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Do natural mortality and availability decline with age? An alternative yield paradigm for juvenile fisheries, illustrated by the hake *Merluccius merluccius* fishery in the Mediterranean

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Abstract

The paper explores the apparent contradiction between a high trawling pressure on juveniles and sustained production of hake that has occurred over the last decade in many Mediterranean fisheries. The practical consequences are followed of assuming rapid declines in natural mortality rate M in the first few years of life to a low, constant adult natural mortality, as well as the observation, for small-mesh trawl cod ends, of declining availability with age. Several approaches are proposed for fitting declining M-with-age with a reciprocal function for hake, using criteria based on mean life-time fecundity, mean age at egg production, existing estimates of adult M, and vectors based on stock productivity assumptions. All vectors of M-at-age were similar to MSVPA estimates of North Sea stocks.

The implications of the changes in mortality with age for stocks harvested by fine-mesh trawls were explored in yield per recruit calculations under 2 different hypotheses: 1) using current estimates of growth and adult mortality, 2) M-at-age vectors for juveniles, dropping rapidly from age 0+, and declining availability to trawling for older fish. These hypotheses were compared within yield per recruit analyses. Under the new assumptions, given current F>>M (adults), yield isopleths predict no significant increases in Y/R with stretched mesh > 40 mm, but a substantial decline in fecundity per recruit with small increases in effort by gill nets or longlines, aimed at mature fish. These results are linked to the refugium concept for older fish, and it is speculated that this may be in part responsible for the continued productivity of other sustained fisheries for juvenile resources elsewhere.

Keywords: Natural mortality at age, fecundity, spawners/juveniles, yield modelling, Mediterranean hake, fisheries management.

La disponibilité et la mortalité naturelle diminuent-elles avec l'âge ? Un paradigme du rendement pour les pêches de juvéniles, illustré par la pêche du merlu, Merluccius merluccius, *en Méditerranée.*

Résumé

Cette étude explore la contradiction apparente entre une pression intense de chalutage sur les juvéniles et la production soutenue de merlus, lors de la dernière décennie, ce qui est le cas pour de nombreuses pêcheries de Méditerranée. Les conséquences pratiques en sont un déclin rapide du taux de mortalité naturelle, M, dans les toutes premières années de vie, suivi d'un taux de mortalité naturelle des adultes faible et constant, ainsi que l'observation d'une baisse de la disponibilité avec l'âge avec des petits maillages de culs de chalut.

Plusieurs approches sont proposées pour ajuster la baisse de mortalité naturelle par âge avec une fonction réciproque pour le merlu en utilisant un critère basé sur la durée moyenne de la fécondité, l'âge moyen des reproducteurs, les estimations existantes de la mortalité des adultes et des vecteurs basés sur les estimations

de la productivité du stock. Toutes les mortalités naturelles par âge étaient similaires aux estimations de MSVPA des stocks de mer du Nord. Les conséquences des changements dans la mortalité par âge des stocks exploités par des chaluts de petits maillages ont été étudiées pour les calculs de rendement par recrue sous 2 hypothèses différentes : 1) en utilisant des estimations courantes de croissance et de mortalité des adultes, 2) les vecteurs de M par âge pour les juvéniles augmentant rapidement à partir de l'âge 0 et diminuant dans les captures pour des poissons plus âgés. Ces hypothèses sont comparées dans des analyses de rendement par recrue. Avec ces nouvelles suppositions étant donné- F>>M (adultes), les isoplèthes de rendement ne prédisent pas d'augmentation significative dans le rapport Y/R avec une maille étirée de 40 mm, mais un déclin substantiel dans la fécondité par recrue avec des faibles augmentations de l'effort de pêche (filet maillant ou palangre) utilisé pour les poissons adultes. Ces résultats sont reliés au concept de "refuge" pour les poissons âgés et il est supposé que cela pourrait être responsable de la productivité durable des ressources en juvéniles d'autres stocks et lieux de pêche.

Mots-clés: Mortalité naturelle par âge, fécondité, modèle de rendement, merlu, aménagement des pêches, Méditerranée.

INTRODUCTION

Over the past 15 years, technical consultations in the General Fisheries Council for the Mediterranean have discussed assessment and management of demersal fish stocks in the Mediterranean following the conventional paradigm for analytical assessments described for North Atlantic fisheries by Beverton and Holt (1957). In the North Sea, cod-end mesh sizes are generally in the range 70-100 mm. By analogy, it has been assumed that availability to capture by the trawl is also asymptotic in the Mediterranean; partial availability to capture by ages 1-2, as compared with ages 2-5 for the North Sea.

In the Mediterranean, smaller mesh sizes are still commonly used in the cod-end, which finds an explanation in the high market value of small hake and other incidentally-caught species, (especially high-priced small crustaceans and cephalopods) in the Northern Tyrrhenian Sea and elsewhere in the Mediterranean. Table 1 shows some recent representative prices for hake of different sizes, which illustrates that unit price/kg drops on some markets with increasing size, which is one reason why simple yield modelling can be misleading without taking into account bioeconomic consequences. Hake trawl fisheries are aimed at juveniles (total length at 50 % retention by a 40 mm stretched mesh is of the order of 12 cm: roughly equivalent to age 1 year). Individuals less than 3 years old constitute almost all the commercial trawl catch, nearly 99 % of the Viareggio (North Tyrrhenian Sea) landings (*see* Table 2). Thus, exploitation rates for ages 0+ to at least 3 year hake are high, in contrast to age at first maturity for females of around 5 years, corresponding to Lm_{50} (46 cm total length (Cesarini, 1994). It is difficult to reconcile this situation with the above. Particularly if gear selection were asymptotic, the numbers surviving to maturity after five years in the fishery at peak mortality rates would be very low.

Table 1. – Recent representative Italian prices for hake of different sizes.

Size category (median size) g	Price (Italian liras)/kg	Indicative price (lira) per individual
< 350 g (200 g)	14 000	(1 000/200) × 14 000 = £ 2 800/piece
350-700 g (525 g)	18 000	(1 000/525) × 18 000 = £ 9 450/piece
> 1 kg (1 500 g)	10 000	(1 000/1 500) × 10 000 = £ 15 000/piece

Table 2. – Catch composition of hake by age for the port of Viareggio in year 1995.

Age	Proportion in the catch (%)
0+	69.9
1+	27.8
2+	1.6
3+	0.4
>3+	0.3

Gear selectivity of trawls (predominantly of 40 mm stretched cod end mesh and smaller) means that ages $2\text{-}5^{+}$ hake should be fully represented in the trawl. However, several studies, using: (*a*) variants of length-based cohort analysis based on Jones (1983); (*b*) the MSFLA program used by Aldebert *et al.* (1993); (*c*); the VIT program (Lleonart and Salat, 1992) used by Oliver *et al.* (1990) and Martin (1989), as well as (*d*) the length-based cohort analysis implemented in an EXCEL spreadsheet (this paper), have all illustrated that the availability (and/or vulnerability) of older hake to small-mesh trawl fisheries, drops off with age (Fig. 1).

