Aquat. Living Resour., 1996, **9**, 197-207

Modelling natural mortality with age in short-lived invertebrate populations: definition of a strategy of gnomonic time division

John F. Caddy

FAO, Vialle delle Terme di Caracolla 00100 Rome, Italy.

Received June 7, 1995; accepted April 30, 1996.

Caddy J. F. *Aquat. Living Resour.*, 1996, **9**, 197-207.

"When we speak of the rate of change, we refer to the number of events crowded into an arbitrarily fixed interval of time. Thus we need to define the 'events'. We need to select our intervals with precision" [from "Future shock" Toffler, 1971].

Abstract

Most highly fecund marine fish show a steep decline in natural death rate from egg to first maturity, after which the natural mortality rate remains constant, or may even increase with age for old animals. Relatively few investigations have quantified early life-history mortality vectors for short-lived invertebrate stocks, but this overall picture is also true here for species with planktonic life stages such as penaeid shrimps, and for squids. If M decreases rapidly with age, one logical approach to demographic analysis is by subdividing the lifespan into intervals which increase in duration in proportion to the age up to the start of each interval. This time subdivision strategy is referred to as 'gnomonic'. Earlier work (Caddy, 1990) showed that if a reciprocal mortality function applies with age, the product of the instantaneous annual rate of natural mortality and interval duration should be roughly constant for gnomonic intervals. This working hypothesis is shown to produce similar results to the reciprocal function for M_t, but allows a simpler approach to generating realistic life history M_t vectors in the absence of direct estimates of M for stock assessment. Values of a constant probability of death, $G = M_t \Delta_t$ were used to generate vectors of M-at-age for a gnomonic series of intervals from hatching up to the mean parental age. The value of G is found by iteration that results in 2 survivors from the mean population fecundity by 1 year of age, under the assumption of steady-state population replacement for an unexploited stock. The natural mortality rate in the final, longest interval was assumed to correspond to the 'constant adult M' value used in stock assessment. Two extremes of reproductive strategy were chosen by comparison with data from for annual species of cephalopods or penaeid shrimps: cephalopods such as *Sepia* sp. and *Rossia* sp., with few, large yolky eggs (and/or parental care), occupy one extreme, and are contrasted with high fecundity penaeid shrimps and at least some *Illex* squids.

The first category has a low fecundity (130-150 eggs, and a K-selected reproductive strategy). Values of 'adult M' of the order of 1.0-1.3 are predicted for the last 60-80% of the annual life span. The high fecundity category (200 000 eggs or more) are opportunistic spawners such as many penaeids and some oceanic squids, and follow an r-selected reproductive strategy. An instantaneous value for pre-spawning M of the order of 2.8-3.4 is predicted for the same period mentioned above. Neither range of values falls outside those in the literature, for which a brief summary is presented.

An important research question relates to the order of magnitude of post-hatching mortality under population stability: it is suggested that irrespective of the specific model used for changes in M with age, this falls rapidly from an initial rate of some 50-75% per day for short-lived, high fecundity species in the 2 days following hatching, unless adult M values are much higher than above, and of the order of 25-40% for the low fecundity organisms over the same initial interval.

Aquat. Living Resour. ISSN 0990-7740/96/03/$ 4.00/© IFREMER-Gauthier-Villars

Modélisation de la mortalité naturelle en fonction de l'âge, chez des populations d'invertébrés à vie courte : définition d'une stratégie de division gnomonique du temps.

Résumé

La plupart des poissons marins les plus féconds présente une baisse importante du taux de mortalité naturelle aux premiers stades de la vie de l'œuf à la première maturité sexuelle, après quoi la mortalité naturelle reste constante ou peut même augmenter avec l'âge pour les animaux les plus âgés.

