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A survey of stock assessment methods and results

Pamela M. Mace

MAFFish Fisheries Research Centre
P O Box 297
Wellington

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MAFFish, N.Z. Ministry of Agriculture and Fisheries

This series documents the scientific basis for stock assessments and fisheries management advice in New Zealand. It addresses the issues of the day in the current legislative context and in the time frames required. The documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

A SURVEY OF STOCK ASSESSMENT METHODS AND RESULTS

Pamela M. Mace

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I. INTRODUCTION

The purpose of this report is to outline the stock assessment methods used by selected well-established stock assessment agencies, and compare these to the methods currently applied at the Fisheries Research Centre (FRC). Estimates of common biological reference points are compiled and related to corresponding estimates adopted by FRC. This analysis is used as a basis for suggesting modifications to some aspects of FRC's approach to stock assessments.

The survey of fish stock assessment methods and biological reference points used by other fisheres research institutions was conducted in part during an overseas trip in August 1987, when I visited the Bedford Institute of Oceanography, Halifax, Nova Scotia, Canada and the Northeast Fisheries Center of the National Marine Fisheries Service at Woods Hole, Massachusetts, USA. I concentrated on three stock assessment agencies that conduct regular assessments on a wide variety of fish stocks: the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC, Canada), the International Council for the Exploration of the Sea (ICES, Europe) and the Northeast Fisheries Center (NEFC, USA).

II. STOCK ASSESSMENT METHODS

The main sources of information for this survey were CAFSAC (1987), ICES (1987) and NEFC (1986). In 1986, the ICES Advisory Committee on Fishery Management reviewed the status of more than 80 fish stocks in the northeast Atlantic Ocean and Baltic Sea (ICES 1987). In total, ICES is responsible for the assessment of about 160 fish stocks. CAFSAC provides annual assessment advice on about 90 fish, invertebrate and marine plant stocks in the northwest Atlantic (CAFSAC 1987). NEFC assesses the status of about forty fish and invertebrate stocks off the northeast coast of the United States (NEFC 1986).

The three agencies differ in complexity. ICES is the only one of the three agencies that is international in participation and scope. It is required to coordinate and synthesise the research activities of several European nations. Fisheries scientists from other countries, particularly the USA and Canada, also participate in stock assessment meetings. CAFSAC and NEFC are smaller organisations. CAFSAC involves three eastern Canadian regions, each with similar research capability and assessment responsibility. In the northeastern United States, there is a single federal agency (NEFC) that conducts most of the research and analysis, with smaller inputs from fisheries agencies in the northeastern coastal states.

There are also differences in the fishery management systems under which the agencies operate. Both ICES and CAFSAC operate under quota systems managed by government agencies. Advice to fishery managers is usually formulated in terms of Total Allowable Catches (TACs). NEFC operates under a Council system of fisheries management. The New England Fisheries Management Council and the Mid Atlantic Fisheries Management Council are comprised of representatives of both government and industry. The New England Council mostly uses indirect methods, such as minimum fish size, minimum mesh size, and closed areas and seasons, to control fishing effort. The Mid Atlantic Council sets quotas for selected species (butterfish, mackerel, squid and surf clams). NEFC focuses on reviewing the status of the stocks in relation to various reference points, rather than providing explicit advice on how the stocks should be managed.

Calculation of biomass

There are numerous methods available for the calculation of relative or absolute biomass. They include virtual population analysis (VPA), trawl surveys, commercial catch per unit effort (CPUE), ichthyoplankton surveys, acoustics and tagging. Brief descriptions of each of these methods are provided in Appendix I.

All three stock assessment agencies focus on VPA for the estimation of absolute biomass. ICES uses VPA for almost all stocks for which it provides explicit advice on management. CAFSAC uses VPA for most of its major stocks, and NEFC uses VPA for about one half of the stocks it assesses. ICES now utilises a version of VPA called separable VPA (Appendix I) for more than fifty percent of its stocks (F.M. Serchuk, NEFC, personal communication). CAFSAC has experimented with separable VPA, but has not yet adopted the technique for general use. Use of separable VPA is still being explored by NEFC.

To evaluate current stock status it is necessary to "tune" (calibrate) the VPA using a time series of indices of relative abundance. The types of data that can be used for tuning include commercial catch and effort data, egg surveys, larval surveys, juvenile surveys, trawl surveys, aerial surveys, acoustics and tagging. All three agencies use commercial CPUE and trawl survey data extensively for this purpose. ICES makes more use of young fish (pre-recruit) and acoustics surveys than the other two agencies. NEFC has the enviable record of having the longest time series of annual multispecies trawl surveys of any stock assessment agency worldwide. An autumn series of surveys has been conducted continuously since 1963, and a spring series since 1968. These have provided extended time series of abundance indices for most of the assessed stocks.

Nowadays, none of the agencies estimate absolute biomass from time series of relative abundance indices alone.

Calculation of biological reference points

Biological reference points can be grouped into categories based on target constant fishing mortality (TCF) strategies, target constant catch (TCC) strategies and target constant biomass (TCB) strategies (Mace 1988). Biological reference points associated with TCF strategies include F_{msy}, $F_{0.1}$, F_{max} (the latter two being derived from yield per recruit analysis), F_{rep} (F-replacement, Sissenwine and Shepherd 1987) and F = M, where M is the instantaneous rate of natural mortality. MSY is the main reference point that has been associated with TCC strategies, while B_{msy} or B_{MESY} (Getz et al. 1987), the target biomass that maximises long term average yields, has been used for TCB strategies. Appendix II contains descriptions of some of the methods commonly used to calculate these reference points.

All three agencies base their assessments on either $F_{0.1}$ or F_{max} whenever there are adequate data to conduct yield per recruit (YPR) analysis. $F_{0.1}$ is the most common reference point used, although ICES also makes extensive use of F_{max}. Although not surveyed in detail, two other international stock assessment groups also base most of their assessments on $F_{0.1}$. These are the Northwest Atlantic Fisheries Organisation (NAFO), formerly the International Council for Northwest Atlantic Fisheries (ICNAF), and the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). At present, $F_{0.1}$ is the most widely accepted reference point for assessing and managing fish stocks. The current status of a fishery can be readily evaluated by comparing estimates of recent fishing mortality ($F_{current}$) derived from VPA or other methods to $F_{0.1}$ (or F_{max}).

In recent years (since 1986), NEFC has begun to consider F_{rep} (Appendix II), also called F_{med} (F-median), as a basis for assessing the status of selected stocks. This reference point is calculated in conjunction with the target spawning stock biomass per recruit (SSB/R) derived from YPR analysis. F_{med} is also beginning to be calculated and reported regularly by ICES (F.M. Serchuk, personal communication). At present F_{med} is not used by ICES as a basis for recommendations. The main reason is that it is often higher than F_{max} (Table 1), and there is a general reluctance to exceed the latter level of fishing mortality. Also, for stocks with a long history of heavy exploitation (which includes numerous ICES stocks) F_{med} will result in the maintenance of biomass at low levels, whereas a lower fishing mortality might promote stock rebuilding and consequent increases in yields.

The deterministic MSY is never used explicitly as a biological reference point. For some assessments (e.g. redfish) CAFSAC has devised a reference point from stock production models, specified as the yield corresponding to two-thirds of the effort exerted at the deterministic MSY. This is, however, intended to be a reference point of a TCF strategy, not a TCC strategy. It is believed to approximate $F_{0.1}$ yield levels for stocks at equilibrium with stable age distribution. The validity of this assumption is currently being investigated (CAFSAC 1987).

The three stock assessment agencies surveyed do not consider TCB (constant escapement) policies. Such strategies are more appropriate for anadromous species where spawning habitat is limited, and the number of spawning adults can be readily estimated throughout the season. Constant escapement strategies are most commonly used for Pacific salmon on the west coast of Canada.

Calculation of yields

Implicit in the fact that ICES, CAFSAC and NEFC express biological reference points in terms of fishing mortality levels is that yields will vary in accordance with fluctuations in stock size. Yields are generally calculated from the Baranov catch equation:

$$C = \sum_{t=t_r}^{t_{max}} \frac{P_t F_{ref}}{P_t F_{ref} + M} \left(1 - e^{-(P_t F_{ref} + M)}\right) N_t W_t \quad (1)$$

where
- C = catch in weight
- t = age
- t_r = age of recruitment
- t_{max} = maximum age in the population
- P_t = the proportion of age class t that has recruited to the fishery
- F_{ref} = instantaneous rate of fishing mortality (reference level)
- M = instantaneous rate of natural mortality
- N_t = the number of fish of age t that will be present during the next fishing year
- W_t = average weight of fish of age t

When the sum of F_{ref} and M is less than about 0.6-0.8, this equation can be approximated by:

$$C = F_{ref} B_{current} \quad (2)$$

where $B_{current}$ = an estimate of the mid-season recruited biomass (i.e. the average recruited biomass) that will be present during the next fishing year.

