

THE LIMITS OF EXPLOITATION: A PRECAUTIONARY APPROACH

R. A. MYERS¹ AND G. MERTZ

*Science Branch, Department of Fisheries and Oceans, P.O. Box 5667,
 St John's, Newfoundland, Canada A1C 5X1*

Abstract. As is well known, the biological limit to the exploitation rate of a fish stock is determined by the maximum per capita reproductive rate and the age selectivity of the fishery. Customarily, the selectivity is treated as fixed when the biological limit to harvesting is estimated. From a precautionary perspective, one should control selectivity. A simple model is used to demonstrate the safety benefits of prohibiting the harvesting of juvenile fish. The model leads to a natural rescaling of the maximum per capita recruitment rate, and it is shown that if this quantity is >1 , then a spawn-at-least-once policy will prevent a collapse of the stock if fishing mortality targets are exceeded. (A spawn-at-least-once policy requires that fish become vulnerable to commercial gear only after having spawned once.)

Key words: age of maturity; age of recruitment; biological limit of exploitation; collapse of fish stocks; exploitation; fishing mortality; mortality; recruitment; reference fishing mortality; Ricker model; spawner; stock–recruitment relationships.

INTRODUCTION

Increasingly, fisheries scientists are emphasizing the utility of management policies that ensure that replacement can be achieved at the observed average recruitment rate or a specified minimum recruitment rate (e.g., Beddington and Cooke 1983, Sissenwine and Shepherd 1987, Gabriel et al. 1989, Jakobsen 1992, Clark 1993, Goodyear 1993, Thompson 1993, Myers et al. 1994, Caddy and Mahon 1995). These studies focus on achieving replacement through the control of fishing mortality, but give less emphasis to the safety benefits of controlling the age of entry into the commercial fishery. We will demonstrate that there is much to be gained, from a precautionary standpoint, by delaying the harvest until after the fish have spawned at least once.

The desirability of delaying harvest until after maturity was recognized by Holt (1895), based on his studies of North Sea plaice (*Pleuronectes platessa*). However, this proposal was eclipsed by theories positing the independence of recruitment and spawner abundance, leading to an emphasis on maximization of the yield from somatic growth (Petersen 1903). We hope to revive interest in the Holt approach, and we will give the first quantitative demonstration of the safety dividends accruing from prohibiting the harvest of juvenile fish.

We will formulate a simple model that permits a ready appreciation of the influence of age of first harvest on the sustainable fishing mortality. It will be assumed that selectivity is knife-edge, but the age of entry into the fishery will be allowed to vary (Beverton and Holt 1957). The model will be used to calculate the limiting (maximum sustainable) fishing mortality, F_r (Mace and Sissenwine 1993, Mace 1994). For reference, the model will be used to calculate the fishing mortality at which observed levels of recruitment permit replacement to be achieved, designated as F_{med} (Sissenwine and Shepherd 1987). Since F_{med} has been suggested as a defensible target fishing mortality (FAO 1993) it is important to compare F_{med} to F_r to establish the margin of safety (which is a function of age at first harvest).

FORMULATION

The limits to sustainable fishing will be expressed in terms of the maximum reproductive rate for the population, or, equivalently, the maximum slope of the stock–recruitment curve, which is realized as the origin (zero stock size) is approached. A sufficiently general relation between recruitment (R) and spawner biomass (S), a proxy for egg production, would take the form

$$R = \alpha S f(S) \quad (1)$$

where α is the slope at the origin, and $f(S)$, assumed to be monotonically decreasing such that $f(0) = 1$, represents density-dependent mortality (Fig. 1). (Note that Myers et al. [1995] found virtually no evidence that the behavior of $f(S)$ is compensatory [rather than monotonically decreasing] for commercially exploited stocks.)

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¹ Present address: Killam Chair in Ocean Studies, Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1.