La mortalité dès les premiers stades de développement a été relativement peu étudiée de façon quantitative pour les stocks d'invertébrés à durée de vie courte mais ceci est aussi vrai pour les espèces présentant des stades de vie planctonique, tels que les crevettes pénéides et les calmars. Si M décroît rapidement avec l'âge, une approche logique à l'analyse démographique consiste à subdiviser le temps en intervalles dont la durée augmente proportionnellement avec l'âge. Ce mode de subdivision du temps est connu sous le nom de « gnomonique ». Des travaux antérieurs (Caddy, 1990) ont montré réciproquement que le produit du taux instantané de mortalité naturelle annuel par la durée de l'intervalle devrait être approximativement constant pour des intervalles gnomoniques. On montre que cette hypothèse de travail produit des résultats similaires à ceux de la fonction réciproque pour M_t mais permet une approche plus simple pour générer des vecteurs M_t réalistes sur l'ensemble du cycle vital, en l'absence d'estimations directes de M pour l'évaluation des stocks. Les valeurs d'une probabilité constante de mortalité, $G = M_t \Delta_t$, ont été utilisées pour générer des vecteurs de M à chaque âge, sur des séries d'intervalles gnomoniques, depuis l'éclosion jusqu'à l'âge adulte moyen. La valeur de G est trouvée par itération, de façon à laisser survivre 2 individus d'un an, en partant d'une population moyenne, sous hypothèse de renouvellement stabilisé pour un stock non-exploité. Le taux de mortalité naturelle dans le dernier intervalle, le plus long, est supposé correspondre à la valeur constante pour les adultes, telle qu'utilisée dans les évaluations des stocks.

Deux stratégies de reproduction extrêmes ont été choisies pour des comparaisons, en utilisant des données relatives à des espèces annuelles telles *Sepia* sp. et *Rossia* sp., avec des œufs riches en vitellus mais peu nombreux (et/ou des soins parentaux) représentent un extrême, l'autre étant caractéristique des crevettes pénéides à haute fécondité et de quelques céphalopodes du genre *Illex*.

La première catégorie a un taux de fécondité faible (130-150 œufs) et a une stratégie de reproduction de type K. Les valeurs de M des adultes sont de l'ordre de 1,0-1,3 pour les derniers 60-80 % du cycle vital. La catégorie de forte fécondité (200 000 œufs ou plus) comprend des reproducteurs opportunistes tels que de nombreux pénéides et quelques calmars océaniques, qui suivent une stratégie de type r. La valeur instantanée de mortalité avant la ponte de l'ordre de 2,8-3,4 est prédite pour la même phase finale du cycle vital. La littérature scientifique, dont une courte synthèse est donnée, ne mentionne pas de valeurs extérieures à ces intervalles.

Une question importante concerne l'ordre de grandeur de la mortalité après la ponte pour une population stable. L'étude suggère que, quel que soit le modèle utilisé pour représenter les variations de la mortalité naturelle avec l'âge, celle-ci décroît rapidement à partir d'un taux initial d'environ 50 à 75 % par jour pour les espèces à vie courte et à forte fécondité dans les 2 jours suivant la ponte (sauf si les valeurs de M pour les adultes sont beaucoup plus élevées que celles indiquées ci-dessus), le taux étant de 25 à 40% pour les organismes à faible fécondité sur la même période.

Mots-clés : Modélisation, mortalité, céphalopodes, Pénéidés.

INTRODUCTION

Current perceptions of changes in natural death with age

The problem of estimating the natural mortality rate from field observations on resources that are simultaneously harvested, appears to be largely intractable. In the current fisheries literature, empirical methods of prediction based on regressing earlier estimates of adult M on more easily measured population variables such as maximum age or growth rate, outnumber new direct estimations of adult natural mortality rate. This, despite the observation (*e.g.* Pascual and Iribarne, 1993) that even assuming no error in the original mortality estimates, empirical methods incorporate a substantial unrecognized error term.

Estimates of natural mortality for short-lived species appear to be less common and less substantiated than for multi-age fish stocks. The assumption of constant natural mortality of adults, while perhaps valid for finfish at or around the age of maturity, is supported by little experimental evidence for short-lived species; nor are explicit estimates provided of the duration of the fixed adult mortality rate used in most stock assessments. Estimates based on assumptions of generational replacement at equilibrium may be useful in bracketing feasible adult mortality rates.