For most stocks the reference level of fishing mortality, F_{ref}, is equated with $F_{0.1}$. Ocassionally F_{max} may be used instead, particularly by ICES. When available, data from young fish surveys are used in the catch projections to provide estimates of the number of new recruits that will enter the fishery in future years. Otherwise, it is usually assumed that recruitment will correspond to average historic levels.

Recommendations are often formulated in terms of fishing mortality levels. For example, for heavily exploited stocks it may be recommended that F not be allowed to exceed current levels, or that it should be reduced down to the level of F_{max} or $F_{0.1}$. Where possible, ICES and CAFSAC base TAC recommendations on $F_{0.1}$ projections from VPA. NEFC performs similar computations, but does not recommend TAC levels. They may, however, make qualitative predictions about future stock status under various fishing mortality options. When there are inadequate data to construct or tune a VPA, ICES usually makes no explicit recommendations at all. In other cases they may recommend a precautionary or pre-emptive TAC based on previous catch figures. In a few isolated cases, CAFSAC derives TAC recommendations from reference points from stock production models (see above). As a final resort, they also base some TACs on recent catches. NEFC does not make catch projections when no VPA is available. Survey data, on their own, are considered to be indices of relative abundance only.

All three agencies may sometimes conduct analyses on subsidiary management measures as alternative or additional controls. Such measures include closed areas, closed seasons, minimum mesh size, and other indirect methods of controlling fishing effort. NEFC places more emphasis on these methods of control than either ICES or CAFSAC.

III. METHODS USED BY FRC

The first series of formal stock assessment meetings conducted by FRC took place in 1985 (Colman et al. 1985). For lack of better data, more than half of the assessments were based on current or recent landings. Sometimes these assessments resulted in TAC recommendations that were similar to the highest landings on record. Often there was no indication that such levels would be sustainable.

The second most common approach adopted was to calculate yields from the equation:

$$PSY = pB \qquad (3)$$

where PSY = "present sustainable yield"
p = productivity, expressed as a fraction of biomass
B = an estimate of biomass, usually calculated as the mean of doorspread and wingtip estimates derived from aerial expansion of trawl survey data

(Hurst 1985). Productivity, p, was usually assigned values of either 0.05, 0.10 or 0.15 per year. The term PSY has been criticised by Mace (1988). It is unclear whether PSY is a reference point for a TCC strategy or a TCF strategy. If it is intended for use in a TCC strategy, there is nothing to indicate that it will be sustainable beyond the immediate future. In fact, Mace (1988) has shown that the values of p used are probably too high for a TCC strategy, but too low for a TCF strategy.

For new fisheries, yields were calculated from the formulation, $MSY = 0.5MB_0$, where B_0 is virgin biomass (Gulland 1971). Other approaches that were used infrequently include stock reduction analysis, tagging and yield per recruit analysis.

In the two subsequent annual assessments (Baird and McKoy 1986, 1988), there have been few changes made to TAC recommendations. The only substantial changes in methods have been the addition of one new assessment based on an acoustic survey, and one based on a stock production model. FRC is now required to provide annual advice on the management of 31 species, comprising about 170 "stocks" or management units. In most cases, there are insufficient data to determine whether a particular TAC level has had a detrimental impact on a fish stock.

IV. SOME COMPARISONS OF RESULTS

In part, this survey was motivated by the analogy between equations 2 and 3. Productivity, p, in equation 3 can be equated with the reference level of fishing mortality, F_{ref}, from equation 2. Both parameters implicitly depend on the level of natural mortality (M) assumed. p has been assigned values of 0.05, 0.10 or 0.15 depending on whether a stock is expected to have low, medium or high productivity, respectively (Hurst 1985). Most stock assessment agencies would consider that low, medium and high productivity correspond to natural mortality estimates of 0.1 (or less), 0.2, and 0.3 (or more), respectively. This seems to be FRC's approach as well, although the connection has not usually been made explicitly. Consideration of the analogy between p and fishing mortality, the values of p that have been adopted (0.05, 0.10 and 0.15) and their likely correspondence to natural mortality levels leads to the conclusion that:

$$p = F_{ref} = 0.5M \qquad (4)$$

The most common estimates of F_{ref} are $F_{0.1}$ and F_{max} (Section II). Both $F_{0.1}$ and F_{max} are highly sensitive to M (Appendix III). To determine the validity of equation 4, estimates of M, $F_{0.1}$ and F_{max} were compiled for a variety of fish stocks assessed by ICES, CAFSAC and NEFC (Tables 1-3). Other information relevant to productivity and stock status has also been included whenever it was reasonably easy to extract it from the reports. This task was very straightfoward for NEFC, which has adopted an appealing standard format in its reports on the status of fishery resources. Tabulated information includes nominal catches, long term potential catch, status of exploitation, age and size at 50% maturity, M, $F_{0.1}$, F_{max} and $F_{current}$. Graphical data include survey indices and commercial landings or CPUE.

It is obvious from Tables 1-3 that estimates of M are often approximate. It is a difficult parameter to estimate, and may often be inferred from the maximum age, or from empirical relationships between M and other parameters such as the Brody growth coefficient, K. The "default" value of M is 0.2. $F_{0.1}$ is usually at least as large as M (Tables 1-3). It is interesting to note that $F_{0.1}$ values tend to be lower, relative to M, in ICES assessments than they are in CAFSAC and NEFC assessments. This is probably because fish tend to be caught at a lower age (size) in ICES management areas.

The survey (Tables 1-3) indicates that equation 4 gives extremely conservative estimates of reference fishing mortalities.

V. DISCUSSION AND CONCLUSIONS

This survey of stock assessment methods and results cannot be used to evaluate FRC's method of biomass estimation by the aerial expansion method described in equation 3. The agencies surveyed have all substituted VPA for aerial expansion methods of estimating absolute biomass. But since wingtip estimates are often considered to be minimum estimates of biomass (Sissenwine 1988), it seems likely that FRC's usual approach of using the mean of wingtip and doorspread estimates is conservative. It has been suggested that this conclusion could be tested by conducting a survey and analysis of VPA and trawl survey data from stock assessment agencies such as ICES, CAFSAC and NEFC (Sissenwine 1988). Regressions of biomass estimates from VPA on trawl survey catch-per-tow would provide indices of trawl efficiency.

I suggest that FRC should also attempt to develop their own VPA for selected fisheries. This would considerably enhance the credibility of estimates of absolute biomass. The aerial expansion method requires much guesswork about the vulnerability and availability of fish to trawl gear. But if VPA was adopted, several new data collection facilities would need to be established. VPA requires representative sampling and ageing of the commercial catch and the development of a time series of appropriate data for tuning; for example, commercial CPUE, research survey catch-per-tow or indices of larval or juvenile abundance. Annala et al. (1987) have already recommended development of VPA for orange roughy fisheries.

FRC also needs to further develop appropriate biological reference points for use in stock assessments. If productivity, p, in equation 3 is considered as loosely equivalent to some reference level of fishing mortality, F_{ref}, in equation 2, then Tables 1-3 suggest that FRC has been far more conservative than other stock assessment agencies. However, if it is not intended that estimates of biomass be updated periodically, it is possible that yields derived from equation 3 will not be sustainable (Mace 1988).

I suggest that FRC make greater use of the biological reference points, $F_{0.1}$ and F_{max}, from yield per recruit (YPR) analysis. $F_{0.1}$, in particular, is widely accepted as a reference fishing mortality that optimises long term yields. YPR analysis is described in Appendix II. The only data required as input to YPR analysis are natural mortality (M), weights at age, age at recruitment and the number of age classes to be used in the computations. An analysis of the sensitivity of $F_{0.1}$ and F_{max} to these inputs is outlined in Appendix III. Tabulated values of $F_{0.1}$, F_{max}, YPR and biomass per recruit (BPR) are also provided (Appendix III and Tables 4-7). The purpose of these tables is to enable assessment biologists to find approximate values of YPR variables when there are insufficient data to construct individual YPR analyses. A reasonable alternative is to use the approximation, $F_{0.1} = M$, which will generally give somewhat conservative estimates of $F_{0.1}$ (Tables 1-3).

Further development of an appropriate framework for the formulation and computation of biological reference points at FRC is the subject of a second document (Mace 1988).

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APPENDIX I. METHODS FOR ESTIMATING BIOMASS

There are several methods for estimating the biomass of a fish population. Some methods estimate biomass in absolute terms (e.g. biomass in 1988 is 10 000 t), whereas other methods estimate it relative to another point in time (e.g. biomass in 1988 is half of the 1987 level).

Virtual population analysis (VPA)

VPA is a method for estimating absolute population size in numbers by age (Pope 1972). Biomass estimates are calculated by applying estimates of weights at age. The method requires data on the age composition of the entire (commercial and/or recreational) catch over several years (usually 10 or more) and an estimate of the natural mortality rate. If fishing mortality is high relative to natural mortality, VPA results are robust.