Comparative fishing experiments with different mesh sizes (mentioned in Caddy 1990), suggest that larger mature fish are less vulnerable to fine mesh gear, or are distributed in areas (*e.g.* the outer shelf and slope) where they are less vulnerable to trawling. From

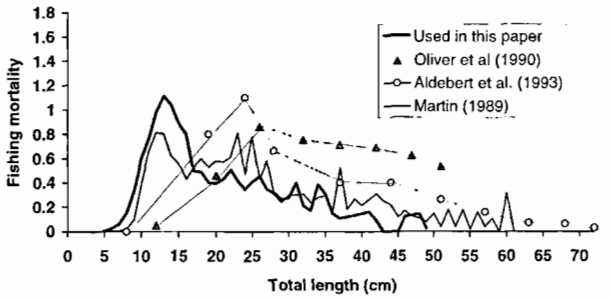

Figure 1. – Estimates of fishing mortality rate by length for hake in Western Mediterranean fisheries, based on 4 independent analyses, showing overall trends in fishing mortality at size (Some results have been converted from F-at-age estimates using the von Bertalanffy growth parameters furnished in the relative papers).

multiple tagging experiments in the Northwest Atlantic, Myers and Hoenig (1997) showed that similar effects occurred there in the past, even at mesh sizes significantly larger than 40 mm.

Studies of other methods of fishing in the Gulf of Lions fishery (Aldebert *et al.*, 1993) and in Southern Spain (Martin, 1989) show that the few older hake surviving to maturity may accumulate with age and constitute a significant spawning potential, and that they are not normally caught in trawls on the shallow shelf. This relatively numerically limited pool of mature fish is however vulnerable to gill nets and long lines; especially along the edge of the shelf and slope. Gillnetting and longlining is practised in the Mediterranean over some slope areas but bottom trawling is currently the only important harvesting technique for hake in the study area and catches with other gear are negligible, unlike in some other areas of the Mediterranean where these methods are expanding in application.

The conventional 'North Sea' paradigm assumes that the fishery is aimed at mature, older fish, and that small fish have no market value, escape through the mesh to survive, or are discarded dead. Yield per recruit and virtual population analysis calculations performed on Mediterranean demersal stocks from the 1970s onwards have also assumed constant M and full availability to the gear from recruitment onwards, and where bioeconomic considerations are included in the calculations, it is assumed that small fish are without market value or are discarded. The lack of validity of these assumptions for most Mediterranean demersal fisheries has already been pointed out in the literature, and summarized in Caddy (1990, 1993).

With respect to the appropriate natural mortality to use in yield modelling, while it has been acceptable to assume constant M-values at age for the North Sea, in the Mediterranean, the effects of higher juvenile natural mortality rates on the available yield have to be considered. This is done in the paper by comparing the North Sea hypothesis of constant M and asymptotic selectivity with the selectivity-mortality situation believed to apply with fine meshed trawl nets common in Mediterranean fisheries.

By first recruitment, the natural mortality rate has usually dropped from high values mainly due to predation by larger fish to a lower, more or less constant annual value, assumed to be of the same order of M = 0.1-0.3 as for the North Sea groundfish; a conclusion in agreement with indirect methods of adult mortality estimation such as that of Pauly (1980).

The situation for North Sea fisheries with respect to the above assumptions, has changed following cooperative ICES studies in the 1980s of stomach contents of the groundfish community (ICES, 1988), leading to so-called MSVPA (Multi-Species Virtual Population Analysis: *e.g.* Gislason and Sparre, 1987). The MSVPA experience as described by Sparholt (1990), is used as a point of reference here, and shows that larger groundfish and other predators on small fish exert much higher natural mortality rates on juveniles than apply for adults of the same species. Given that high research budgets are needed for the detailed stomach sampling studies that underlie MSVPA estimates, these methodologies are not available for many world fisheries, including those in the Mediterranean. There is a need therefore to develop other approaches to obtaining indicative M-vectors for use in yield modelling of juvenile fisheries, which are more realistic than assuming constant M from the 0 + age group onwards.

Estimation of natural mortality rates for adults is possible using classical methods such as Paloheimo (1958), and earlier methods described, for example, in Ricker (1975). To the authors' knowledge, such direct estimates of natural mortality rate have never been made for adult Mediterranean demersal fish, although the assumption has been made by earlier analyses that adult natural mortalities are of the same order of magnitude as for the species outside the Mediterranean. Given that assessments need to be made, there seems no obvious alternative to this assumption, which finds support from similar lifespans for Mediterranean stocks as for the same species outside the Mediterranean. With respect to choosing an appropriate level of natural mortality to use for adult hake, the values in the world literature are summarized in papers within Alheit and Pitcher (1995). In some cases, the difference in growth rate of male and female hake may also be accompanied by a difference in the value of natural mortality rate (*e.g.* Caddy and Defeo, 1995). No such difference has yet been demonstrated for Mediterranean hake, and seems unlikely to be important for juveniles, especially since most of the catch is made well before maturity. For Mediterranean hake, adult values in the range M = 0.1 to 0.3 are routinely used in assessment, apparently largely by analogy with other areas, or are obtained by using empirical formulas such as those in Pauly (1980) and Rikhter and Efanov (1976). As for most other fishery resources elsewhere, current practice is to choose 'suitable' values of M that are compatible with what we know about 'longevity';

(*e.g.* Hoenig *et al.*, 1983), and from this perspective these current values seem reasonable for the adults, but leave the question unanswered of what M-values to use for juveniles. Unfortunately, this constant M assumption is not a sufficient precondition for performing realistic stock assessments for those small-mesh fisheries for juveniles that are common in the Mediterranean, as well as in many tropical areas.

In a study of the limited data available on natural mortality rate at age for a variety of invertebrates and fish, Caddy (1991) showed that a simple reciprocal relationship reasonably describes the decline in natural mortality rate with age to the adult value of M used in assessments of mature fish, and that this function also provides a fairly good fit to the North Sea MSVPA results. This methodology was included as an option in Sparre and Venema (1993) and has been used in Thompson-Bell calculations by Sanders (1995), but several new approaches to fitting this function are provided here that are compatable with life history information.

The general lack of methodologies for assessing natural mortality at age for juvenile groundfish has been a major reason why assessments 'with constant M' have continued to be applied, despite clear evidence from MSVPA, which show that mortality rates typically drop steeply from very high values shortly after hatching, towards a low value for adults, that can reasonably be assumed constant for iteroparous species. Given that direct M estimates for the Mediterranean are lacking, we propose several approaches to obtaining indicative values for natural mortality rate at age that are not incompatible with experience elsewhere and assume the reciprocal M-at-age model proposed in Caddy (1991). To refer to this process as 'fitting the reciprocal model' is to use the word 'fitting' in a loose sense: here we are looking for indicative vectors of M that do not contravene what we know about the life history of hake and other groundfish species, and are ecologically more reasonable than the classic 'constant M' assumption.