The concept that for fecund marine organisms, natural mortality falls off rapidly from very high values for the egg and larval stages to a relatively constant level at or around the age at maturity, seems widely established for most commercially important marine fish and invertebrates. Reliable estimates of natural death rate at more than one age are extremely rare however, and difficult to obtain for commercially exploited species where an overriding fishing mortality rate also applies. The situation is worse if anything, for larger, short-lived, essentially annual, species such as the larger penaeid shrimps, and for most squid species of commercial importance. There is a tendancy in the literature to assume (without much analysis) a single indicative value for 'adult death rate' that does not take into account even what little we know of life histories of these organisms.

It is probably reasonable to conclude for annual species producing large numbers of eggs, that M-at-age also drops off more or less steeply in the early life history, levelling off as sexual maturity is approached, and then for semelparous species, rise steeply following spawning.

Of course, divergences may occur after maturity and spawning, and for many cephalopod species, a post-spawning catastrophic mortality soon leads to a rapid increase in M, so that, with certain exceptions (*see* Juanico, 1983), it is assumed that for these normally semelparous species, most spawners are dead within a month of egg laying (Fig. 1*a*). For squid, the attraction of this assumption has led to the commonly-followed suggestion (originally made by Au, 1975), that if survival is exponential, then for unexploited stocks, $M = 1/\bar{t}$; where $\bar{t}$, the supposed mean life expectancy, is less than 12 months. Recent experience (*e.g.* Rodhouse and Hatfield, 1990, and Hatanaka *et al.* 1984) tends to confirm a close to annual maximum life span, which is also generally accepted for most penaeid shrimps (Garcia and Le Reste, 1981), although here a short life span seems more a function of high rates of predation (Fig. 1*b*).

The assumption that a constant natural mortality is a simple function of mean lifespan is however suspect for short-lived organisms, as a couple of simplistic examples will illustrate. A constant annual value of M of around 3.0 will result in 5% survivors after 1 year, which is higher than needed for stock replacement, while a constant annual M, yielding 2 survivors from 200 000 eggs, would be in excess of $M = 11$ (Fig. 2). Neither of these values seem particularly useful for stock assessment purposes.

It is not presumed that a unique vector for M-at-age has been obtained in this study, given that this depends on the assumptions followed; and more than one approach gives apparently realistic results. This paper postulates an approach to calculating an indicative vector of natural death rates at age which is mathematically simple, and satisfies population replacement, where it is believed that initial death rate is high, and falls off steeply in the early months of life to a plateau later on.

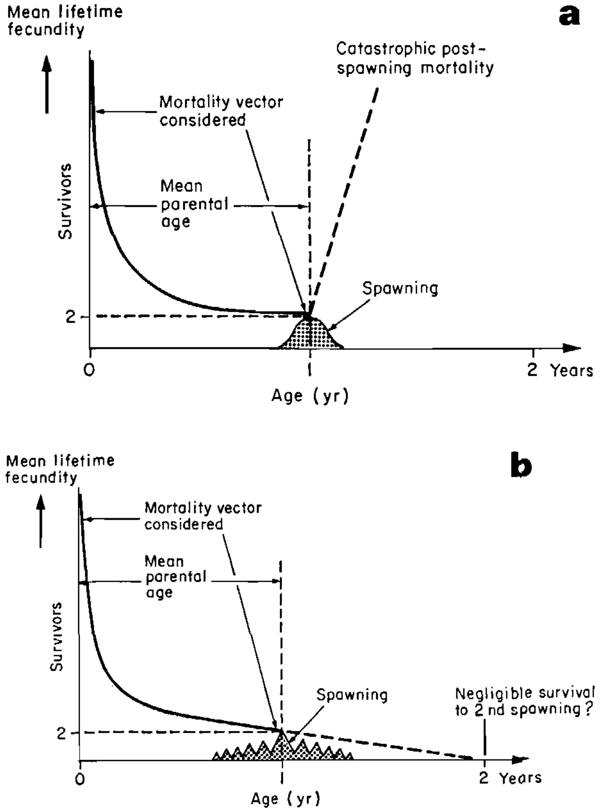

Figure 1. – Schematic for two common life history strategies for annual species. a: Semelparous, typical of many cephalopods; b: Iteroparous, but not surviving in sufficient numbers for spawning in the second year to be of importance (*e.g.* many penaeid shrimps). In both cases, only the mortality vector in the first years is considered in this study as being relevant to population replacement.