VPA is based on the truism that the minimum population size at some time in the past equals the number of fish alive at that time that were eventually caught. Absolute population size is calculated by taking into account the number of fish that have not been caught (i.e. they may have died naturally or they may still be in the sea). The implication is that VPA is only useful for estimating population size historically. VPA is usually combined with a time series of relative abundance data in order to estimate current absolute biomass. The relative biomass estimates are calibrated by comparing them to absolute biomass over the period when VPA estimates are applicable.

A relatively new version of VPA called separable VPA is currently being developed. This is a statistical version of VPA that takes account of the error structure in the model assuming a pattern of exploitation with age that is invariant over time.

Trawl surveys

Trawl surveys randomly sample the density of fish (number or weight per unit area). If all of the fish in the population are available to trawls (i.e. they are in the area sampled by trawls) and their vulnerability (fraction in the path of the net that were caught) is known, then a trawl survey can be used to estimate absolute biomass. This is rarely the case. Trawl surveys are usually used to estimate relative abundance. They can be integrated with VPA to estimate absolute abundance.

Commercial catch per unit effort (CPUE)

Commercial CPUE is also a source of relative abundance data. The assumption is that catch rate is linearly related to population size, which may or may not be true since fisheries do not randomly sample populations. There are many example of non-linear relationships, particularly for fisheries on highly aggregated populations.

Ichthyoplankton surveys

The concentration of ichthyoplankton (eggs or larvae) collected during surveys may be used to estimate the biomass of spawners. Sampling should be random in both time (over the spawning season) and space. In order to estimate the spawning biomass from ichthyoplankton surveys, it is necessary to know the mortality rate of eggs and larvae and the sex ratio and fecundity of adults. If sampling of ichthyoplankton is sufficiently intense and growth rates are known (either from analysis of daily growth rings in otoliths or from laboratory experiments), mortality rate can be estimated from the stage of eggs or the length frequency of larvae. Otherwise, only relative abundance can be estimated and the precision of the index suffers from variability in mortality rate and fecundity. The precision of ichthyoplankton survey estimates of biomass depends on the frequency of sampling during the spawning season.

Acoustics

Acoustic surveys use beams of sound energy transmitted into the water to sample fish. The amount of energy reflected back is related to the number and size of fish that are sampled by the acoustic signal. The most critical information needed to estimate the biomass of fish is the target strength (i.e. the amount of energy reflected by a fish of a specific size). This depends on the species and orientation of the fish.

Tagging

Mark and recapture experiments are also used to estimate the number of fish, although rarely for oceanic populations. Population size is estimated by relating the proportions of fish caught with and without marks. There are many potential sources of bias; e.g immigration or emigration, tag loss, tagging mortality, and incomplete reporting of tag recoveries. There are various methods for correcting for these sources of bias.

APPENDIX II. METHODS FOR ESTIMATING BIOLOGICAL REFERENCE POINTS

Biological reference points can be grouped into categories based on target constant catch (TCC) strategies, target constant fishing mortality (TCF) strategies and target constant biomass (TCB) strategies (Mace 1988). The main biological reference point associated with TCC strategies is the maximum sustainable yield, or MSY. Biological reference points associated with TCF strategies include F_{msy}, $F_{0.1}$, F_{max} F_{rep} and F = M. B_{msy}, the target biomass that maximises long term average yields, is a reference point for TCB strategies.

This section provides brief descriptions of the methods most commonly used to estimate these biological reference points.

TCC strategies

MSY is the only biological reference point of a TCC strategy that will be considered here. The most straightfoward, universal method for calculating MSY yields is based on surplus production (stock production) models (e.g. Schafer 1954, Pella and Tomlinson 1969). These models describe the relationship between surplus production and population biomass. They do not usually consider age structure explicitly. Surplus production is the excess of growth and recruitment over natural mortality. In an unfished stock at equilibrium, growth and recruitment balance natural mortality and there is zero surplus production. This means that it is theoretically impossible to fish a stock while at the same time maintaining it at virgin biomass. Surplus production is created as the stock is fished down. Presumably, as the biomass decreases there is less competition and so productivity increases. This compensatory effect results in surplus production. If biomass is reduced too much, surplus production will begin to decrease. MSY is defined as the maximum surplus production. For the most commonly-used surplus production model (Schafer 1954), MSY occurs at a stock size of $B = 0.5B_0$, where B_0 is the virgin biomass (Figure 1). This assumption has also been used by Gulland (1971) in his suggestion of the use of $0.5MB_0$ as an approximation to MSY. In practice, MSY is usually estimated by fitting models to catch and fishing mortality (F) data, or catch and fishing effort (f) data.

MSY estimates from surplus production models have been criticised on several grounds. The production function is often difficult to determine. A long time series of data is required. In practice, MSY can only be estimated after it has been exceeded at least once. Near the maximum, yield increases relatively little for relatively large increases in effort. This means that economic rent (profit) declines as MSY is approached. Relatively small increases in yield are also accompanied by relatively large decreases in stock biomass. This makes the stock more vulnerable to stochastic environmental effects.

These undesirable effects can be alleviated by taking the more conservative approach of setting yields as some fraction of the deterministic MSY estimated from stock production models. For example, one approach is to adopt as a biological reference point the yield corresponding to two thirds of the effort at the deterministic MSY level (CAFSAC 1987).

<u>TCF strategies</u>

The biological reference points of TCF strategies that will be discussed here are F_{msy}, $F_{0.1}$, F_{max}, F_{rep} and $F = M$.

F_{msy} can be derived from surplus production models as the fishing mortality rate corresponding to the deterministic MSY level. The deterministic F_{msy} may not be sustainable in stochastic stock production models, although it is usually so in stochastic age-structured simulation models. F_{msy} is difficult to estimate when the form of the stock-recruitment relationship is unknown. For this reason, $F_{0.1}$ and F_{max}, the reference points from yield per recruit analysis, are often used as approximations to F_{msy}.

Yield per recruit (YPR) analysis (Thompson and Bell 1934, Beverton and Holt 1957) is derived from a class of models called dynamic pool models. These are age-structured models that describe cohorts or year classes once they have recruited to a fishery. At each age the cohort is subjected to growth, natural mortality and fishing mortality. The yield for a standard number of recruits (usually one) at a specified age can be calculated for various levels of fishing mortality to give a yield per recruit graph (Figure 2). Natural mortality (M), weights at age, the number of age classes to be used in the computations, and the age-related pattern of recruitment to the fishery (e.g. knife-edge recruitment at age 2; (0% before age 2, 100% thereafter); or 50% recruitment at age 2, 100% recruitment for ages 3+) are required as inputs to YPR analysis (Appendix III).

If the YPR curve is dome-shaped (Figure 2a) it is possible to calculate the level of fishing mortality (F_{max}) that results in the maximum yield per recruit. In the (frequent) case where the YPR curve is asymptotic (Figure 2b), F_{max} cannot be defined. Even when F_{max} can be calculated, it is often not used as biological reference point because it ignores the possibility that recruitment may decline with spawning stock size. The sensitivity of yields near F_{max} is similar to the sensitivity of yields near the deterministic MSY level in surplus production models. As F_{max} is approached, large increases in fishing mortality result in relatively small increases in yield per recruit and relatively large decreases in stock size (Figure 2). For this reason the biological reference point preferred by most stock assessment agencies is $F_{0.1}$ (Figure 2), the level of fishing mortality at which the slope of the YPR curve is 1/10 of the slope at F = 0 (no fishing). Although somewhat arbitrary, $F_{0.1}$ has been widely applied as an "optimum" biological target because it results in yields only slightly smaller than F_{max}, maintains higher levels of spawning stock biomass at lower levels of effort, and may be closer to the economic optimum.

The yields corresponding to F_{max} and $F_{0.1}$ can be calculated from the product of YPR and average recruitment. It must, however, be remembered that they are not necessarily good estimates of F_{msy}. Surplus production models implicitly account for the existence of a relationship in which recruitment is dependent on stock size; YPR analysis does not. If recruitment is a monotonically increasing function of stock size, then F_{msy} is always less than F_{max}. If the stock recruitment relationship is dome shaped, F_{msy} may be larger than F_{max}. F_{msy} is often between $F_{0.1}$ and F_{max}, but sometimes even less than $F_{0.1}$ (Mace 1988). Overall, $F_{0.1}$ is probably the better approximation to F_{msy}.

A relatively new reference level of fishing mortality, F_{rep} (F-replacement) (Sissenwine and Shepherd 1987) or, equivalently, F_{med} (F-median) is being developed by some stock assessment agencies, particularly ICES. A simplified description of the procedure for estimating this reference point follows. Spawning stock biomass per recruit (SSB/R) is calculated from YPR analysis for a range of fishing mortality levels. Straight lines with slopes equal to the inverse of these values (i.e. R/SSB) are then superimposed on a plot of R vs. SSB data (Figure 3). The line that bisects the data (equal number of points above and below) is the median. F_{rep} (F_{med}) is simply the calculated fishing mortality corresponding to this line. It represents the level of fishing mortality at which a spawning stock of a given size can be expected to replace itself on average (assuming that the median is a robust estimator of the mean). F_{low} (the 10% percentile) and F_{high} (the 90% percentile) may also be useful reference points in some situations.

