt (1957) where approximately linear increases in M with age are shown for a number of fish species. In practice, it is usually difficult enough just to estimate a constant average natural mortality rate for a fish species, so predictions of yield will usually be based on an assumed constant M . Kirkwood *et al* (1994) investigated the extent to which allowing for M to increase with age will affect the results presented for constant M .

In order to examine the size of the bias incurred by erroneously assuming a constant M , it is necessary to calculate an appropriate constant average M that would correspond to a given age-dependent M . The well-known Heincke (1913) estimator of mortality has been used as the equivalent M by Kirkwood *et al* (1994). As detailed there, it was found that an erroneous assumption of a constant M leads to a negative bias in the yield-biomass ratios. That bias increased with increasing age-dependency, but it never exceeded around 25% in the cases examined.

The conclusion reached was that an erroneous assumption of constant M with age is likely to result in a slightly conservative prediction of potential yield when in fact M actually increases with age.

6. The special case of very short-lived species

On the surface, the results presented apply equally for all values of M . However, we have already seen that the proportional relationship between yield-biomass ratios and M can break down for high M when recruitment is not constant. The argument for treating at least some very short-lived species as special cases is unanswerable when one considers annual species like squid, which die immediately after spawning. Such species can be considered to present extreme cases of age-dependent natural mortality: M is effectively infinite for all ages above the age at maturity.

The difficulty that occurs is not that any of the preceding calculations are incorrect, but rather that the values calculated for the exploitable or total biomass in an virgin population using the standard methods no longer correspond to anything really measurable.

The biomasses as calculated both here and in Kirkwood *et al* (1994) actually represent an average value throughout a year. When M is relatively small, these biomasses really are approximately constant throughout the year, and it is reasonable to treat an estimate of abundance in an unexploited population made at virtually any time throughout a year as an acceptable estimate of the annual average biomass. As M increases (and thus lifespan decreases), however, the population biomass can vary considerably throughout the year. For annual species not only do these biomasses vary considerably throughout the year for ages up to the age at maturity, but they are zero for the remainder of the year. This means that interpretation and estimation of average biomasses throughout the year are rather difficult.

In such circumstances, it is more realistic to examine ratios of yield to the biomass in an unexploited population at time t_c (i.e. at the start of what would be the fishing season in an exploited stock). Apart from being much more easily interpretable, this biomass has the additional virtue of being practically measurable, e.g. by pre-season surveys of abundance or retrospectively via within-season stock assessments. As usual, there is a cost to pay. Yield-biomass ratios and values of F_{MSY} are perfectly well defined when using this new measure of exploitable biomass. However, the close-to-proportional relationship between yield-biomass ratios and M for species with the same l_c and M/K unfortunately no longer holds.

Table 6.1 presents numerical results for the case where $d=0.75$, $M=K=3$, $l_m=0.8$, and l_c ranges from 0.2 to 0.8, obtained for two dynamics models: the standard one as described earlier, and an alternative where M is infinite for all $t > t_m$. The high value used for l_m is more typical of very short-lived species. Shown in the table are yield-biomass ratios with calculated as either the average value throughout the year or the biomass of exploitable fish at the start of the fishing season.

Table 6.1 Yield-biomass ratios when $d=0.75$, $M=K=3$ and $l_m=0.8$ for the standard dynamics model and for one in which all fish die immediately after spawning. ExB_0 is the average exploitable biomass throughout the year in an unexploited population, and $Init ExB$ is the exploitable biomass measured at the start of the fishing season.

l_c	Standard model		Death occurs after spawning	
	MSY / ExB_0	$MSY / Init ExB$	MSY / ExB_0	$MSY / Init ExB$
0.2	0.68	1.34	1.01	12.71
0.4	0.87	1.11	1.39	1.82
0.6	1.19	0.82	2.20	0.94
0.8	1.89	0.84	6.61	0.92

The first thing to note in this table is that, when using the average biomass, yield-biomass ratios increase with length at first capture, and often they exceed 1.0. Both features arise from the inappropriate method of averaging biomass throughout a year when in fact it varies during that time. When biomass is measured at the start of the fishing season, the yield-biomass ratios initially decrease with increasing length at first capture, as is to be expected. For the smaller values of l_c , the ratio of MSY to the exploitable biomass at

the start of the season can still be substantially greater than 1.0, especially when death occurs after spawning. This may seem somewhat bizarre, but it simply reflects the fact that fishing has started well before the population has reached its maximum biomass for the year.