In the eastern Mediterranean, landings of hake have been growing almost exponentially over the last two decades. More recently, a positive trend has also been observed in the western Mediterranean. Various reasons have been proposed for this, including improvements in reporting, or a general eutrophication of Mediterranean environments (Caddy, 1993) which may have improved environmental conditions for hake. Rates of mortality due to fishing of age groups targetted by trawlers are much higher than commonly accepted values for the rate of adult natural mortality in the literature.

According to Gulland (1971), assuming the logistic model of population growth, the approximation F≅M applies under MSY conditions although later experience (*e.g.* Caddy and Csirke, 1983; Die and Caddy, in press) has suggested that for some species, F(MSY) can be either significantly higher or lower than adult M. From conventional population dynamic theory, given conventional values of M, and recent F values, it is difficult to avoid the conclusion for Mediterranean hake that *F(MSY) >> adult M*. This must have some validity, since recruitment of juvenile hake to the fishery appears to have significantly increased in the Mediterranean as a whole as illustrated by Figure 2 which shows the trends in landings of hake since 1950 in the Eastern and Western Mediterranean Sea. Spawning potential appears not to have been a constraint over the last 2 decades, although it would be unwise to assume that this conclusion will apply if effort levels continue to rise further, and target mature fish.

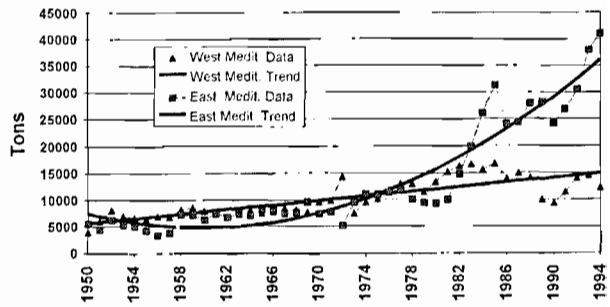

Figure 2. – Trends in recorded landings of hake since 1950 in the Mediterranean ("West trend" and "East trend" show hake landings from GFCM Statistical Divisions 1 and 2 respectively) (FAO, 1993).

MATERIALS AND METHODS

Data

Data central to this study come from the Viareggio and Livorno commercial bottom trawl fleets fishing for hake, and from 22 seasonal trawl surveys in the corresponding area of the Northern Tyrrhenian Sea. A catch assessment survey was performed in 1990-1996 to determine total landings, effort, catch rates and (in Viareggio in 1995), size frequency of the catch. A literature review for which some key references are cited, showed that for growth, selectivity and fecundity, the values derived from these studies are typical of other fisheries for demersal fish, and in particular hake, elsewhere in the Mediterranean. (Oliver *et al.*, 1990; Papaconstantinou *et al.*, 1991; Aldebert .and Recasens, 1995) Finally, 35 years of statistical data on hake landings from the Western and Eastern Mediterranean (FAO, 1993) were utilized.

For species showing divergence of growth rates with sex, M may be different between males and females (Caddy 1984). In the approach developed here we have attempted to develop reasonable natural mortality rates for females and although a divergence in natural mortality rates may occur by sex for some hake species it has not been documented in the Mediterranean. We

feel that using the mortality vectors for both sexes combined in this paper, is probably not misleading for juvenile age groups as a whole, since these make up the large majority of the yield.

Stock assessment models

A comparative approach was adopted in order to test the consequences of conventional versus new assumptions that are, in the authors' opinion, more relevant to Mediterranean hake assessments; these included yield-per-recruit analyses, and Jones (1981) length-cohort analyses based on the 1995 landings, using values for population parameters derived from the data which are compatible with those from the literature. The pseudocohort equilibrium assumptions appeared justified in this case since the fleet size, fishing strategy and level of recruitment have all remained relatively constant in the local fishery in recent years. The two analyses compared were constant M and asymptotic selectivity, against an M vector derived using the method of Caddy (1991) and a selectivity at size relationship derived from the Jones analysis. The results of this analysis were backed up by similar conclusions in the literature which also support a domed selectivity curve at size for small mesh trawls (Oliver *et al.*, 1990; Aldebert and Recasens, 1995, 1996). For the yield per recruit analyses we have chosen to use the values for the von Bertalanffy growth and length -weight relationship given in Abella *et al.* (1995) Parameter estimates were K = 0.185 and L_∞ = 79.1 and for the length/weight relationship, a = 0.0041 and b = 3.192. These values compare well with these reported by Alemany and Oliver, 1995; Aldebert and Recasens. 1995) but imply higher growth rates than earlier studies. Yield per recruit isopleths could have been generated for any of the large number of options for M-at-age and selectivity generated by the above methods but to avoid confusion, and to make more evident the contrast with the conventional approach, yield per recruit isopleths were only constructed for two cases:

1) Making the conventional assumptions of a constant M and assymptotic retention by the trawl (Fig. 3*a*) referred to in the following as the "conventional assumption").

2) Introducing an M vector and F values reflecting an overall declining availability at age, that represent the gradual diminution in natural mortality and gear efficiency over the size range of capture by the trawl; (referred to as the "new hypothesis") (Fig. 3*b*).

The analysis of yield per recruit was carried out using the Thompson-Bell format (Ricker, 1975; Sanders, 1995), with recruits added to the array at age 0.5 (about 9 cm of total length). In both approaches reported here, the effects of increasing size at first capture was approximated to by knife-edged 'slicing' of the length distribution at 5 cm intervals.

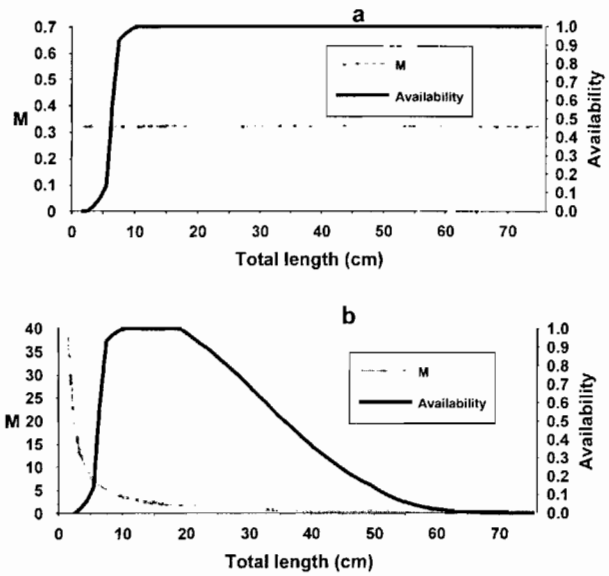

Figure 3. – Illustration of the two assumptions made as to the shape of the vectors of natural mortality, and availability to fishing, compared in the paper: Constant M and asymptotic availability (a) is compared with variable M with age and declining availability at age (b).