F_{rep} can assume a wide range of values relative to $F_{0.1}$ and F_{max} (Table 1). The range depends on the relationship between stock and recruitment and the history of exploitation of the stock. In a lightly exploited stock F_{rep} will probably be low and in a heavily exploited stock it will be high. It is a biological reference point that can be equated with the maximum sustainable fishing mortality rate. For a stock that has persisted despite being fished at levels in excess of F_{msy}, F_{rep} will obviously be larger than F_{msy}. Examination of YPR and SSB/R curves may suggest truncating the data series to obtain estimates of F_{rep} that more nearly approximate F_{msy}, and thus result in increased yields.

The reference point, F = M, is based on the observation that estimates of $F_{0.1}$ are often similar to M (Gulland 1971 and

Tables 1-3). It may be a useful approximation when there are insufficient data to construct individual YPR analyses.

TCB strategies

TCB strategies have often been shown to produce higher long term average yields than either TCC or TCF strategies (Ricker 1958, Reed 1979, Ruppert et al. 1985). They were not used by any of the stock assessment agencies surveyed here.

The target biomass, B_{msy}, of a TCB strategy is usually estimated from a stock recruitment relationship (e.g. Ricker 1954, Beverton and Holt 1957). Stock recruitment models describe the relationship between spawning stock and the number of surviving progeny or recruits they produce. They are generally not age-structured but can be formulated so that they account for such factors as time lags between spawning and recruitment and increases in egg production with fish age or size. The Ricker (1954) stock recruitment relationship can be monotonically increasing or dome shaped (Figure 4); the Beverton-Holt (1957) curve is asymptotic.

A population is at equilibrium when recruits replace spawners. For species that spawn once and die (e.g. Pacific salmon) the replacement line (F = 0) is at 45 degrees to the origin (Figure 4). The population will increase in size at stock levels for which the stock recruitment relationship is above the replacement line, and decrease below it. The maximum equilibrium yield is attained at the level of spawning stock size (B_{msy}) where the distance between the stock recruitment curve and the replacement line is maximised (Figure 4).

In an equilibrium situation, the maximum sustainable yield would be achieved by capturing all fish in excess of B_{msy} prior to spawning, thus ensuring that exactly B_{msy} fish contribute to subsequent recruitment. Due to variability in stock size, the excess of spawners over B_{msy} cannot usually be predicted in advance. One strategy for maximising long term average yields in an uncertain environment is to conduct real-time management based on the appropriate target escapement level. The number of fish already on the spawning grounds and the number yet to arrive are estimated at intervals of several days and the fishery is opened for the appropriate duration to catch the predicted excess. This is essentially the management strategy used for Pacific salmon.

In practice, stock recruitment models usually fit the data very poorly. For many species, there is little evidence of a decline in the number of recruits as spawning stock size decreases. This makes it difficult to obtain good estimates of the optimal target biomass.

APPENDIX III. A SENSITIVITY ANALYSIS OF YIELD PER RECRUIT

The inputs to yield per recruit (YPR) analysis are natural mortality, weights at age, age at recruitment, and the number of age classes to be used in the computations. In the following analyses I used a von Bertalanffy growth function to describe weights at age:

$$w_t = w_\infty (1 - e^{-Kt})^3$$

where t	=	age in integer years
w_t	=	average weight at age t
w_∞	=	average maximum weight
K	=	Brody growth coefficient

To illustrate the sensitivity of the analysis to changes in inputs, I defined a standard cohort with:

w_∞	=	1.0 kg
K	=	0.2
M	=	0.2
A_r	=	age at recruitment = 4
Number of ages	=	20

and then varied each parameter (except w_∞) in turn while holding the others constant. The average maximum weight, w_∞, was not varied because it can be considered simply as a scaling factor.

The sensitivity of $F_{0.1}$, F_{max}, and the corresponding estimates of YPR and biomass per recruit (BPR) to changes in input parameters are illustrated graphically in Figure 5. The important points to note are:

(i) F_{max} is often undefined.

(ii) As F increases from $F_{0.1}$ to F_{max}, relatively small increases in equilibrium yield result in relatively large decreases in equilibrium BPR.

(iii) As M increases, so do both $F_{0.1}$ and F_{max}. At the same time corresponding equilibrium YPR and BPR decrease (Figure 5a). Thus species with higher natural mortality can be fished at higher levels of F, but with lower YPR and BPR. The lower levels of YPR should be offset by higher levels of recruitment per spawner.

(iv) As K and A_r increase, $F_{0.1}$, F_{max}, YPR and BPR all increase (Figures 5b and 5c). Thus species with higher growth rates can be harvested at higher levels of exploitation, as can species where exploitation is restricted to older ages.

(v) As the number of ages used in the analysis increases, $F_{0.1}$, F_{max}, YPR and BPR values all converge (Figure 5d).

YPR analysis does not take account of stock recruitment relationships. If the age of sexual maturity is close to A_r, it may be necessary to reduce fishing mortality in order to conserve spawning stock biomass.

In essence, the age of recruitment acts as a proxy for the amount of growth potential left in a cohort at the time it recruits to a fishery. If fish size is already close to w_∞ there is no point in using conservative fishing mortalities, because at this point M exceeds growth and cohort biomass will be declining. Similarily, if A_r is too high, the YPR at age A_r may be high but the YPR at age 1 will be low.

There has been much debate about the appropriate number of ages to include in YPR calculations (Anthony 1982, Scumacher 1982). Too few age classes results in overestimation of $F_{0.1}$ and F_{max}, and underestimation of YPR at particular F values (ICES 1983). Anthony (1982) suggested that the oldest age considered should that age at which 5% of the initial population numbers would survive under conditions of zero exploitation. This translates into calculating the number of ages from the formula 3.0/M. It has subsequently been recommended for use by the ICES working group on methods of fish stock assessment (ICES 1983). The ICES working group concluded that most of their assessments used too few age groups.

This recommendation on the use of 3.0/M to determine the number of ages for YPR analysis has been adopted for the preparation of tables giving $F_{0.1}$, F_{max}, YPR and BPR values for various combinations of M, K and A_r (Tables 4-7). The purpose of these tables is to enable assessment biologists to find approximate values of YPR variables given what is known or assumed about natural mortality and growth. A value of w_∞ = 1.0 kg was used in all tables. $F_{0.1}$ and F_{max} are independent of the the value of w_∞, whereas YPR and BPR values should be multiplied by w_∞. Greater accuracy can be achieved through use of empirical weights at age and an age-specific partial recruitment vector (instead of the knife-edge recruitment assumption used in the tables).

REFERENCES

Annala, J.H., P. Breen, P. Henriques, P.M. Mace and K. Sullivan. 1987. Report of the working group on stock assessment and monitoring data needs. Unpublished report, Fisheries Research Centre, Ministry of Agriculture and Fisheries, New Zealand. 127 pp.

Anthony, V. 1982. The calculation of $F_{0.1}$: a plea for standardisation. Northwest Atlantic Fisheries Organisation Scientific Document 82/VI/64.

Baird, G.G. and J.L. McKoy. 1986. (comps. and eds.) Background Papers for the Total Allowable Catch Recommendations for the 1986-87 New Zealand Fishing Year. Fisheries Research Centre, Ministry of Agriculture and Fisheries, New Zealand. 177 pp.

Baird, G.G. and J.L. McKoy. 1988. (comps. and eds.) Papers from the Workshop to Review Fish Stock Assessments for the 1987-88 New Zealand Fishing Year. Fisheries Research Centre, Ministry of Agriculture and Fisheries, New Zealand. 300 pp.

Beverton, R.J.H. and S.J. Holt. 1957. On the Dynamics of Exploited Fish Populations. Fisheries Investigations of the Ministry of Agriculture, Fisheries and Food (G.B.), Series II, 19. 533 pp.

CAFSAC 1987. Canadian Atlantic Fisheries Scientific Advisory Committee Annual Report. Department of Fisheries and Oceans, Halifax, Canada.

Colman, J.A., J.L. McKoy and G.G. Baird. 1985. (comps. and eds.) Background Papers for the 1985 Total Allowable Catch Recommendations. Fisheries Research Division, Ministry of Agriculture and Fisheries, New Zealand. 259 pp.

Getz, W.M., R.C. Francis and G.L. Swartzman. 1987. On managing variable marine fisheries. Canadian Journal of Fisheries and Aquatic Sciences 44: 1370-1375.

Gulland, J.A. 1971 (comp.). The Fish Resources of the Ocean. West Byfleet, Surrey, Fishing News (Books) Ltd., for the Food and Agriculture Organisation (FAO). 255 pp. (Revised edition of Food and Agriculture Fisheries Technical Paper (97): 425 pp, 1970).