Comparing the results across dynamics models, the yield-biomass ratios are considerably higher when the fish die immediately after spawning, particularly for low values of l_c . This is because even for this high M , there are sufficiently many survivors into a second year to influence the size of the exploitable biomass at the start of the season. There are no survivors to a second year if death occurs after spawning.

The tables of constants of proportionality presented in sections 3 and 4 were calculated for $M=1$, a value of M for which there is not that much difference between the two methods of calculating exploitable biomasses. The findings in this section indicate that for larger M problems do arise. In the following section we present estimates of yield-biomass ratios for selected species from FISHBASE for which estimates of all or most of the biological and fishery parameters are available. A number of these species are short-lived tropical species. Accordingly we include estimates of yield-biomass ratios calculated in both ways in the results.

7. Estimates of yield-biomass ratios and F_{MSY} for selected species

The FISHBASE database being jointly developed by ICLARM and FAO is intended to be, on release, the most up-to-date and comprehensive collation of both biological and fisheries information existing anywhere. The decision by MRAG to become a collaborator was in considerable part taken with a view that information from that database could be used to obtain direct estimates of yield-biomass ratios and optimum fishing mortality rates for a wide range of commercially important marine species, particularly those found in the tropics and fished by developing countries. As is well known, it is for these species that it is most difficult to obtain appropriate information.

The table of estimates that concludes this section has been assembled by extracting estimates of the cited parameters from the database and then using the computer program developed during this project to perform the necessary calculations. It must be emphasised, however, that these estimates should be considered as preliminary only, for a number of reasons. First, the FISHBASE database is still under development, and the version we have used to extract information is still preliminary. The final version released will not only cover more species and contain more information about species already in the database, but will also be subject to more rigorous checking. That said, however, the database is intended to record faithfully biological and fisheries information as recorded in the literature. No attempt has been made to review the likely accuracy of that information. Before estimates of yield-biomass ratios were to be used for management purposes for a particular species, it would be vital to undertake such a review. In the time available, we have not attempted to do so for the species in the table, although a couple of species have been omitted where the recorded biological parameters are clearly quite inconsistent.

The version of the database used has a total of 1200 fields available to record quantitative and qualitative information for each species, and information of some sort is available for nearly 9000 different species of the roughly 24000 fish species existing in the world. We firstly restricted attention to commercially exploited or potentially exploitable marine species. In terms of the biological parameters needed, fields are available in the database records for a species to contain estimates of M , K , L_{∞} , t_0 , and I_m . The principal fishery parameter needed is l_c , the length at first capture. This is actually not recorded explicitly, but a related parameter, l_{com} , the "common" length in the catch, is recorded. The true value of l_c clearly will be less than l_{com} , but by how much is unclear.

Ideally, one would seek to select stocks of a species for which appropriately calculated estimates of all these parameters are recorded using consistent units. In practice, this only occurred very rarely in the development version of the database available. The most commonly available parameter estimates are for M , K , and L_{∞} , and in the table below we have required that estimates of those three parameters are available for a specified stock of a species before it can be included in the table. Where corresponding estimates of t_0 are recorded, these have been used, but otherwise t_0 was taken to be zero. Where multiple estimates of parameters exist on the database, a judgement was made as to which were the most reliable. Estimates of I_m (relative to L_{∞}) were rather less frequently available for the same stock and species. If a consistent estimate of I_m was available for other stocks of the same species, or if necessary for related species, this has been used in the table below for important tropical species. In a few cases indicated with a superscript asterisk, a value of 0.5 has been assumed for I_m .

Values of l_c were chosen according to the following rule:

If an estimate of l_{com} exists and $l_{com} < 0.8 I_m$, then $l_c = l_{com}$

Otherwise, $l_c = 0.8 I_m$

This is to a large extent arbitrary, but it is relatively rare for fish not to be exploited before they become mature, and the above rule ensures that is avoided.

The database does not include any estimates of potential stock-recruitment relationships. As already noted, estimates of stock-recruitment parameters have been gathered by Myers *et al* (1994), but these are mainly for species exploited in developed countries. In the table below, we have included estimates of the parameter d of the Beverton-Holt stock-recruitment relationship where it can be estimated for a species and stock, but otherwise, we have calculated yield-biomass ratios and fishing mortality rates for a Beverton-Holt relationship with $d=0.5$ and for a Ricker-type relationship with $R_m/R_0=1.2$, taking these to represent relatively low levels of density dependence. In these cases, yield-biomass ratios and F_{MSY}

estimates are given as a range of values, the lower end corresponding to the Beverton-Holt relationship, and the upper end to the Ricker-type relationship, and no specific value of d is recorded.