Fitting' the reciprocal model for M-at-age

All the methods described in the following sections rest on three assumptions:

1) A common assumption to all methods, namely that the natural mortality rate decline is a reciprocal function of age.

2) Biological assumptions differ between methods (*e.g.* FOREM, BACKM models are based on fecundity considerations, while PROBIOM follows assumptions for productivity.

3) Algorithms described later are applied sequentially to successive size classes or age groups, between age at hatching $t = 0$, and maximum age of commercial importance, t_{max}

Modern spreadsheet packages contain routines for non-linear solving which permit one or more mathematical constraints to be introduced, which need to be satisfied in seeking numerical values for population parameters. These are perfectly suited to solving a multiple set of optima or constraints. In the case in point (table 4) the SOLVER routine in EXCEL 5.0 was used to arrive at vectors of M-at-size or M-at-age following different sets of assumptions.

Changes in mean M-at-age have been represented by $M_t = A + B/t$ (Caddy, 1991), where A was referred to as the asymptotic natural mortality rate but is not equivalent to the conventional adult M value (*see* Caddy, op. cit.), while the parameter B determines the concavity of the curve. Caddy's equation is empirical, and parameter values A and B were first derived as linear regression parameters, fitted directly for those few

cases where several estimates of M_t were available at different ages. The data for such a fitting does not yet exist for Mediterranean fishery resources, hence the simulation approach required here. Regression fits can result in negative values of A and caution must be exercised in the use of this empirical equation for older fish in these cases. The equation will only give positive values for M_t up to a maximum age (t_λ) in the population if the values of A and B obtained satisfy the constraint $A + B/t_\lambda > 0$.

In order to estimate the M values for different life history stages, following Caddy (1991), the mean M was determined for each interval t_1 - t_2 by the integration of $M_t = A + B/t$:

$$M = I(t_2 - t_1) \text{ where:}$$

$$I = \int_{t_1}^{t_2} (A + B/t)dt$$

$$I = \int_{t_1}^{t_2} A \cdot dt + \int_{t_1}^{t_2} (B/t)dt \text{ so that}$$

$$\bar{M} = [1/(t_2 - t_1)][B \ln (t_2/t_1) + A(t_2/t_1)]$$

and finally we obtain:

$$\bar{M} = [B/(t_2 - t_1)] \ln (t_2/t_1) + A \quad (\text{for } t > 0)$$

Parameters of the von Bertalanffy Growth equation, and of the length/weight relationship are known, as noted earlier.

Computations estimate survivals from a cohort expressed as a length frequency which is 'sliced' into constant size classes, but equivalent non-uniform time intervals, using the von Bertalanffy equation:

Due to the nature of the equation used for estimationg the value of mean M, a very short positive time delay has to be imposed in arbitrarily setting the lower limit of the first time interval. This avoids the indeterminate nature of equation 10 of Caddy (1991) when the first time interval starts at time $t = 0$. In practice, this initial time value has no significant influence on the estimates of the A and B parameters.

Otherwise:

$$t = (1/K) \ln (1 - L_t/L_\infty) + t_0$$

All calculations were carried out on a spreadsheet that specifies the following operations for each length interval:

– the time spent to grow from L_{t_1} at the start of an interval to L_{t_2}, the size at the end of the interval:

$$\Delta_t = (t_2 - t_1) = (1/K) \ln [(L_\infty - L_{t_1})/(L_\infty - L_{t_2})]$$

– the number of survivors at the end of the length interval

$$N_{t_2} = N_{t_1} \exp(-M\Delta_t)$$

Program PROBIOM

In order to maintain a stable biomass, overall losses of biomass in the unfished population must be equal to gains in production through the cohort life history. In these computations, the number lost by natural causes is approximated by:

$$D_t = N_t(1 - \exp(-M\Delta_t)) \text{ for all age classes,}$$

the mean individual weight of each class interval is:

$$w_t = [1/(L_{t_2} - L_{t_1})][a/(b+1)][L_{t_2}^{(b+1)} L_{t_1}^{(b+1)}]$$

the biomass lost due to natural mortality between L_{t_1} and L_{t_2} is

$$\Delta B_t = \bar{M}_t \cdot \bar{N}_t w_t \cdot (t_2 - t_1) \text{ for each age class}$$

and the biomass of survivors is calculated as $\bar{B}_t = \bar{N}_t w_t$

The production for each length interval L_{t_1} to L_{t_2} is then calculated as the product of the instantaneous rate of growth $G = (\ln w_{t_2} - \ln w_{t_1})$ and the mean biomass:

$$P_t = G \cdot B_t$$

The overall production (OP) summed over the life history will then be given by:

$$OP = \sum_{t=t_1}^{t_\lambda} P_t$$

where the overall losses in biomass due to natural mortality between the first interval t_1 and the maximum age t_λ, is given by:

$$OBL = \sum_{t=t_1}^{t_\lambda} M_t B_t \Delta_t$$

The estimation of the parameters A and B of the reciprocal M equation are estimated by the SOLVER option of the EXCEL5 spreadsheet, with the goal of obtaining identical values for Overall Biomass Losses (*OBL*) and Overall Production (*OP*).

Programs FOREM and BACKM

Both use the fecundity at length equation from Cesarini (1994):

$$\text{No. eggs} = 2.55\ TL^{3.07}$$

where TL is total length (cm).

Both methods also assume that the population is unfished and at equilibrium, and follow the assumption of Caddy (1991) that one female and one male survive to the Mean Parental Age; MPA, (or equivalent length) from an initial cohort size at age $t = 0$, equivalent to the

Mean Lifetime Fecundity or average egg production throughout life. This is mathematically equivalent to a 1:1 sex ratio to the more conventional assumption that if half of the eggs are female, one female survives to spawn at MPA

In order to estimate the Mean Lifetime Fecundity (MLF) and the Mean Parental Age (MPA), the above mentioned fecundity at age equation for Mediterranean hake (Cesarini, 1994) was utilized. The adult population structure for females was reconstructed from an arbitrary starting number of 1 000 individuals at age of first sexual maturity and assuming a 'seed' value for constant natural mortality rate of 0.2 for the individuals older than the age of maturity. This rate is generally accepted in the literature for adult natural mortality of Mediterranean hake with values in the range M = 0.17 to 0.35 (0.15-0.2 in Aldebert and Recasens, 1995; 0.23 in Dintheer, 1982; 0.165-0.3 in Papaconstantinou *et al.*, 1991; 0.17 in Petrakis *et al.*, 1991). In general, these estimates were obtained by using empirical formulas such as those in Pauly (1980) and Rikhter and Efanov (1976). The 'seed' value of adult M can be changed in order to perform a sensitivity analysis on the impact of this assumption on the final values for MPA and MLF.