Hurst, R.J. 1985. Estimation of yields from trawl survey data. pp 9-10 in J.A. Colman, J.L. McKoy and G.G. Baird (comps. and eds.): Background Papers for the 1985 Total Allowable Catch Recommendations. Fisheries Research Division, Ministry of Agriculture and Fisheries, New Zealand. 259 pp.

ICES 1983. Report of the working group on methods of fish stock assessment. International Council for the Exploration of the Sea C.M. 1983/Assess: 17.

ICES 1987. Reports of the ICES Advisory Committee on Fishery Management, 1986. International Council for the Exploration of the Sea Cooperative Research Report No 146. 388 pp.

Mace, P.M. 1988. The relevance of MSY and other biological reference points to stock assessments in NZ. New Zealand Fisheries Assessment Research Document 88/6. 42 pp.

NEFC 1986. Status of the Fishery Resources off the Northeastern United States for 1986. National Oceanic and Atmospheric Administration Technical Memorandum NMFS - F/NEC-43, USA. 130 pp.

Pella, J.J. and P.K. Tomlinson. 1969. A generalised stock production model. Bulletin of the Inter-American Tropical Tuna Commission 13: 419-496.

Pope, J.G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. International Commission for Northwest Atlantic Fisheries Research Bulletin 9: 65-74.

Reed, W.J. 1979. Optimal escapement levels in stochastic and deterministic harvesting models. Journal of Environmental Economics and Management 6: 350-363.

Ricker, W.E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11: 559-623.

Ricker, W.E. 1958. Maximum sustained yields from fluctuating environments and mixed stocks. Journal of the Fisheries Research Board of Canada 15: 991-1006.

Ruppert, D., R.L. Reish, R.B. Deriso and R.J. Carroll. 1985. A stochastic population model for managing the Atlantic menhaden (Brevoortia tyrannus) fishery and assessing managerial risks. Canadian Journal of Fisheries and Aquatic Sciences 42: 1371-1379.

Schaefer, M.B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Bulletin of the Inter-American Tropical Tuna Commission 1(2): 27-56.

Sissenwine, M.P. 1988. Vulnerability and availability of fish to trawls. New Zealand Ministry of Agriculture and Fisheries. New Zealand Fisheries Assessment Research Document 88/2. 3 pp.

Sissenwine, M.P. and J.G. Shepherd. 1987. An alternative perspective on recruitment overfishing and biological reference points. Canadian Journal of Fisheries and Aquatic Sciences 44: 913-918.

Thompson, W.F. and F.H. Bell 1934. Biological statistics of the Pacific halibut fishery. 2. Effects of changes in intensity upon total yield and yield per unit of gear. Report of the International Fisheries (Pacific Halibut) Commission 8. 49 pp.

TABLE 1. Estimates of parameters related to stock productivity for ICES fish stocks. The fishing mortality estimates $F_{0.1}$, F_{max} and F_{85} (the most recent estimate of F) were extracted from ICES (1987). This document did not include estimates of natural mortality (M), which were obtained from Beddington and Cooke's (1983) Table 2 and K. J. Sullivan (FRC, pers. comm.), and may not be identical to the estimates used in the yield per recruit analyses. Estimates of F_{med} were obtained from unpublished summaries of recent ICES assessments (F. M. Serchuk, NEFC, pers. comm.).

Stock/Region	M	$F_{0.1}$	F_{max}	F_{85}	F_{med}(1986)
Cod (*Gadus morhua*)					
N.E. Arctic	0.20	0.15	0.32	0.55	-
Farce Plateau	0.20	0.19	0.42	0.57	-
Kattegat	0.20	?	0.34	1.26	-
Skagerrat	0.20	?	0.26	0.96	-
North Sea	0.20	0.11	0.18	1.00	0.65
West of Scotland	0.20	0.14	0.25	0.72	0.60
Irish Sea	0.20	0.17	0.28	0.57	0.60
Celtic Sea	0.20	0.16	0.25	0.46	0.38
Baltic, Subdiv 22,24	0.20	0.13	0.20	1.07	-
Baltic, Subdiv 25-32	0.20	0.21	0.59	0.84	-
Haddock (*Melanogrammus aeglefinus*)					
N.E. Artic	0.20	0.15	0.30	0.20	-
Faroe	0.20	0.23	0.63	0.39	-
North Sea	0.20	0.21	0.34	1.08	0.80
West of Scotland	0.20	0.18	0.26	0.90	-
Saithe (*Pollachius virens*)					
N.E. Arctic	0.20	0.18	0.31	0.37	-
Iceland	0.20	0.15	0.57	0.32	-
Faroe	0.20	0.19	0.41	0.56	-
North Sea	0.20	0.18	0.29	0.69	-
West of Scotland	0.20	0.14	0.23	0.54	-
Whiting (*Melangius merlangus*)					
North Sea	0.20	0.23	0.67	0.74	1.20
West of Scotland	0.20	?	?	0.49	-
Irish Sea	0.20	0.22	?	1.12	0.90
Greenland Halibut (*Hippoglossus hippoglossus*)	?	0.17	?	0.46	-
Plaice (*Pleuronectes platessa*)					
Irish Sea		0.11	0.25	0.45	0.39
North Sea	0.10	0.13	0.25	0.51	-
Sole (*Solea vulgaris*)					
Celtic Sea	0.10	0.16	0.30	$>F_{max}$	0.20
North Sea	0.10	0.14	0.28	0.61	-
Div VIId	0.10	0.15	0.31	0.26	-
Golden redfish (*Sebastes marinus*)					
Subareas V & XIV	0.05?	0.03	0.08	0.19	-

TABLE 1. continued

Stock/Region	M	$F_{0.1}$	F_{max}	F_{85}	F_{med} (1986)
Herring (*Clupea harengus*)					
Iceland (spring spawners)	0.10	0.22	?	0.16	-
Iceland (summer spawners)	0.10	0.22	0.50	0.24	-
Norwegian	0.16	0.18	?	0.13	-
North Sea Div IVa & b	0.10	0.12-0.14	0.26-0.44	0.38	0.35
North Sea Div IVc & VIId	0.10	0.14	?	0.63	-
Div IIIa		0.32	0.68	0.86	-
West of Scotland	0.20	0.14	?	0.21	0.28
Clyde		0.14	?	0.15	-
Div VIa & VIIb,c		0.16	?	0.40	0.18
Baltic Subdiv 22-24		0.32	0.68	0.86	-
Baltic Subdiv 25-27		0.20	?	0.14	-
Baltic Subdiv 28,29s		0.24	?	0.43	-
Baltic Subdiv 29NE & 30E		0.17	?	0.20	-
Baltic Subdiv 31E		0.18	?	0.22	-
Baltic Subdiv 32		0.20	?	0.39	-
Sardine (*Sardinia pilchardus*)					
Div VIIIc & IXa		0.52	?	0.40	-
Mackerel (*Scomber scombrus*)					
North Sea	0.15	0.18	0.47	0.85	-
Western	0.15	0.18	0.47	0.31	0.14

TABLE 2. Estimates of parameters related to stock productivity for CAFSAC fish stocks. All estimates were extracted from CAFSAC (1987). F_{85} refers to the most recent estimate of fishing mortality (1985).

Stock/Region	M	Approx. age at 50% recruitment (years)	Approx. weight at 50% recruitment (kg)	$F_{0.1}$	F_{max}	F_{85}
Cod (*Gadus morhua*)						
4R, 4S, 3Pn	0.20	6	1.4	0.20	?	0.40
4Vn, 4T	0.20	6	?	0.20	?	0.40
4Vs, 4W	0.20	4	1.0	0.20	0.33	0.30
4X	0.20	3	1.4	0.20	0.29	0.40
5Z,6	0.20	2	1.4	0.15	?	0.45
2J,3K,3L	0.20	?	?	0.20	?	?
Haddock (*Melanogrammus aeglefinus*)						
4VW	0.20	4	0.7	0.25	?	0.40-0.60
4X	0.20	4-5	1.0-1.4	0.25	?	0.38
4TVW	0.20	5	1.0	0.21	?	1.00
5Z	0.20	2	1.0	0.26	?	0.50
Redfish (*Sebastes* sp.)						
4RST	0.10	12-13	?	0.10	?	0.08
American Plaice (*Hippoglossoides platessoides*)						
4T	0.20	~10	?	0.30	?	0.40

TABLE 2. continued

Stock/Region	M	Approx. age at 50% recruitment (years)	Approx. weight at 50% recruitment (kg)	$F_{0.1}$	F_{max}	F_{85}
Witch Flounder (*Glyptocephalus cynoglossus*)						
2J,3K,3L	0.20	?	?	0.35	?	0.81
Pollock (*Pollachius virens*)						
4V,4W,4X,5	0.20	4	1.9	0.28	?	0.55
White hake (*Urophycis tenuis*)						
4T	?	5	2.0	0.32	?	0.40
Herring (*Clupea harengus*)						
4WX	0.20	3	0.1	0.30	?	0.25
4T	0.20	3-4	0.2	0.30	?	0.25-0.30
4R	0.20	5-6	0.3	0.30	?	0.15-0.35
Mackerel (*Scomber scombrus*)						
3-6	0.30	?	?	0.41	?	<0.10
Arctic Charr						
Labrador:Nain	0.20	8	1.8	0.40	?	0.45
Voisey	0.20	8	2.1	0.40	?	0.45
Okak	0.20	9	2.0	0.40	?	0.45

TABLE 2. continued

Stock/Region	M	Approx. age at 50% recruitment (years)	Approx. weight at 50% recruitment (kg)	$F_{0.1}$	F_{max}	F_{85}
Alewife (*Alosa* sp)						
Miramichi River, NB	0.20	3	?	0.45	?	2-3 x $F_{0.1}$
Margaree River, NS	0.20	4	?	0.42	?	2 x $F_{0.1}$
Scallops (*Placopecten magellanicus*)						
Georges Bank	0.10	4	?	0.46	0.70	1.20

TABLE 3. Estimates of parameters related to stock productivity for NEFC fish stocks. All estimates were extracted from NEFC (1986). F_{85} refers to the most recent estimate of fishing mortality (1985).