When these results were first calculated, we had initially calculated ranges of estimates corresponding to Beverton-Holt parameters of $d=0.5$ and $d=1.0$, the latter corresponding to a constant recruitment. While the yield-biomass ratios are often not that different for the constant recruitment and the Ricker-type relationship (those for the Ricker-type are usually higher), the values of F_{MSY} for the constant recruitment relationship can often be either very large or infinite. This only occurs because there is no penalty for reducing the spawning stock biomass to very low levels. Basing management on such an extreme assumption is clearly not conservative, so we have opted to base upper ranges on a Ricker-type relationship.

One other biological parameter needed in the computer program is the exponent b in the length-weight relationship $L \propto W^b$. In some cases, this was not recorded in FISHBASE, in which case we have assumed the conventional value of 3 for b .

As indicated in section 6, the difficulties that arise in interpretation of yield-biomass ratios for high M values require that we include in the table ratios of MSY to both measures of initial exploitable biomass: ExB_0 , which is the average exploitable biomass in an unfishery population throughout the year, and $Init ExB$, which is the exploitable biomass in an unfishery population estimated at the start of the fishing season.

Table 7.1 lists estimates obtained for a total of 53 commercially exploitable marine species.

Table 7.1 Yield-biomass ratios and F_{MSY} for selected species. For explanation of column headings, see text on previous page

Species	Common name	Country	M	K	t_0
<i>Dicentrarchus labrax</i>	European seabass	Ireland	0.10	0.14	-0.2
<i>Cetengraulis mysticetus</i>	Pacific anchoveta	Colombia	2.40	2.09	0.0
<i>Encrasicholina devisi</i>	Devis' anchovy	Papua N	7.20	2.10	-0.7
<i>Encrasicholina heteroloba</i>	Shorthead anchovy	Papua N	6.20	2.60	0.0
<i>Engraulis mordax</i>	Californian anchovy	USA	0.92	0.35	-2.4
<i>Engraulis ringens</i>	Peruvian anchovy	Peru	1.52	1.70	0.0
<i>Cepola macrophthalma</i>	Red bandfish	Greece	0.68	0.21	0.0
<i>Notothenia coriiceps</i>	Yellowbelly rockcod	Antarctica	0.36	0.09	-1.7
<i>Gadus macrocephalus</i>	Pacific cod	Canada	0.91	0.27	0.0
<i>Gadus morhua</i>	Atlantic cod	Faeroe Is	0.17	0.19	-0.4
<i>Pollachius virens</i>	Saithe	Iceland	0.30	0.13	-0.9
<i>Theragra chalcogramma</i>	Alaska pollack	USA	0.40	0.32	0.0
<i>Trisopterus minutus</i>	Poor cod	UK	0.90	0.40	0.0
<i>Squalus acanthias</i>	Piked dogfish	Canada	0.09	0.03	-7.3
<i>Callionymus lyra</i>	Dragonet	UK	0.96	0.43	0.0
<i>Lethrinus enigmaticus</i>	Blackeye emperor	India	0.20	0.18	-1.1
<i>Coracinus capensis</i>	Galjoen (male)	South Africa	0.29	0.19	0.0
<i>Coracinus capensis</i>	Galjoen (female)	South Africa	0.36	0.13	0.0
<i>Amblygaster sirm</i>	Spotted sardinella	N Caledonia	2.90	1.58	0.0
<i>Clupea harengus</i>	Atlantic herring	UK	0.16	0.44	-1.3
<i>Clupea pallasii</i>	Pacific herring	USA	0.56	0.36	0.0
<i>Sardinops caeruleus</i>	California pilchard	USA	0.45	0.40	-2.1
<i>Sprattus sprattus</i>	European sprat		1.20	0.70	0.0
<i>Galeorhinus galeus</i>	Tope shark	Australia	0.12	0.16	-1.3
<i>Caranx lugubris</i>	Black jack	N Marianas	0.58	0.08	-0.5
<i>Caranx ruber</i>	Bar jack	Jamaica	1.40	0.24	0.0
<i>Rastrelliger brachysoma</i>	Short mackerel	Indonesia	4.56	2.28	0.0
<i>Rastrelliger kanagurta</i>	Indian mackerel	Indonesia	4.44	2.76	0.1