Mean parental age and mean lifetime fecundity

The effective lifetime fecundity is an important indicator that will allow us to judge whether a particular mortality vector is reasonable or not. In the case of large penaeid shrimps, for example, Garcia and Le Reste (1981) estimated that individual fecundity is between 100 000 and 500 000 eggs, and probably not less than 200 000. Given that penaeids may be iteroparous, mean lifetime fecundity (MLF) could be considerably higher than this. An age at first spawning of from 7 months to just over one year, and a maximum life span for the oldest individuals of around 2 years seems indicated. However, evidence of individual females spawning in two successive years was not found in the literature. Smaller tropical shrimp species have shorter lifespans and presumably higher values of natural mortality rate. There may also be differences between the sexes, but neither is this taken into account in the indicative approach adopted here. Rarely is it possible to accurately determine sex ratios at age from catches, but where major differences in death rate by sex apply, the present approach could only be used (assuming sex ratio in hatching eggs is 1:1) to provide a mortality vector for females in the cohort.

In comparison with penaeid shrimps, the range of species-specific fecundity in cephalopods is apparently

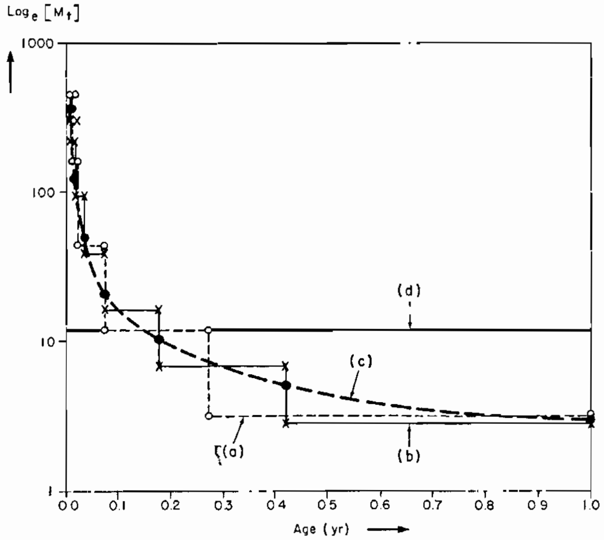

Figure 2. – Comparison of 4 vectors of natural mortality that result in roughly 2 survivors from 200 000 eggs: a) constant value of G with 4 gnomonic intervals; [$\Delta_1 = 2/365$; a = 1.382, $G = 2.878$], b) with 7 intervals, [$\Delta_1 = 2/365$, $a = 1.382$, $G = 1.645$], c) M as a continuous reciprocal function of age (t): $M_t = 1.342 + 1.493/t$; d) constant $M = 11.51$.

wider, but egg numbers are generally lower, and often much lower. A relatively small number of large eggs is found in many Sepiidae, but high fecundities are reported for some squids and octopi. There also seem some indications (Anon, 1988) that "squid appear to have higher survivorship than fish in comparable environments. Most squid produce fewer eggs per clutch than fish, and since most are semelparous, this means fewer eggs per female". The report by Anon (1988) also notes that cephalopod eggs are less vulnerable than in many fish due to 'packaging', and in some cephalopods there is parental care. It is not clear however for either cephalopods or penaeids, whether fecundity estimates in the literature represent estimates of eggs laid, or those fertilized and viable. If not, this may also contribute to the high early mortality rates postulated here. More recent evidence (*e.g.* Laptikhovsky and Nigmatullin, 1993), supports the idea that some cephalopods such as *Illex*, like some penaeids, may be serial spawners, and hence have a much higher net fecundity than cited by earlier authors, or used in the simulations reported here.

For many cephalopods, maximum life span is rarely supposed to exceed 1 year. Although actual data on the maximum lifespan is scanty, Table 1 gives some probably very provisional estimates taken from Roper, Sweeney and Nauen (1984). As for penaeid shrimps, there is the possibility that for some species (*see* Juanico, 1983), multiple (partial) spawnings could take place. Some squids may possibly 'skip' spawning at around 1 year of age, to spawn later. From the perspective of stock recruitment however, the assumption of 'stable population replacement' is applied; namely, that beginning with one female of Mean Lifetime Fecundity (MLF), a realistic mortality vector should result in an average survival by the Mean Parental Age (MPA) (Caddy, 1990), of at least one female; and since sex ratios differing from equality are not considered here, one survivor also from the males in the cohort.