Stock/Region	M	Age at 50% maturity (years)	Size at 50% maturity (cm)	$F_{0.1}$	F_{max}	F_{85}
Cod (*Gadus morhua*)						
Gulf of Maine	0.20	4	50-54	0.16	0.30	≥0.80
Georges Bank & South	0.20	3	44-52	0.15	0.30	≥0.65
Haddock (*Melanogrammus aeglefinus*)						
Gulf of Maine	0.20	2	38	0.26	0.55	$>F_{max}$
Georges Bank	0.20	2	38	0.26	0.55	$>F_{max}$
Redfish (*Sebastes* sp.)						
Gulf of Maine & Georges	0.05	8-9	22-23	0.07	0.14	0.17
Silver Hake (*Merluccius bilinearis*)						
Gulf of Maine-N.Georges	0.40	2	24-25	0.44	>2.00	?
S. Georges-mid Atlantic	0.40	2	25-26	0.43	>2.00	?
Red Hake (*Urophycis chuss*)						
Gulf of Maine-N.Georges	0.40	2	28	?	>2.00	?
S. Georges- mid Atlantic	0.40	2	28	?	>2.00	?
Pollock (*Pollachius virens*)						
Gulf of Maine-Georges	0.20	4	50	0.19	0.45	0.34

TABLE 3. continued

Stock/Region	M	Age at 50% maturity (years)	Size at 50% maturity (cm)	$F_{0.1}$	F_{max}	F_{85}
Yellowtail Flounder (*Limanda ferruginea*)						
Georges Bank	0.20	2	26	0.30	0.50	$>F_{max}$
S. New England-mid Atlantic	0.20	2	26	0.30	0.50	$>F_{max}$
Summer Flounder (*Paralichthys dentatus*)						
Georges-mid Atlantic	0.20	2	32	0.16	0.19	?
American Plaice (*Hippoglossoides platessoides*)						
Gulf of Maine-Georges	0.20	3-4	26-30	0.17	0.34	?
Scup (*Stenotomus chyrysops*)						
S. New England-mid Atlantic	0.20	2	21	0.20	0.35	?
Tilefish (*Lopholatius chamaeleonticeps*)						
Georges-mid Atlantic	0.15	5-8	55-65	0.17	0.27	?
Herring (*Clupea harengus*)						
Gulf of Maine	0.20	3	26	0.24	?	0.40
Georges	0.20	3	26	0.36	?	<0.01
Mackerel (*Scomber scombrus*)						
Labrador-North Carolina	0.20	2	33	0.29	0.62	0.05

TABLE 3. continued

Stock/Region	M	Age at 50% maturity (years)	Size at 50% maturity (cm)	$F_{0.1}$	F_{max}	F_{85}
Butterfish (*Perilus triacanthus*)						
Gulf of Maine-mid Atlantic	0.80	1.5	14	1.60	>2.50	?
Black Sea Bass (*Centropristis striata*)						
Gulf of Maine-mid Atlantic	0.30	3	27	0.20	0.30	?
Skates (*Raja* sp.)						
Gulf of Maine-mid Atlantic	0.40	4	40	0.49	1.00	?
American Lobster (*Homarus americanus*)						
Gulf of Maine-mid Atlantic	0.10	?	10	?	0.18-0.23	$>F_{max}$
Ocean Quahogs (*Arctica islandica*)						
New England-mid Atlantic	0.01-0.10	8-11	5	?	0.03-0.05	<0.10
Sea Scallops (*Placopecten magellanicus*)						
Gulf of Maine	0.10	?	?	0.14	0.22	$>F_{max}$
Georges Bank	0.10	3-4	60-90	0.15	0.26	$>F_{max}$
mid Atlantic	0.10	3-4	60-90	0.14	0.25	$>F_{max}$

TABLE 4. Fishing mortality (F), yield per recruit (YPR) and biomass per recruit (BPR) calculations for two points on the yield per recruit curve (slope 0.1 of that at the origin; maximum YPR) for various combinations of the Brody growth coefficient (K) and age of recruitment (A_r), with w_∞ = 1 kg, natural mortality M = 0.05 and 60 age classes.

			0.1			max		
			F	YPR	BPR	F	YPR	BPR
K = .1	A_r =	1	0.036	0.124	3.450	0.051	0.130	2.577
		2	0.037	0.138	3.719	0.054	0.144	2.652
		3	0.039	0.153	3.887	0.059	0.160	2.711
		4	0.042	0.169	4.051	0.065	0.178	2.750
		5	0.044	0.187	4.211	0.072	0.198	2.765
		6	0.047	0.206	4.363	0.080	0.220	2.753
		7	0.051	0.226	4.507	0.090	0.243	2.713
		8	0.053	0.247	4.642	0.101	0.270	2.642
		9	0.056	0.269	4.767	0.116	0.294	2.541
		10	0.060	0.291	4.883	0.134	0.322	2.410
K = .2	A_r =	1	0.046	0.235	5.094	0.071	0.248	3.492
		2	0.050	0.264	5.281	0.081	0.281	3.477
		3	0.055	0.297	5.447	0.094	0.318	3.397
		4	0.060	0.333	5.589	0.111	0.361	3.246
		5	0.065	0.369	5.706	0.134	0.406	3.028
		6	0.070	0.406	5.799	0.165	0.453	2.751
		7	0.075	0.441	5.872	0.207	0.502	2.426
		8	0.080	0.475	5.929	0.267	0.551	2.061
		9	0.085	0.505	5.974	0.360	0.599	1.664
		10	0.089	0.533	6.010	0.524	0.646	1.234
K = .3	A_r =	1	0.054	0.310	5.711	0.089	0.330	3.716
		2	0.060	0.353	5.865	0.107	0.381	3.563
		3	0.067	0.401	5.978	0.133	0.438	3.291
		4	0.074	0.448	6.058	0.172	0.501	2.920
		5	0.081	0.493	6.103	0.228	0.564	2.475
		6	0.087	0.533	6.135	0.316	0.623	1.982
		7	0.092	0.567	6.146	0.470	0.687	1.460
		8	0.097	0.595	6.154	0.851	0.744	0.873
		9	0.100	0.618	6.158	-	0.811	-
		10	0.103	0.636	6.160	-	0.858	-

TABLE 5. Fishing mortality (F), yield per recruit (YPR) and biomass per recruit (BPR) calculations for two points on the yield per recruit curve (slope 0.1 of that at the origin; maximum YPR) for various combinations of the Brody growth coefficient (K) and age of recruitment (A_r), with w_∞ = 1 kg, natural mortality M = 0.10 and 30 age classes.