L_m/L_∞	L_c/L_∞	b	d	F_{MSY}	MSY / ExB_0	MSY / Init ExB
0.57	0.45	3.0		0.08 - 0.14	0.03 - 0.04	0.03 - 0.04
0.90	0.72	3.0		1.77 - 3.04	0.68 - 1.28	0.39 - 0.73
0.55	0.44	3.5		5.33 - 9.75	1.77 - 2.93	0.72 - 1.20
0.65	0.52	3.0		5.50 - 10.03	1.83 - 3.10	0.64 - 1.09
0.85	0.68	3.0	0.92	1.48	0.43	0.32
0.80	0.64	3.0		1.65 - 3.19	0.49 - 0.84	0.39 - 0.66
0.40	0.32	2.0		0.58 - 1.17	0.18 - 0.32	0.16 - 0.28
0.64	0.51	3.0		0.20 - 0.34	0.08 - 0.16	0.07 - 0.14
0.59	0.47	3.0		0.62 - 1.14	0.22 - 0.41	0.18 - 0.34
0.48	0.38	3.0	0.78	0.20	0.05	0.05
0.55	0.44	3.0	0.71	0.35	0.09	0.09
0.60	0.48	3.0	0.94	0.76	0.14	0.14
0.54	0.43	3.0		0.69 - 1.36	0.22 - 0.37	0.19 - 0.33
0.78	0.62	3.0		0.04 - 0.07	0.02 - 0.04	0.02 - 0.04
0.70	0.56	3.0		0.70 - 1.28	0.25 - 0.46	0.20 - 0.37
0.59	0.48	3.0		0.15 - 0.29	0.05 - 0.09	0.05 - 0.08
0.62	0.49	3.1		0.21 - 0.39	0.07 - 0.12	0.07 - 0.12
0.48	0.39	3.1		0.24 - 0.46	0.08 - 0.14	0.08 - 0.13
0.74	0.59	3.2		2.58 - 4.72	0.84 - 1.46	0.51 - 0.87
0.76	0.61	3.2	0.72	0.28	0.07	0.07
0.79	0.64	2.9		0.40 - 0.72	0.15 - 0.28	0.13 - 0.25
0.61	0.48	3.0	0.25	0.19	0.07	0.07
0.77	0.62	3.5		0.91 - 1.68	0.32 - 0.58	0.25 - 0.46
0.61	0.48	3.0		0.10 - 0.18	0.03 - 0.05	0.03 - 0.05
0.50	0.32	3.0		0.22 - 0.36	0.10 - 0.19	0.08 - 0.17
0.46	0.37	3.2		0.97 - 1.81	0.33 - 0.61	0.25 - 0.46
0.74	0.59	2.9		3.84 - 6.82	1.32 - 2.33	0.55 - 0.96
0.79	0.64	3.2		3.98 - 6.98	1.41 - 2.54	0.49 - 0.89