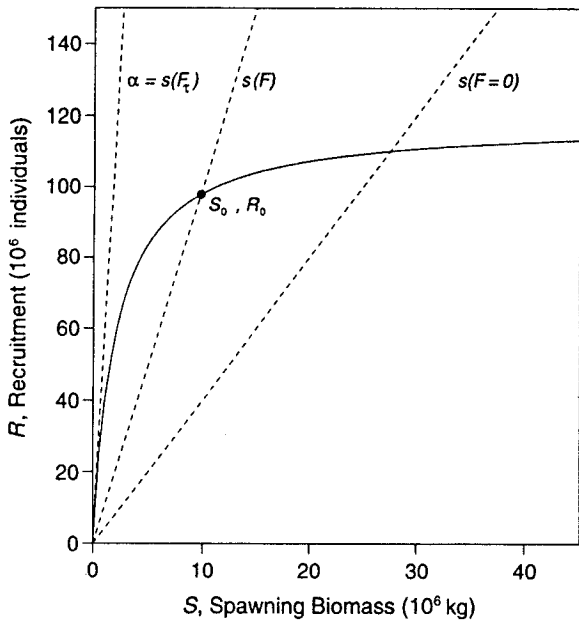


FIG. 1. Recruitment vs. spawning biomass (solid line) and the replacement line (dashed) for three fishing mortalities ($F = 0$; an intermediate value of F ; and $F = F_r$, the limit of sustainable fishing). The equilibrium for the intermediate level of fishing (S_0, R_0) is shown. Units and the curve are typical of a cod or herring population.

This is the standard formulation used in fisheries, but requires some explanation for the general ecologist. First, the units of R and S are different: numbers of fish and biomass, respectively. The reason for this convention is that egg production is usually more closely related to the biomass than the numbers of spawners. The two values are related by the slope at the origin, which gives the number of recruits, typically in 10^6 individuals, per unit of spawning biomass, typically in 10^6 kilograms of spawners. This slope, α , when suitably rescaled, determines the largest fishing mortality that can be sustained in a deterministic equilibrium (stochastic effects will be briefly discussed at the end of the *Results* section). In this section, we explicitly formulate the limiting fishing mortality.

A second point is worth noting for ecologists not familiar with fisheries research: we assume that all density-dependent mortality occurs during the larval or juvenile stage. That is, density-dependent mortality occurs before the fish recruit to the fishery, which will be defined at a_{rec} . This approximation is consistent with most analyses of data for marine fish (Myers and Cadigan 1993). Note that R is the number of fish at age a_{rec} .

For equilibrium, the spawning biomass needed to produce a recruit must equal the spawning biomass yielded by each recruit (SPR_F , where the subscript F indicates dependence on fishing mortality). We designate $s(F)$ as the slope of the line joining the origin and the point of equilibrium in the R, S plane (thus

$s(F) = R_0/S_0$, where the subscripts indicate equilibrium). It follows that the spawning biomass required to produce a recruit is $s(F)^{-1}$ and thus the above stated criterion for equilibrium may be written as $s(F)^{-1} = SPR_F$. This equation can also be expressed as

$$\frac{1}{s(F)} = SPR_F \equiv \sum_{a_{rec}}^{\infty} w_a l_a p_a \quad (2)$$

where we have used Mace's (1994) definition of SPR_F , and where l_a is survival from recruitment to age a (which depends upon F), p_a is the proportion of fish mature at age a , w_a is the mass at age a , and a_{rec} is the age of recruitment. For explicitness, we must state that a_{rec} represents the first age at which abundance can be estimated, and it is also generally the first age at which it is feasible to harvest. However, the age at which fish are first selected for commercial harvest (a_{sel}) may be greater than the age of recruitment ($a_{sel} \geq a_{rec}$ in general) due to restrictions imposed by management policy.

It is helpful to simplify this equation by assuming knife-edge maturity at age a_{mat} (at mass w_{mat}), no growth occurs after maturation ($w_a = w_{mat}$ for $a \geq a_{mat}$), and that natural mortality (M) and fishing mortality (F) are constant for mature fish and rewrite Eq. 2, after summing a geometric series, as

$$\frac{1}{s(F)} = \frac{w_{mat} l_{a_{mat}}}{1 - e^{-(M+F)}} \quad (3)$$

Here, $l_{a_{mat}}$ is survival from a_{rec} to a_{mat} . Note that we have assumed that density-dependent mortality occurs before the fish are recruited to the fishery; e.g., M and $l_{a_{mat}}$ are constants.