			0.1			max	
		F	YPR	BPR	F	YPR	BPR
K = .1	A_r = 1	0.057	0.053	0.936	0.079	0.055	0.699
	2	0.062	0.064	1.041	0.088	0.067	0.760
	3	0.067	0.077	1.149	0.099	0.081	0.816
	4	0.073	0.092	1.261	0.113	0.097	0.859
	5	0.080	0.110	1.374	0.131	0.117	0.889
	6	0.087	0.130	1.483	0.155	0.139	0.898
	7	0.095	0.151	1.591	0.186	0.164	0.883
	8	0.103	0.174	1.693	0.228	0.192	0.840
	9	0.111	0.199	1.791	0.290	0.222	0.768
	10	0.119	0.225	1.884	0.386	0.256	0.663
K = .2	A_r = 1	0.072	0.131	1.818	0.105	0.137	1.307
	2	0.081	0.161	1.984	0.124	0.169	1.364
	3	0.092	0.197	2.143	0.152	0.209	1.377
	4	0.104	0.237	2.287	0.192	0.256	1.332
	5	0.117	0.281	2.412	0.253	0.309	1.225
	6	0.130	0.326	2.517	0.348	0.367	1.056
	7	0.142	0.370	2.608	0.520	0.429	0.825
	8	0.158	0.413	2.685	1.095	0.494	0.451
	9	0.164	0.452	2.749	-	0.581	-
	10	0.174	0.488	2.803	-	0.646	-
K = .3	A_r = 1	0.085	0.196	2.306	0.129	0.207	1.602
	2	0.099	0.245	2.484	0.163	0.261	1.599
	3	0.115	0.302	2.633	0.219	0.328	1.499
	4	0.132	0.362	2.745	0.310	0.403	1.302
	5	0.149	0.421	2.831	0.477	0.484	1.015
	6	0.164	0.475	2.893	0.925	0.568	0.614
	7	0.177	0.521	2.939	-	0.675	-
	8	0.188	0.560	2.974	-	0.751	-
	9	0.197	0.590	3.000	-	0.811	-
	10	0.204	0.615	3.020	-	0.857	-

TABLE 6. Fishing mortality (F), yield per recruit (YPR) and biomass per recruit (BPR) calculations for two points on the yield per recruit curve (slope 0.1 of that at the origin; maximum YPR) for various combinations of the Brody growth coefficient (K) and age of recruitment (A_r), with W_∞ = 1 kg, natural mortality M = 0.20 and 15 age classes.

			0.1			max		
			F	YPR	BPR	F	YPR	BPR
K = .1	A_r =	1	0.100	0.017	0.172	0.137	0.018	0.130
		2	0.113	0.025	0.218	0.161	0.026	0.160
		3	0.129	0.035	0.269	0.196	0.037	0.187
		4	0.147	0.048	0.326	0.245	0.051	0.208
		5	0.167	0.065	0.385	0.319	0.068	0.212
		6	0.189	0.084	0.446	0.448	0.093	0.207
		7	0.210	0.107	0.507	0.766	0.121	0.158
		8	0.231	0.131	0.568	-	0.167	-
K = .2	A_r =	1	0.119	0.059	0.494	0.168	0.061	0.365
		2	0.141	0.085	0.603	0.214	0.089	0.418
		3	0.168	0.120	0.714	0.291	0.129	0.443
		4	0.200	0.164	0.821	0.430	0.180	0.418
		5	0.233	0.213	0.917	0.768	0.242	0.315
		6	0.264	0.266	1.005	-	0.341	-
		7	0.294	0.318	1.083	-	0.427	-
		8	0.320	0.368	1.152	-	0.507	-
K = .3	A_r =	1	0.137	0.104	0.758	0.199	0.108	0.545
		2	0.169	0.153	0.901	0.277	0.162	0.585
		3	0.210	0.216	1.031	0.431	0.236	0.548
		4	0.253	0.288	1.139	0.841	0.328	0.390
		5	0.293	0.360	1.227	-	0.468	-
		6	0.328	0.426	1.298	-	0.580	-
		7	0.357	0.484	1.353	-	0.674	-
		8	0.380	0.531	1.398	-	0.750	-

TABLE 7. Fishing mortality (F), yield per recruit (YPR) and biomass per recruit (BPR) calculations for two points on the yield per recruit curve (slope 0.1 of that at the origin; maximum YPR) for various combinations of the Brody growth coefficient (K) and age of recruitment (A_r), with w_∞ = 1 kg, natural mortality M = 0.30 and 10 age classes.

			0.1			max		
			F	YPR	BPR	F	YPR	BPR
K = .1	A_r =	1	0.145	0.008	0.055	0.199	0.008	0.042
		2	0.171	0.014	0.079	0.249	0.142	0.057
		3	0.204	0.022	0.109	0.330	0.024	0.071
		4	0.242	0.034	0.142	0.467	0.037	0.080
		5	0.281	0.050	0.179	0.835	0.056	0.067
		6	0.321	0.070	0.219	-	0.092	-
		7	0.359	0.093	0.259	-	0.127	-
K = .2	A_r =	1	0.166	0.033	0.198	0.232	0.034	0.147
		2	0.207	0.056	0.271	0.321	0.060	0.184
		3	0.259	0.091	0.350	0.500	0.098	0.196
		4	0.316	0.136	0.428	1.275	0.153	0.120
		5	0.373	0.188	0.503	-	0.252	-
		6	0.426	0.244	0.573	-	0.340	-
		7	0.471	0.300	0.637	-	0.426	-
K = .3	A_r =	1	0.187	0.065	0.348	0.269	0.068	0.252
		2	0.245	0.112	0.458	0.415	0.119	0.288
		3	0.317	0.178	0.563	0.826	0.199	0.240
		4	0.391	0.256	0.654	-	0.340	-
		5	0.458	0.335	0.732	-	0.467	-
		6	0.511	0.407	0.796	-	0.580	-
		7	0.553	0.469	0.849	-	0.674	-

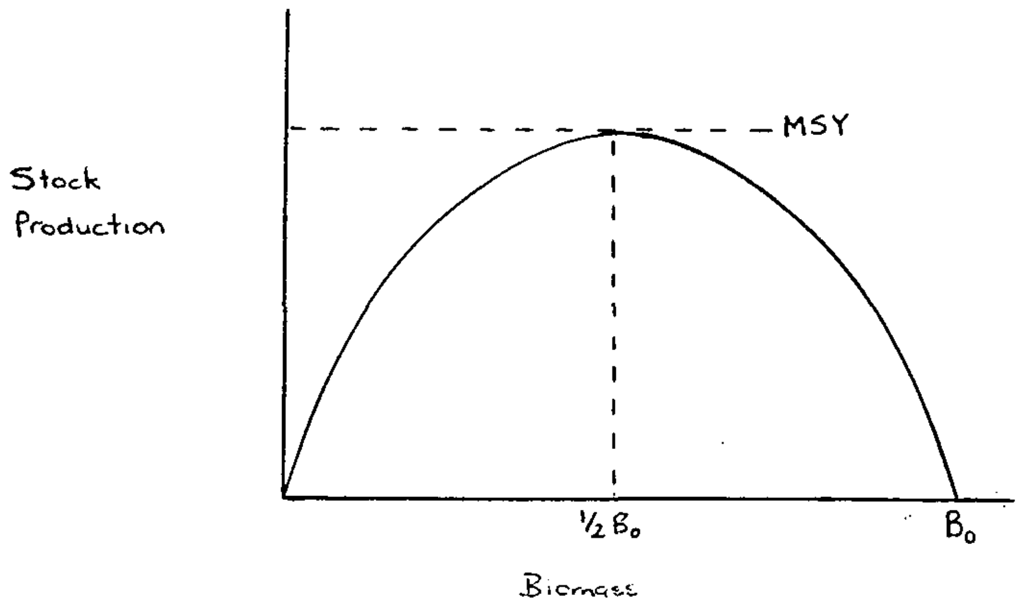

Figure 1. Symmetric surplus production model showing location of MSY.

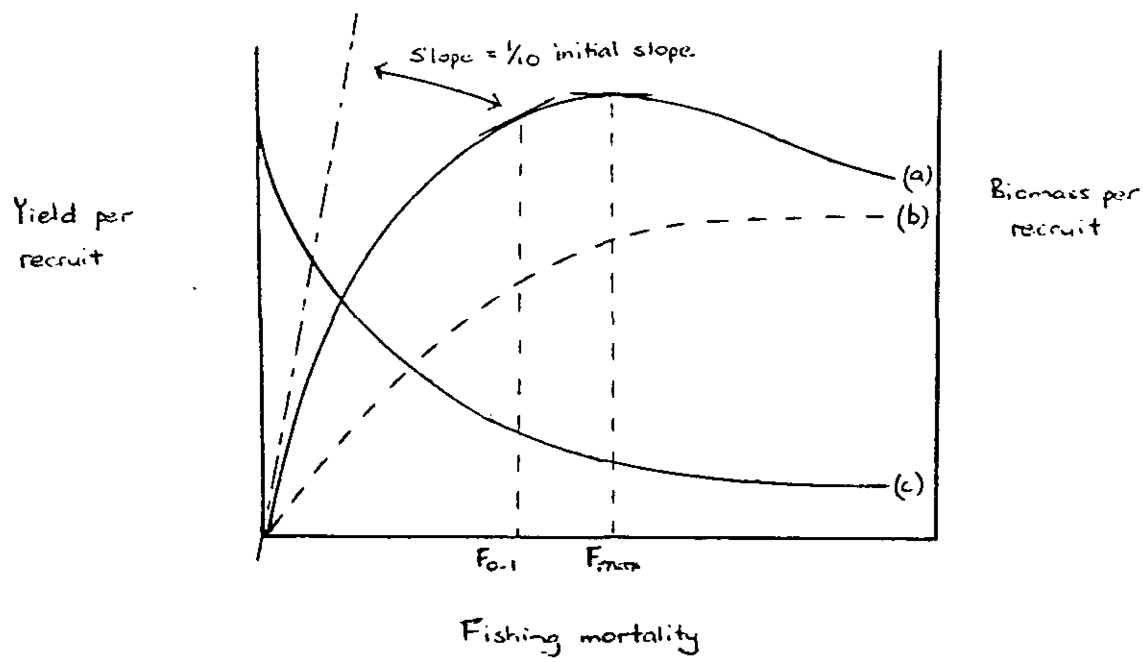

Figure 2. Relationship between yield per recruit and fishing mortality, showing location of $F_{0.1}$ and F_{max} reference points. a) YPR curve with F_{max} defined; b) YPR curve with F_{max} undefined; c) BPR curve corresponding to a).