Species	Common name	Country	M	K	t_0
<i>Scomber japonicus</i>	Chub mackerel	USA	0.50	0.24	0.0
<i>Scomber scombrus</i>	Atlantic mackerel	USA	0.30	0.27	-1.7
<i>Scomberomorus cavalla</i>	King mackerel	USA	0.37	0.14	-2.1
<i>Thunnus alalunga</i>	Albacore	USA	0.22	0.17	-1.9
<i>Thunnus albacares</i>	Yellowfin tuna	Mexico	0.77	0.66	0.0
<i>Thunnus thynnus</i>	Northern bluefin tuna	Tunisia	0.18	0.09	0.0
<i>Merluccius merluccius</i>	European hake	Tunisia	0.20	0.19	-0.9
<i>Cheilodactylus macropterus</i>	Morwong	N Zealand	0.15	0.10	-4.3
<i>Platichthys flesus</i>	Flounder	Germany	0.18	0.30	-0.3
<i>Pleuronectes platessa</i>	Plaice		0.12	0.08	0.0
<i>Oncorhynchus keta</i>	Chum salmon	Canada	1.20	0.45	0.0
<i>Salmo trutta trutta</i>	Sea trout	UK	0.94	0.36	0.0
<i>Sebastes alutus</i>	Rockfish	USA	0.10	0.18	1.1
<i>Mallotus villosus</i>	Capelin	Canada	1.30	0.48	0.0
<i>Apsilus dentatus</i>	Black snapper (male)	Jamaica	1.90	0.65	0.0
<i>Apsilus dentatus</i>	Black snapper (fem)	Jamaica	0.80	0.30	0.0
<i>Etelis coruscans</i>	Flame snapper	N Marianas	0.36	0.12	-1.2
<i>Lutjanus buccanella</i>	Blackfin snapper	Jamaica	2.20	0.70	0.0
<i>Lutjanus campechanus</i>	Northern red snapper	USA	0.20	0.17	-0.1
<i>Lutjanus purpureus</i>	Southern red snapper	Brazil	0.37	0.10	-1.2
<i>Ocyurus chrysurus</i>	Yellowtail snapper	Jamaica	0.62	0.25	0.0
<i>Pristipomoides auricilla</i>	Goldflag jobfish	N Marianas	0.62	0.36	-0.9
<i>Pristipomoides filamentosus</i>	Crimson jobfish	Hawaii	0.25	0.15	-1.7
<i>Pristipomoides zonatus</i>	Oblique-banded	N Marianas	0.48	0.23	-0.9
<i>Rhomboplites aurorubens</i>	Vermilion snapper	USA	0.20	0.20	0.1
<i>Nemipterus japonicus</i>	Japanese threadfin	India	2.52	1.00	0.0
<i>Balistes vetula</i>	Queen triggerfish	Jamaica	2.60	0.57	0.0

L_m/L_∞	L_c/L_∞	b	d	F_{MSY}	MSY / ExB_0	MSY / Init ExB
0.73	0.59	3.4	1.00	5.88	0.24	0.21
0.74	0.59	3.0	0.83	0.57	0.12	0.11
0.56	0.45	3.0		0.25 - 0.47	0.09 - 0.16	0.08 - 0.15
0.63	0.51	3.0		0.17 - 0.32	0.06 - 0.10	0.05 - 0.09
0.69	0.55	3.0		0.67 - 1.32	0.21 - 0.37	0.19 - 0.33
0.30	0.24	3.0		0.09 - 0.17	0.03 - 0.05	0.03 - 0.05
0.56	0.45	3.2		0.14 - 0.27	0.05 - 0.08	0.05 - 0.08
0.50	0.40	3.0		0.10 - 0.19	0.03 - 0.06	0.03 - 0.06
0.73	0.43	3.0		0.13 - 0.23	0.05 - 0.08	0.04 - 0.08
0.40	0.32	3.0	0.65	0.10	0.03	0.03
0.71	0.55	3.0		0.76 - 1.34	0.29 - 0.55	0.22 - 0.42
0.80	0.64	3.0		0.51 - 0.86	0.22 - 0.43	0.16 - 0.33
0.79	0.63	3.0		0.10 - 0.18	0.03 - 0.06	0.03 - 0.06
0.90	0.72	3.0		0.48 - 0.78	0.23 - 0.50	0.15 - 0.32
0.76	0.61	3.0		1.19 - 2.03	0.47 - 0.92	0.29 - 0.56
0.71	0.57	3.0		0.52 - 0.92	0.20 - 0.38	0.16 - 0.31
0.61	0.37	3.0		0.16 - 0.28	0.06 - 0.12	0.06 - 0.12
0.48	0.39	3.0		2.11 - 4.37	0.58 - 0.93	0.44 - 0.71
0.50	0.40	3.0		0.14 - 0.26	0.05 - 0.08	0.05 - 0.07
0.50*	0.40	3.0		0.24 - 0.44	0.08 - 0.15	0.08 - 0.14
0.50	0.40	3.0		0.44 - 0.85	0.14 - 0.24	0.13 - 0.23
0.50*	0.40	3.0		0.44 - 0.85	0.14 - 0.23	0.13 - 0.22
0.67	0.53	3.0		0.17 - 0.32	0.06 - 0.11	0.06 - 0.11
0.50*	0.40	3.0		0.33 - 0.65	0.11 - 0.18	0.10 - 0.17
0.30	0.24	3.0		0.12 - 0.20	0.04 - 0.06	0.04 - 0.06
0.48	0.38	3.0		2.31 - 4.67	0.64 - 0.97	0.53 - 0.81
0.56	0.44	2.9		1.85 - 3.27	0.67 - 1.23	0.38 - 0.70

8. Stochastic recruitment

While deterministic results set a scale on yield levels and indicate how these vary for species with differing biological parameters, the actual yields that will be taken in the presence of a varying environment can differ substantially from those suggested by the deterministic results. For many fish species, the primary focus of variability is in the annual recruitment; for temperate species the recruitment resulting from the same or similar levels of spawning stock can vary by more than an order of magnitude. Kirkwood *et al* (1994) therefore examined the effect of a varying environment by allowing for stochastic variability in the stock-recruitment relationship. The same approach was taken by Beddington and Cooke (1983).