Rescaled slope

Equilibrium represents a balance between reproductive and mortality rates. It is natural to express the reproductive rate in per capita terms, analogous to the mortality rates. To this end, consider the product ($l_{a_{mat}} w_{mat} s(F)$); it represents the number of spawners arising in year $t + a_{mat}$ from one fish spawning in year t . For our purposes it is beneficial to factor $l_{a_{mat}}$ into components related to natural (l_{nat}) and fishing mortality ($\gamma(F)$); i.e., $l_{a_{mat}} \equiv l_{nat} \gamma(F)$. The survival before reproduction associated with fishing mortality, $\gamma(F)$, will be equal to 1 if $F = 0$, and will be a monotonically decreasing function of F . We now define $\bar{s}(F) \equiv (l_{nat} w_{mat}) s(F)$, which may be interpreted as the number of spawners arising in year $t + a_{mat}$ from one fish spawning in year t , in the absence of harvesting of juveniles. For computational purposes, it is helpful to recast this in terms of $SPR_{F=0}$ (which is readily obtained for individual stocks from the literature). From Eq. 2, it is easily shown that $w_{mat} l_{nat} = SPR_{F=0} (1 - e^{-M})$ and thus $\bar{s}(F)$ may be written as

$$\bar{s}(F) \equiv (l_{nat} w_{mat}) s(F) = [SPR_{F=0} (1 - e^{-M})] s(F). \quad (4)$$

Note that $s(F_r) = \alpha$ (Fig. 1), and $\bar{s}(F_r) = \bar{\alpha}$, where $\bar{\alpha}$ is defined in accord with Eq. 4.

Completion of formulation

To calculate $\bar{s}(F)$, the number of replacement spawners produced per spawner if fishing does not occur on juveniles, we substitute Eq. 3 into the middle term of Eq. 4 to obtain

$$\bar{s}(F) = \frac{1 - e^{-(M+F)}}{\gamma(F)} \tag{5}$$

For illustration, consider $F = 0$: in this limit we have $\bar{s}(0) = 1 - e^{-M}$, so that each spawner produces $1 - e^{-M}$ replacement spawners per year. Thus, summed over its spawning lifetime (a span of $(1 - e^{-M})^{-1}$), each spawner produces one replacement, as required.

We now allow the age of selection (a_{sel}) to the fishery to vary while maintaining the assumption that the selectivity is knife-edge. Accordingly, $\gamma(F) = \exp[-F(a_{mat} - a_{sel} + 1)]$. (A separate case, $\gamma(F) = 1$ will be presented in *Results*.) It follows that Eq. 5 becomes

$$\bar{s}(F) = e^{F(a_{mat}-a_{sel}+1)}(1 - e^{-(M+F)}) \tag{6}$$

This equation describes equilibrium for the specified level and pattern of fishing.

A number of recent approaches assume that a safe fishing mortality is one that permits replacement to be achieved with the number of recruits per spawner being equal to the observed median of $\bar{s}(F)$. This fishing mortality is usually designated as F_{med} (Sissenwine and Shepherd 1987), it follows from Eq. 6 that it is given by

$$\bar{s}(F_{med}) = e^{F_{med}(a_{mat}-a_{sel}+1)}(1 - e^{-(M+F_{med})}) \tag{7}$$

When the stock is sufficiently depleted that $\bar{s}(F) = \bar{\alpha}$, the equilibrium fishing mortality is the maximum possible that can be imposed on a stock without causing extinction. Mace and Sissenwine (1993) and Mace (1994) have designated this to be F_r , and using Eq. 6 it is given by

$$\bar{\alpha} = e^{F_r(a_{mat}-a_{sel}+1)}(1 - e^{-(M+F_r)}) \tag{8}$$

That is, the biological limit of fishing is given by the scaled slope at the origin, $\bar{\alpha}$, or in ecological terms, the maximum annual reproductive rate.

RESULTS

Two simple analytical results follow from this formulation, and are presented in the next two paragraphs.