The weighted mean age of spawning (MPA) was estimated considering the number of spawners surviving at age. For the estimation of the lifetime fecundity (MLF) both fecundity at age and the number of adults surviving at age have been considered. This is done by summing the eggs produced through a female reproductive life history, between t_m (age at first maturity) and MPA. The mean lifetime fecundity corresponds to the eggs produced on average by a female surviving to maturity. This departure value of "recruits" (eggs) is set at the initial population size for the first class and the program then uses a classical size- or age-subscripted equation for exponential mortality to calculate the number of survivals through each age (length) interval which would result in two survivors at the estimated mean age (length) of reproduction, as a result of changing the values of the A and B parameters of the Caddy (1991) equation. The estimate of mean age at spawning then allowed the estimation of the lifetime fecundity by summing the eggs produced by a female from t_m (age at first maturity) to the mean age of spawning.

The main assumptions and equations used in program FOREM are as described above for PROBIOM. The FOREM approach, as well as BACKM, are based on female life histories, and therefore female growth parameters have been used. As noted earlier, the results of the M vectors obtained by these two methods strictly speaking apply to females, although a similar declining M trajectory is expected for males also. PROBIOM is based on other considerations however, and could in theory allow separate estimation of M_t values by sex if data were available, but as used here, applies to the two sexes combined.

In the case of FOREM, the departure is from the MLF, with the goal of finding an M vector that allows two individuals to survive at the MPA, by changing the values in the cells corresponding to parameters A and B in Caddy (1991). BACKM follows the inverse procedure: departing from 2 surviving individuals at the length equivalent to MPA , it searches for the M vector that generates the estimated MLF. This last method reconstructs the population by back-calculations involving a change in sign of the survival equation.

In order to avoid multiple solutions, some reasonable constraints can be introduced into the computations of any one of the 3 programs described here. For instance, if we have reliable estimates of the natural mortality rate for adults, it is possible to take this into account, and constrain the choice of the A and B parameters by SOLVER, so that the mortality trajectory passes through or close to these values.

The results of the three fitting procedures were compared with estimates of M-at-age for 3 species of North Sea groundfish species; cod, haddock and whiting (from Sparholt, 1990). The values for M's-at-age for these 3 North Sea gadoids were felt to provide a standard for natural survivorship of species which are believed to be similar in the shape of the vector of M-at-age to Mediterranean hake, and to provide a broad standard for interspecies comparison for demersal fish in north-boreal seas.

RESULTS

Fecundity at age relationships for Mediterranean hake

By using the fecundity at length equation and estimates of adult M = 0.2, a mean age at spawning (MPA) of 8 years (or roughly 61 cm TL) was predicted. A corresponding meanlife fecundity (MLF) of 3.182×10^6 eggs was then estimated for each mature individual in the unfished stock. From successive trials, it seems that the sensitivity analysis described earlier is robust which makes the choice of a suitable 'seed value' for adult M not very critical; at least for low values of adult M. Although the estimate of MLF varies with seed M value, any pair of values of MLF and MPA determined on the basis of a reasonably wide range of adult M from 0.05-0.4, gave practically identical results for the parameters of the reciprocal equation (Fig. 4).

Another simulation allowed us to evaluate the sensitivity of the M vector to different input estimates of MLF. Several widely varying values of MLF were tested with only small variations in the resulting M-at-age values, which become less evident at older ages (Fig. 5).

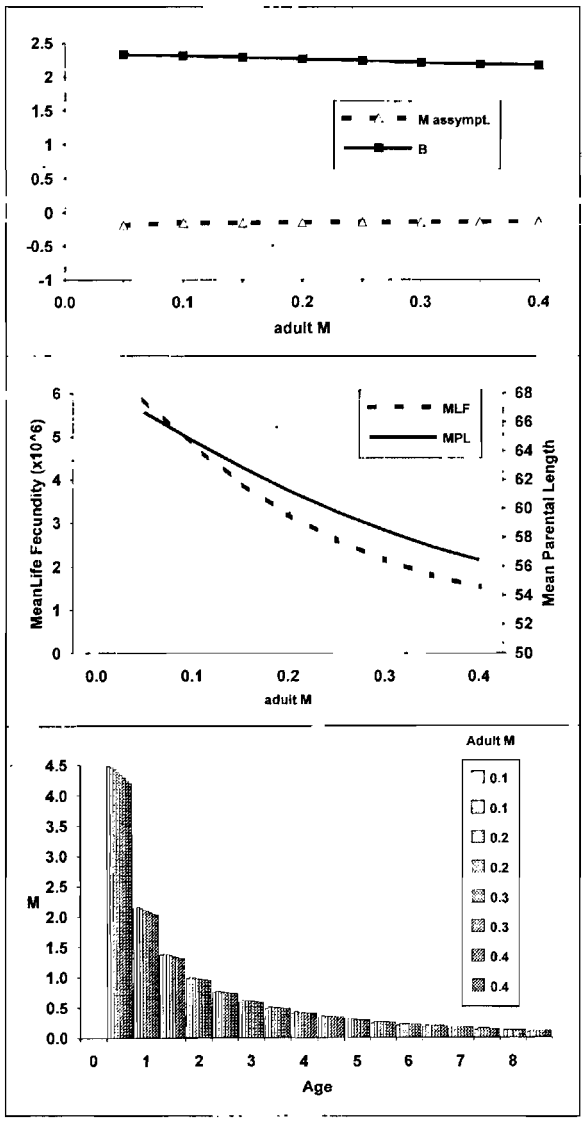

Figure 4. – Sensitivity of the FOREM model to changes in adult M input.

Generating natural mortality at age vectors under different assumptions

The results of the 3 methods of fitting the reciprocal relationship for mortality agree fairly closely with the estimates of *M* for North Sea groundfish derived from the North Sea MSVPA experiments (Fig. 6, Table 3). Even if all the 3 procedures showed similar trends in relative values of natural mortality at age, the fitting with PROBIOM seemed to show the closest correspondence, and was used as a basis for the following yield per recruit analysis.

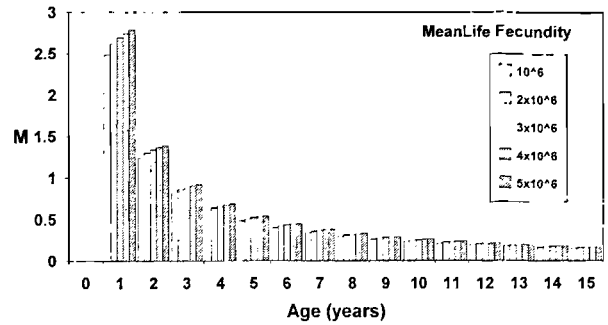

Figure 5. – Sensitivity of the M vector to different input estimates of meanlife fecundity (MLF).