Two scenarios were examined. In the first, the annual recruitment arising from given levels of spawning stock biomass is taken to be log-normally distributed. The second examines the ability of species of different lifespans to recover from an extreme case of environmental variability, in which the spawning stock suffers an episode of catastrophic mortality.

8.1 *Environmental variability in recruitment*

In their examination of the statistical properties of recruitment in some commercial fish species, Hennemuth, Palmer and Brown (1980) found that recruitment was highly variable and that its skewed frequency distribution was similar to a log-normal distribution. Similar conclusions have been reached in other studies. Accordingly, we investigated the probability distribution of annual yield when the annual recruitment is log-normally distributed with mean equal to that predicted by the deterministic Beverton-Holt stock-recruitment relationship. The coefficient of variation of the log-normal errors was taken to be 0.5 (Beddington and Cooke, 1983).

The procedure for generating series of stochastic annual yields and characterising them for each combination of parameters was as follows. A simulated population was set up at time zero in deterministic equilibrium, harvested at the fishing mortality rate that produced the deterministic MSY for that parameter combination. Annual log normal variation about the stock-recruitment curve was then introduced, and sufficient time was allowed to elapse for the effects of the stochastic recruitment to spread through all age classes in the population. Then the values of annual yield were collected for the next 100 years. This process was repeated 100 times, and the median, 5th and 95th percentiles of the pooled distribution of annual yields was determined. These statistics of the distribution of annual yield were determined in Kirkwood *et al* (1994) for parameter combinations $l_c=0.4$, $l_m=0.5$, $d=0.2$ and 0.8 , and M taking selected values in the range 0.05 to 3.0. Results were presented in terms of the ratios of annual yield to the deterministic exploitable biomass.

For low values of M , the median annual yield exploitable biomass ratio was very close to the corresponding deterministic value, but as M increased, the median began to fall below the deterministic value. This tendency is more marked when the degree of density dependence in the stock-recruitment relationship was much smaller ($d=0.2$).

There was a strong tendency for increased skewness in the distribution of annual yield biomass ratios as M increased. The lower 5th percentile of this distribution stayed remarkably constant for M above 0.5, but in contrast the 95th percentile increased rapidly with M . The increasing skewness with increasing M was expected; when M is high, the exploitable stock consists of only one or two age classes, each of which has been subject to highly skewed log-normal variability, while when M is low, the exploitable stock is the sum of many age classes and its distribution will be more symmetric.

A direct result of the increasing skewness with M is that, while in most cases the annual yield biomass ratio will be much less than $\frac{1}{2}M$, in an important minority of cases it can exceed $\frac{1}{2}M$, sometimes substantially. This ability to gain benefits in terms of high yields during good years flows directly from the assumption that fishing mortality (or equivalently fishing effort) is the variable that is used to control the level of harvesting. The figures in Kirkwood *et al* (1994) show clearly that once M gets large, application of a constant fishing mortality can lead to yield-biomass ratios considerably in excess of $\frac{1}{2}M$. However, the very high variation in recruitment has tended to be documented for species with relatively low mortality.

8.2 *Recovery from a stock collapse*

The preceding sub-section examined the effect of stochastic variation of recruitment about a stock-recruitment relationship. One feature of that relationship was that recruitment was non-zero for all positive stock biomasses. This would be an optimistic assumption if there existed a critical spawning stock biomass below which recruitment fell to zero; i.e. if there is critical depensation in the stock-recruitment

relationship. Here, Kirkwood *et al* (1994) examined the ability of a population to recover from a catastrophic mortality episode.

A population was assumed to be in deterministic equilibrium at time zero, and harvested at the fishing mortality rate that produces the deterministic MSY. Just before the start of the spawning season in the first year, the entire spawning stock was killed, so that there was no recruitment at all at the beginning of the second year. Subsequently, the population was allowed to recover, if it can, according to the standard deterministic dynamics and deterministic stock-recruitment relationship. During the recovery period, fishing continued at the F_{MSY} rate.