If fish in their first year of maturity are not harvested until the completion of the spawning season ($a_{sel} \geq a_{mat} + 1$), then $\gamma(F) = 1$. The equilibrium ((Eq. 5) can then be expressed as

$$e^{-F} = (1 - \bar{s}(F))e^M \tag{9}$$

If $\bar{s}(F) = 1$ at sufficiently large F (which will result in

a low stock size), then an equilibrium with $F = \infty$ is possible. Since $\bar{\alpha}$ is the largest value of $\bar{s}(F)$, it follows that if the criterion $\bar{\alpha} \geq 1$ is met, then the stock will not collapse at any fishing mortality, no matter how high (again, provided that the fish are allowed to spawn at least once before they are harvested). To interpret this result consider the following example: suppose there is no survival after spawning, $F = \infty$, and that $\bar{s}(F = \infty) = 1$. In this case, a fish spawns, then perishes, and this spawning results in exactly one replacement spawner, which in turn spawns once and perishes, and thus the stock endures (despite the extreme fishing mortality).

A second analytically tractable case is that of $a_{sel} = a_{mat}$, corresponding to the selection of fish by the fishery in their first year of maturity, but (unlike the previous case) with harvesting prior to the spawning season. Eqs. 7 and 8 yield

$$\begin{aligned} F_{med} &= \ln(\bar{s}(F_{med}) + e^{-M}) \\ F_r &= \ln(\bar{\alpha} + e^{-M}). \end{aligned} \tag{10}$$

The safety margin, the difference between F_r and F_{med} , is easily calculated from Eq. 10:

$$F_r - F_{med} = \ln(\bar{\alpha} + e^{-M}) - \ln(\bar{s}(F_{med}) + e^{-M}) \tag{11}$$

It is evident that an acceptable separation between F_r and F_{med} requires an appreciable difference between $\ln \bar{\alpha}$ and $\ln \bar{s}(F_{med})$, and $\bar{\alpha}$ must be reasonably large compared to e^{-M} .

The following approximation allows a qualitative appreciation of the dependence of the safety margin on $a_{mat} - a_{sel}$. If F_r and F_{med} are large (say ≥ 1) then the terms $\exp[-(M + F_{med})]$ and $\exp[-(M + F_r)]$ may be dropped in Eqs. 7 and 8, respectively. It is then easily shown that

$$F_r - F_{med} \approx \frac{\ln \bar{\alpha} - \ln \bar{s}(F_{med})}{a_{mat} - a_{sel} + 1} \tag{12}$$

It is evident from this relation that the prospects for safe fishing (requiring a wide gap between F_r and F_{med}) are enhanced by minimizing the difference between a_{mat} and a_{sel} .

Myers et al. 1997b reported $\bar{\alpha}$ values for all the north Atlantic cod (*Gadus morhua*) stocks. With a Ricker fit to the stock recruit data, all stocks were characterized by $\bar{\alpha} > 1$ and the median $\bar{\alpha}$ was ~ 4 . A robust fit, utilizing the median *R/S* ratio of the six points closest to the origin, produced much the same results. These estimates of $\bar{\alpha}$ can be used to investigate the dependence of F_r on $a_{mat} - a_{sel}$ for a typical cod stock. In Fig. 2 we have plotted F_r (from Eq. 8) vs. $a_{mat} - a_{sel}$ for $\bar{\alpha} = 2, 4$, and 8. Although the $\bar{\alpha}$ estimates depend on the fitting technique, the range shown should encompass the true $\bar{\alpha}$ values for the bulk of north Atlantic cod stocks. The range $a_{mat} - a_{rec}$ spans the entire domain of feasible values for north Atlantic cod stocks (slow growing cold water cod stocks may become vulnerable