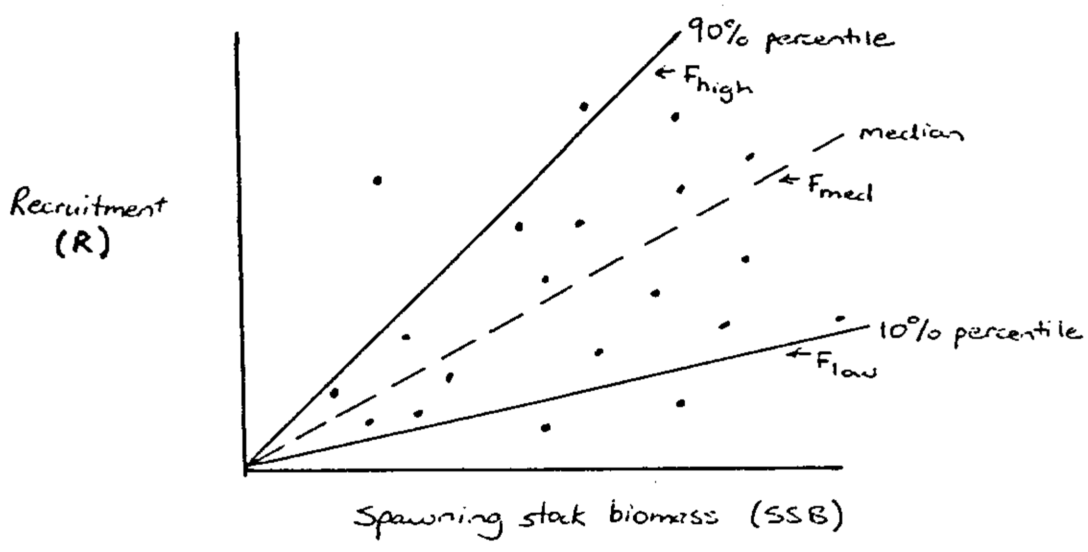

Figure 3. Location of the reference points F_{low}, F_{med} and F_{high} on a spawner-recruit plot. The slope of the straight lines corresponding to these levels of F is R/SSB (the inverse of SSB/R) as calculated from a YPR analysis.

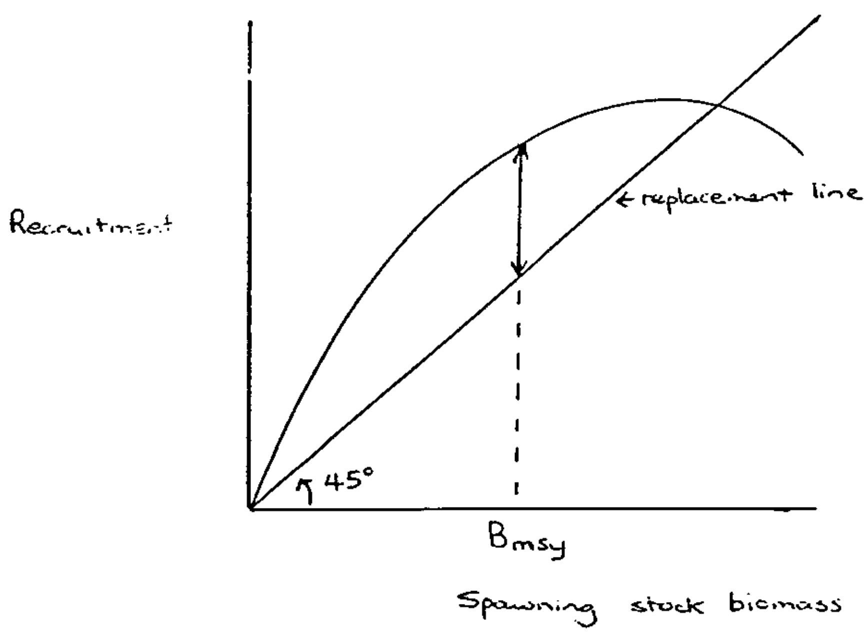

Figure 4. Ricker stock-recruitment curve showing location of optimum spawning stock size, B_{msy}

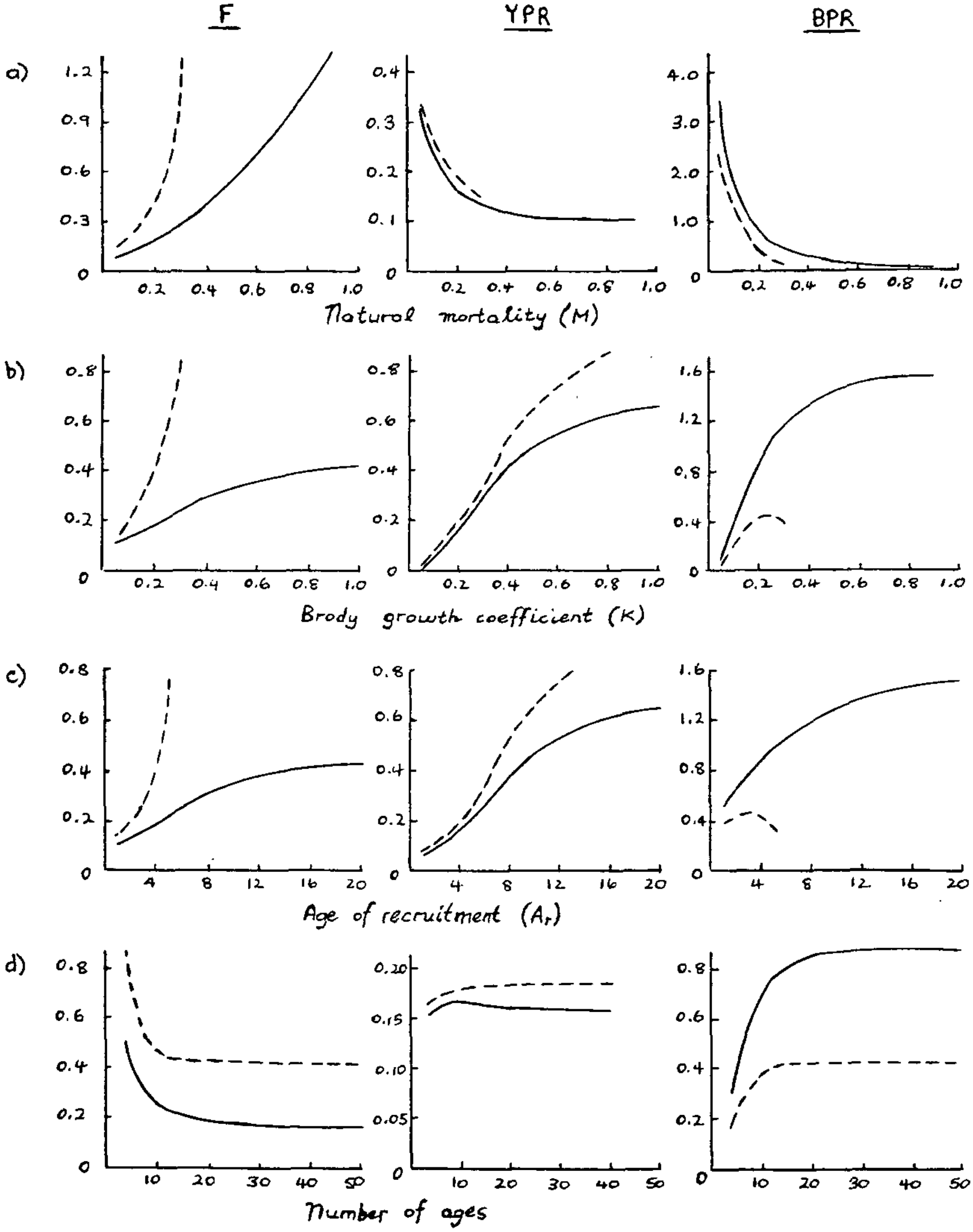

Figure 5. Sensitivity of yield per recruit analysis to a) natural mortality, b) Brody growth coefficient, c) Age of recruitment and d) number of ages used in the analysis. Solid lines represent $F_{0.1}$ and the corresponding YPR and BPR. Dashed lines represent F_{max} and the corresponding YPR and BPR. See text for values assigned to the fixed input parameters (the standard cohort).