The trajectories taken by the annual spawning stock biomasses were investigated for three different natural mortality rates ($M= 0.05, 0.1$ and 0.4). For convenience, the lengths at first capture and at maturity were taken to be equal. A low degree of density dependence in the stock recruitment relationship was used ($d=0.2$), and M/K was set to 1.0. The resulting trajectories are shown in Kirkwood *et al* (1994).

Despite exploitation continuing, in each case the spawning stock biomasses recovered (eventually), initially at a relatively fast rate and then at a rather slower rate. The key to these recoveries lay in the presence of a buffer in the form of unfished immature age-classes in the population, and in the time lags between birth and the age at maturity. For each of the three mortality rates, the age at maturity was more than one year, so that immediately after the catastrophic mortality suffered by the spawning stock, the population consisted of a number of immature unfished age-classes. The number of such age-classes increased with decreasing values of M . One year later, the oldest of these immature age-classes became mature and the process of rebuilding the spawning stock started. This process continued until the annual increment to the spawning stock was roughly balanced by the deaths due to natural mortality and fishing. The spawning stock then recovered at a much slower rate that is consistent with the increase in recruitment flowing from an increased spawning stock implied by the stock-recruitment relationship .

The exclusion of examples with a high M is deliberate. Under the conditions simulated, any species with M sufficiently high that the age at maturity is less than one year will by definition be completely extinguished by the catastrophe hypothesised. This may seem an artifact of an extremely unlikely scenario. While in a strict sense that is true, all that is required to bring about conditions nearly matching those simulated here for short-lived species is for them to have a critical spawning biomass below which recruitment is severely diminished. Then a bout of severe overfishing, for example, could well result in a complete stock collapse.

In contrast, the unfished age-classes in longer-lived species provide a buffer against such catastrophic events. It follows that in this sense, longer-lived species can show a greater resilience than short-lived ones. Further, the greater the number of unfished age-classes, the greater the amount of buffering. Thus extremely long-lived fish species, such as orange roughy, have the ability to withstand occasional major catastrophic events, despite the very low sustainable yields they provide.

9. Conclusions

The primary conclusion that may be drawn from the results obtained during the project is that although there is a clear approximately proportional relationship between sustainable yield and mortality (lifespan), the constant of proportionality is smaller than had originally been proposed by Gulland (1971). Yield taken as a percentage of virgin biomass, even in the case of very strong density dependence (recruitment constant regardless of mature stock size), is more likely to be around $0.3M$, rather than $0.5M$ that Gulland suggested. When more realistic levels of density dependence are considered, the percentage yield is further reduced, perhaps to between $0.1M$ and $0.2M$.

When looked at specifically in terms of lifespans, the non-linear relationship between M and lifespan implies that for longer-lived species, the sustainable yields are both low and almost independent of lifespan. An exception to this ground rule is the behaviour of very short lived species. In these, the details of the life cycle dominate their response to exploitation, such that on sensible and measurable definitions of exploitable biomass, the stock may be capable of producing sustainable yields well in excess of the biomass measured at the start of the fishing season.

Obviously, this analysis sets the scene for more detailed investigations of individual species and the way in which the key parameters that determine yields vary. An initial step has been taken using the information recorded in the FISHBASE database to develop the estimates of yield-biomass ratios and fishing mortality rates for selected species given in section 7 of this summary report. In a more general context, it is interesting to note that Pauly (1980) found a dependence between natural mortality, growth in size, and mean water temperature for a wide range of fish stocks. Such a relationship affords the possibility of further assessment of the potential yield of species in ecosystems of different types.

The deterministic results are a useful guide to expectations in the real world, particularly for relatively long lived species. The investigation of stochasticity in recruitment and its implications for the expected variation in yield complements other findings that a policy of constant effort with a target level of fishing mortality can produce substantial benefits in high yields when recruitment is high. The strength of this effect with increasing mortality (reduced lifespan) is particularly marked. Very short lived species do appear to be exceptions to the general rules outlined above; they can provide high yields. However the brief examination of the effect of catastrophic events on the dynamics does indicate that longer lived species retain a resilience to catastrophes that is not available to the short lived species, which can be particularly vulnerable to a combination of high exploitation and occasional environmental events that devastate the spawning stock.

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