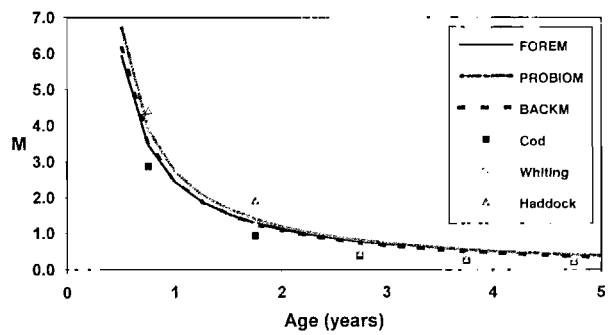

Figure 6. – Comparison of vectors of M estimated with 3 different methods with data for 3 species of North Sea groundfish.

How does yield per recruit vary with Mediterranean selectivity and declining M?

The results of the comparison described in the methods section are shown in Figure 7 respectively, where an approximate point of reference is provided for the current situation where a 40 mm stretched codend mesh is commonly used. Under the "conventional assumption", the optimal mesh size for current mean values of F of around 1.6/year roughly corresponds to 100 mm stretched mesh, assuming a Selection Factor of 3.2 (Jukic and Piccinetti, 1988; Aldebert and Carries, 1990; Oliver *et al.*, 1990). For the "new hypothesis, the optimal mesh size at current fishing mortality rates is much lower; not much different from 40 mm stretched mesh size. For both models, the predicted yield per recruit increases with fishing mortality rate at the optimal L_c (size at knife-edge selection).

The overall value for yield per recruit with the new assumptions is very much smaller than that provided under the "conventional assumption".

Predicted spectra for catch weight and biomass with the two methods

A further comparison was considered useful in illustrating the ecological implications of the two approaches. This was to compare (Fig. 8) the biomass

Table 3. – Results of different fittings of the Caddy (1991) reciprocal equation described in this paper, for three species of North Sea groundfish. Data from Sparholt (1990) and for hake.

Data reported in Sparholt (1990) for M for second half of the year				Overall fitting of Caddy reciprocal equation				Hake		
				Parameters	Cod	Whiting	Haddock	Merged North Sea Groundfish	PROBIOM	FOREM	BACKM
				A	-0.497	-0.522	-0.650	-0.437	-0.153	-0.066	-0.150
				B	2.512	3.521	3.787	3.154	2.493	2.171	2.271
Age (Yrs)	Cod	Whiting	Haddock	Age (Yrs)							
0+	2.86	4.32	4.32	0	2.85	4.17	4.40	3.77	4.83	4.28	4.39
1+	0.93	1.2	1.9	1	0.94	1.49	1.51	1.37	1.51	1.38	1.36
2+	0.36	0.51	0.44	2	0.42	0.76	0.73	0.71	0.84	0.80	0.76
3+	0.23	0.37	0.27	3	0.17	0.42	0.36	0.40	0.56	0.55	0.50
4+		0.29	0.22	4		0.22	0.15	0.23	0.40	0.42	0.35
5+		0.24		5		0.09		0.11	0.30	0.33	0.26
6+		0.22		6		0.00		0.03	0.23	0.27	0.20

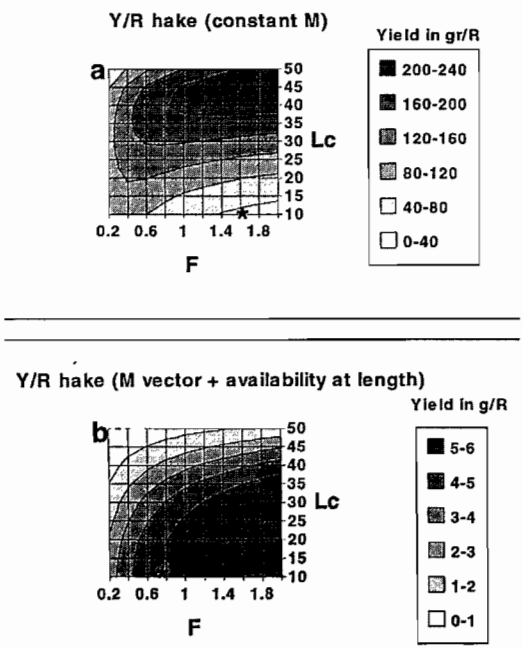

Figure 7. – Yield per recruit isopleths based on the conventional assumptions of a constant M and asymptotic availability (a) and with M and availability declining with age (b). (Lc = mean length of fish at first capture and F= instantaneous rate of fishing mortality).

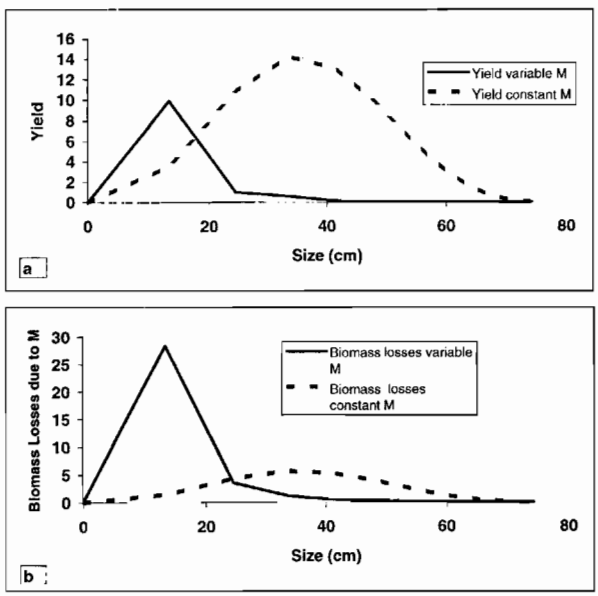

Figure 8. – Predicted spectra of yield (a), and biomass losses due to natural mortality (b) with age and size due to fishing and natural causes on a population of one thousand recruits, under the two hypotheses followed in this paper (var. M = variable M-at-age; const. M = constant M-at-age).

at age and size vectors for both yield and animals dying of natural causes (notably by predation). Under the "conventional assumption, the main contribution by age group to the weight of catch (Fig. 8*b*) is from age 2 fish, and a high contribution is predicted to persist until at least age 3-4. This is of course unrealistic if you examine the typical size and age frequency of Mediterranean hake catches (Fig. 9) using the traditional Italian trawl ("tartana"), and the situation is believed to be similar elsewhere. In contrast, the "new hypothesis" with reciprocal M-at-age and declining availability, shows peak biomass of catch in the first year of life (Fig. 8*a*) dropping rapidly after age 1. This seems to generally fit Mediterranean experience with commercial catches from trawls in shelf areas.

Thus, during almost the whole year, the major component of the commercial catch (nearly 70 %) taken close to Viareggio consists of 0+ age individuals (Table 2) The relative frequency of these individuals under legal size actually landed is much lower of course, because a significant proportion by numbers of the 0+ age are discarded at sea.