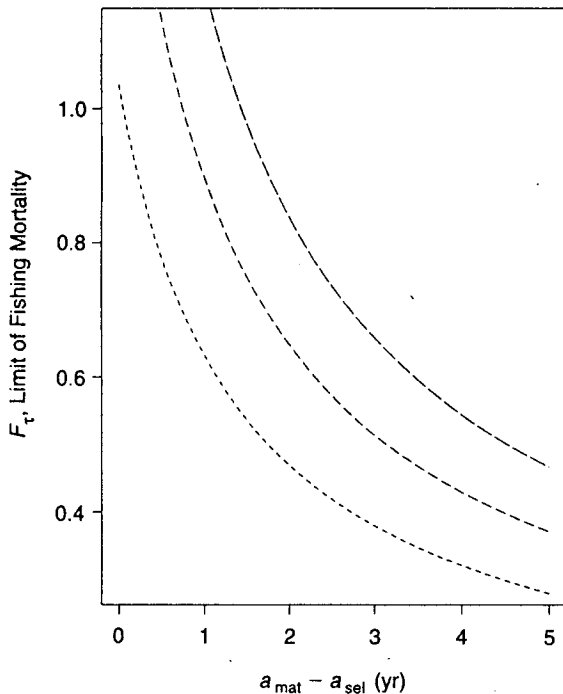


FIG. 2. The biological limit of fishing mortality, F_r , vs. age at maturity minus age at selection to the fishery ($a_{mat} - a_{sel}$) for three levels of $\tilde{\alpha}$ (short dashes, $\tilde{\alpha} = 2$; intermediate dashes, $\tilde{\alpha} = 4$; long dashes, $\tilde{\alpha} = 8$) that bound the values for cod stocks.

to fishing at 3 yr old, while not maturing until they reach 7 or 8 yr old; hence the maximum $a_{mat} - a_{sel}$ value of 5). The message conveyed by Fig. 2 is clear: the maximum sustainable fishing mortality decreases rapidly as $a_{mat} - a_{sel}$ increases, and thus there are obvious safety dividends conferred by insisting that fish not be harvested before they mature.

We have presented a deterministic treatment, which assumes that an average value of the recruitment rate per unit of spawners (estimated from a fit to stock-recruit data) is sufficient to calculate the limits to harvesting. A stochastic treatment would explicitly recognize that recruitment varies about its expected value. The deterministic approach is reasonable when recruitment is not extremely variable and is strongly autocorrelated, so that recruitment will not exhibit protracted excursions away from its expected value (variability and autocorrelation estimates for many of the world's major fish stocks are collated in Myers and Barrowman [1995]). (In fact, this assumption is inherent in the studies of F_{med} and F_r , which are antecedent to this one.)

CONCLUSIONS

Our findings are encapsulated in the following four points.

1) Although there is growing recognition of the need for precautionary approaches to fisheries man-

agement, exactly what measures would be required is seldom made clear. Our analysis permits us to make a concrete recommendation: fish should be permitted to spawn at least once before they become vulnerable to commercial gear. With a spawn-at-least-once policy, there is no extinction threshold (provided that $\tilde{\alpha} \geq 1$) and thus the stock will not collapse if fishing mortality targets are breached.

2) The safety margin—the difference between F_r and F_{med} —is largest when the difference between the age at maturity and the age at selection by the fishery is smallest (Eq. 12). If the spawn-at-least-once policy cannot be imposed, then the next safest strategy is to reduce the selection of younger fish sufficiently to provide a wide gap between F_{med} and F_r .

3) Harvesting at a sustainable rate can, with a small change in age of selection, become unsustainable, leading to commercial extinction of the stock unless remedial action is taken. The likelihood of earlier selection by the fishery will increase as the stock becomes depleted of older fish. This process of the reduction of the age of selection by the fishery as the population collapsed is evident in the collapse of herring (*Clupea harengus*) stocks in the North Pacific (Hourston 1980) and North Atlantic (Saville 1980), walleye (*Stizostedion vitreum*) in Lake Erie (Shuter et al. 1979), and the cod stocks in the Northeast Atlantic (Myers et al. 1997a). Attempts to harvest a constant quota from a declining stock are especially apt to cause increases in selection of younger fish (through alteration of gear or changes in fishing grounds when there is spatial segregation of fish by age). Risk evaluations based on simulations of population trajectories apparently never include this phenomenon, despite the likelihood of its occurrence during stock declines. Realistic evaluations of the risk incurred by employment of a given strategy should not ignore this effect.

4) Populations that can be harvested at a young age and that mature at an old age will be extremely vulnerable to overfishing (Greenland halibut [*Reinhardtius hippoglossoides*], Atlantic bluefin tuna [*Thunnus thynnus*], and some cod stocks fall into this category). The only reported extinction of a marine population by fishing, the elimination of the "common" skate (*Raia batias*) from the Irish Sea, was caused by a by-catch fishery that exposed juvenile skates to a long period of vulnerability, due to the large hatch length (~22 cm; this permitted catches of age zero skates), and late maturity at age 11 (Brander 1981).

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