The comparison of the biomass vector of natural deaths in Figure 8*b* with the yield vector (Fig. 8*a*) is

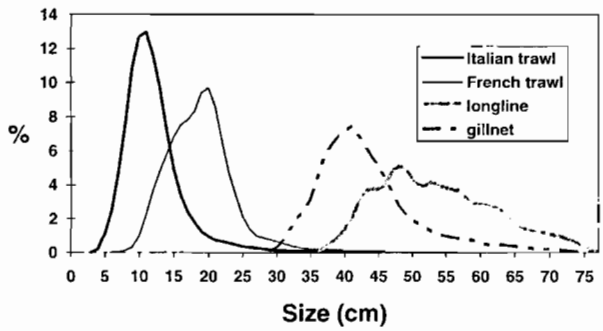

Figure 9. – Characteristic size structure of the catch from the Mediterranean trawl ("tartana"), French trawl ("francese"), longline, and gillnet, for hake.

also revealing: the large majority by number of hake are predicted to be consumed before age 1, fitting what may be expected from a typical 'trophic pyramid'.

What is the ratio of eggs/yield for the constant M and declining M cases?

A detailed comparison of estimations of the biomass per recruit under the different assumptions discussed here was not carried out, but some preliminary results are indicative of the likely effects of size/age selection and fishing mortality if the "new hypothesis" applies. According to these preliminary calculations, there is still a considerable advantage to be gained for hake by increasing mesh size in terms of fecundity per recruit, (and even more so from a reduction in discarding, although this was not investigated explicitly). However, due to the high juvenile mortality rate, the overall numbers of eggs per recruit are much lower than estimated under the constant parameter-asymptotic model (Figs. 10*a*, *b*).

DISCUSSION

This paper has explored the implications of the utilization in yield-per-recruit computations of two different hypotheses for the natural mortality rates at age (a constant value for the species whole life and a vector of *M* based on the above described Caddy reciprocal equation) as well as of the asymptotic or dome-shaped vulnerability-at-age. It is interesting to note, under the conventional assumptions (constant M and asymptotic vulnerability) and the new ones (M vector and dome shaped vulnerability), the quite different results that can be obtained regarding the definition of the current status of the fishery as well as relative to the choice of an optimal combination of fishing mortality rate and mean size at first capture. The Yield-per-recruit analysis made with a "traditional approach" suggests the need of a significant reduction of fishing pressure (to about 50 % of the current level) and a contemporary

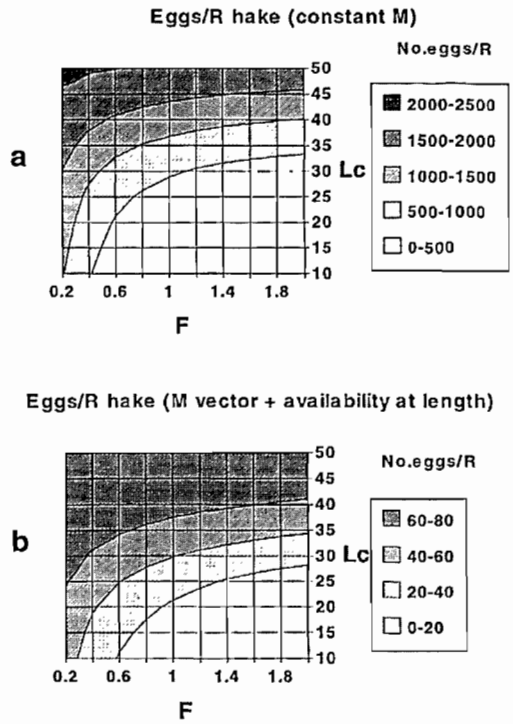

Figure 10. – Egg/recruit analysis under the constant M-assymptotic availability assumption (a) and under the assumptions proposed in this paper (b).

substantial increase in mesh size (from 40 to 100mm stretched mesh size) in order to restore acceptable levels of yields per recruit. (With this new combination of F and tc, an increase of 400 % in Y/R was predicted).

By utilizing the same assessment methodology but under the "new assumptions" a more optimistic scenario is described, suggesting the need for only a light reduction of the current level of effort and a moderate increase of mesh size in order to maximize the yield-per-recruit values. These changes should in contrast only produce a moderate increase in yield-per-recruit of about 10-15 %. Similar results are obtained if bioeconomical aspects as unit price by size are taken in consideration and benefit-per-recruit isopleths are constructed. This is due to the high prizes of small hakes in the Mediterranean markets.

The choice between the traditional or new assumptions for the Yield-per-recruit analysis markedly influence the values of yield per recruit obtained. In fact, with the new assumptions these values are very much smaller than those predicted under the "conventional assumption". This is inevitable, given the high death rates that we suppose mainly occur in the first year of life before full availability to the trawl, and corresponds to a situation where predation on small hake is expected to be more intense than for adults. These low values are at least in part compensated by a higher number of recruits. In fact, a non-traditional Length Cohort Analysis that utilizes the inverse M-at-age

function followed in this paper furnishes an estimated number of recruits that is many times higher than the number estimated with a traditional approach. The reconstructed demographic structure of the stock obtained under the new assumptions and based on catch-at-size data closely resembles the observed size structure obtained with trawl-surveys.

A more generalized comment on yield per recruit analyses is revealed by this study, namely that calculations with constant *M* involving young fish, whether Y/R or VPA, are going to overestimate the proportion of a cohort that is available for harvesting, since a demersal species may occupy several positions in the trophic chain during its lifespan. A simple illustration shows that a steeply declining vector for juvenile M, appears to be more closely in accord with demersal food pyramids than 'constant M' calculations.

It seems to us that the predictions of the "new hypothesis" of declining M and availability proposed here, reflects quite well the situation in the Mediterranean fine mesh trawl fishery. Where this analysis becomes particularly useful we believe is to consider what would happen to population fecundity if a new or expanded fishery began for larger hake along the edge of the slope and shelf targetting older, mature fish, as suggested by Aldebert *et al.* (1993). A selection curve for longline gear is not available, but data from the last-cited authors was used to simulate an increase of the fishing mortality for mature fish of the ages and sizes taken by longline gear (*i.e.* ages 4 to 10). From these preliminary calculations, it is expected that both the number of eggs per recruit and the spawning potential ratio (Current Spawning Biomass/Unfished Spawning Biomass) will show a sharp decline with increased fishing, using gear aimed specifically at adult fish (Fig. 11). This preliminary analysis also suggests that the overall population fecundity is relatively resistant to increasing fishing mortality rates at higher levels of fishing mortality when the mortality-at-age vector generated by trawlers on the juvenile stock component on the shelf is used. There is little room for complacency, but in the figures calculated under this new hypothesis, estimates obtained with a length cohort analysis (LCA) using an *M* vector of the Caddy (1991) type instead of the usual constant *M*, back-calculate a number of recruits many times higher than those estimated by means of traditional LCA with constant *M*, and compensate in part for the reduced number of eggs per recruit predicted. This balance has to be kept in mind in evaluating the absolute potential number of eggs generated by the stock under any given fishing strategy.

Analysis of landings and abundance data series

FAO statistical data on landings (Fig. 2) for either the Western or Eastern Mediterranean do not show the negative trend in landings that should be observed in a recruitment overfished situation. In fact, during the last decade there was a pronounced positive trend in

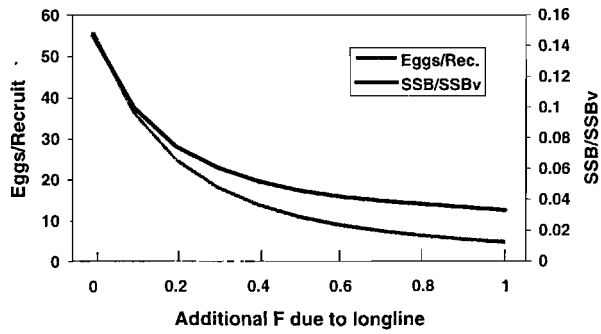

Figure 11. – Inferred effects on the population egg/recruit and exploited spawning stock/unfished spawning stock ratios, caused by increasing the current F values due to longlining.

reported hake landings. This increase could be partially explained by the increase in fishing fleet that occurred during the former two decades. In the local study area, hake catch has not shown any evident trend; either for landings or for catch per unit effort. Nor had relative abundance of hake from trawl surveys during the period 1985-1995. Whether one takes the local or general Mediterranean situation as typical therefore, there seems no evidence, at least until recently, to suppose that the fishery for juvenile hake has not been sustainable. As noted, there may be other reasons than fishing strategy that have contributed to a Mediterranean-wide increase in fishery production.

Implications of M-at-age assumption for population dynamics of hake

Several different methods of arriving at an indicative vector of M with age using the reciprocal model are proposed here. At this early stage in applying a new methodology, it is difficult to decide which is the most realistic. A general similarity to the values obtained empirically for North Sea groundfish offered one of the few standards of comparison, and seems to confirm our results are realistic, at least if current perceptions of similar longevity and growth rates of Atlantic and Mediterranean groundfish species are confirmed. Slightly higher values of M-at-age are suggested by the proposed procedures for intermediate aged (2 + to 4 +) fish than for the North Sea data set, and the reader is left to judge whether these are realistic. One comment in this respect relates to the "hybrid" nature of the North Sea vectors used as a basis for comparison: North Sea data for juvenile ages are apparently from MSVPA, but those from older specimens come from earlier "constant M" estimates; presumably from fitting total mortality against annual effort using a procedure such as that of Paloheimo (1958) This may account for the discrepancy just noted between our estimates and those for the North Sea species at intermediate ages.

Management implications

This communication takes no 'moral' position with respect to the correctness or otherwise of capturing juvenile fish, nor do we take the position that the current exploitation strategy is correct and without serious risk. In our opinion, a management strategy must be judged from its results and not from theoretical preconceptions.

The main objectives of demersal fish management, as spelled out in recent meetings of the General Fisheries Council for the Mediterranean, are to reduce exploitation rates on demersal fish, and to protect nursery areas. While not contradicting the need to avoid catches of very small hake, which currently leads to widespread discarding of very small fish, this analysis points however to another urgent priority, which is to conserve spawning potential so that stock collapse under the *current* fishing strategy, which is *de facto* aimed at juveniles, can be avoided.

It seems, in fact, that the cod-end mesh size of 40 mm stretched mesh recommended by the General Fisheries Council for the Mediterranean in the Second Session of its Committee on Resource Management in 1978 (GFCM, 1978) is not as sub-optimal as previously thought, although we admit that the calculations presented here should be repeated when more precise estimates of discarding, and realistic data on incidental mortality at size for two or more mesh sizes are available. It is also implied here that the inefficiency of the small mesh trawl fishery for capturing large hake may, paradoxically, be one element that has unwittingly helped to conserve the spawning stock. Careful studies need to be carryed out, especially to estimate the size of the spawning stock, before fishing effort is allowed to increase on older hake. (It is not obvious in fact that refocussing the fishery on mature fish is a socially or economically desirable option, given high prices paid for juvenile hake in some parts of the Mediterranean, and given management failures in gadoid fisheries elsewhere where this strategy has been followed). One incidental consequence of this study is to draw attention to the surprising continuity and even increases in yield which the current fishing strategy *de facto* apparently has permitted.

Although fecundity per recruit would be increased somewhat by increasing the mesh size, it is not clear that this will necessarily increase yield per recruit markedly, and would mean that active measures would have to be taken annually to assure that fisheries targetted on larger fish do not deplete the spawning stock. Apart from the difficulties of enforcement, imposing larger mesh sizes is not therefore as precautionary as it seems at first sight, and in the Mediterranean, may not protect the stock from recruitment overfishing. In fact, a precautionary management approach here would be to prevent expansion of such mature fish fisheries, at least until trawl effort has been seriously reduced, and juvenile survival has been greatly improved. Conservation of spawning stock might better be achieved directly by discouraging fisheries on large hake, and protecting deeper water areas of adult concentrations, following a 'refugium' concept.

An effective monitoring and management system does not currently exist, and this would be even more necessary than at present, since a move to targetting mature fish would require a monitoring system for determining minimum spawning biomass, since this would be very vulnerable to overfishing under these conditions, with potentially drastic results.

A comparison of the two length cohort analyses under the "conventional assumptions" and the "new hypothesis" suggests meaningful differences in their management implications. We can observe that the analysis made with the first set of assumptions suggests that F is always much higher than M (especially for the smaller sizes). On the other hand, with the declining M and availability assumptions, the F values remain below the corresponding natural mortality rates over the whole size range.

General implications of the study

We note that fisheries aimed at juveniles may arise in areas where fishing pressure was high prior to the introduction of minimal size and effort regulations, or because small target species or sizes lower in the food chain have resulted from earlier fishery depletion, as in many tropical fisheries, and we would suggest also in the Mediterranean Sea. As a more general observation, it is suggested that the survival of fisheries for juveniles will always depend on the availability of refugia, (whether geographical, or resulting from harvest selectivity), that protects at least a minimum spawning biomass of older mature fish. Where this occurs elsewhere (*e.g.* Northwest Atlantic fisheries for *Homarus americanus* which are predominantly captured in most areas as juveniles; Anthony and Caddy, 1974), the fishery appears to be unusually resistant to high fishing pressure, as appears also to be the case for hake and several other demersal species in intensively trawled areas of the Mediterranean such as the Adriatic.

The new paradigm implied here will not be applicable in all fishery situations however: for example, in areas such as the North Sea where adult demersal fish are readily available to exploitation over a wide shelf without natural refugia (and without those created by gear design), and where markets are not aimed at the sale of individual small fish, such a paradigm may not be applicable. It may, however, have a fairly wide application in some tropical areas, where similar conditions to the Mediterranean prevail. What is clear, however, is that a fishery which allows uncontrolled exploitation of both juvenile and adults from a stock is likely to experience stock declines!

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