Table 1. – Some individual fecundity estimates for several cephalopod species from Roper *et al.* (1984).

Species	Life span	Fecundity (# eggs)
Sepia bertheloti	1-2 y	50-100
Rossia macrosoma	1 y	120-150
Loligo vulgaris	2 y?	<20 000
Illex coindetii	15-18 months?	12 000
Octopus vulgaris	17 months?	120 000-400 000

Under this assumption (Fig. 1), it is not vital that post-spawning mortality should be catastrophic or merely high. Simply, it is important that if iteroparity applies, spawnings can be considered centred around a particular time; say at one year of age, and that by the next annual spawning period, the number of mature females surviving from the previous spawning to make a reproductive contribution should be negligible (Fig. 1*b*).

The assumption that the MPA is around one year for larger short-lived invertebrates such as penaeids and cephalopods, as well as some short-lived fish species, seems then not unreasonable. If this were otherwise, there would be a progressive 'drift' of spawning season between years, or several successive generations might occur in one year: this is true of course for many smaller invertebrates, and the present method could of course be adapted to shorter or longer life spans.

Even in the tropics, pronounced seasonality of spawning usually applies for many fish species. A specific strategy that allows for lifespans other than one year is mentioned for cephalopods by Mesnil (1977), whereby shorter and longer lifespans could alternate, or be successively scheduled between (say) spring and autumn spawning seasons, though Summers (1985) considers such strict scheduling improbable. In the absence of information that this type of interannual scheduling is a widespread phenomenon, the assumption is made in the following calculations that MPA is about 1 year, which places a useful constraint on likely mortality vectors during the life history.

Natural mortality rates in current use

For penaeid shrimps, the short-lived invertebrates of the highest commercial importance at a global level, the values for constant M commonly used in stock assessments tend to fall in the range 1.2-5.4 on an annual basis (Table 2), with values of up to 10 cited for juveniles (Garcia and Le Reste, 1981; Rothschild and Brunenmeister, 1984).

Table 2. – Numbers of annual values of natural mortality rates cited for Penaeid shrimp (from Garcia and Le Reste, 1981).

Annual values of M						
0.00 –0.99	1.00 –1.99	2.00 –2.99	3.00 –3.99	4.00 –4.99	5.00 –5.99	6^+.00 –6.99
1?	3	6	2	2	1	2 (1 Juv.)

For cephalopods, as noted, fewer and probably less well founded values of 'adult M' are in use, and these are generally much lower than for penaeids. Some annual values for pre-spawning adults used in assessments are in the range of 0.35-1.8 (Table 3); however, as for penaeids, few estimates are based on a specific estimation procedure. The lower values may even reflect a dubious extrapolation from values used for temperate fish stocks, and seems an underestimate for annual species where growth rates, when available, imply high metabolic rates often associated with high rates of natural mortality. At the same time, the concept of a constant natural death rate throughout life is clearly not valid, and death for semelparous species, significant numbers may survive to spawn, then die soon afterwards.

Table 3. – Some published values for adult pre-spawning natural mortality rates of squid species, expressed on an annual basis.

Species	Annualized M-value	Author
Todarodes pacificus	0.35-0.45	Osako and Murata (1983)
Loligo pealei	0.12-1.8	Lange and Sissenwine (1983)
Loligo sp.	0.5-1.5	COPACE (1987)
Illex illecebrosus	0.6	Efanov and Puzhakov (1975)
Illex argentinus	1.44	Csirke (1987)
Dosidicus gigas	0.6-0.96	Ehrhardt *et al.* (1983)

A modelling approach

Mortality vectors

For an exploited stock, the total death rate is conventionally split up into components that correspond to natural death and fishing, but we are concerned here with the stock in its unexploited state. The assumption is made that under unexploited conditions, average fecundities, as reported in the literature, should be in equilibrium with unexploited mortality rates. If so, the above 'stable population replacement' axiom applies. It is also necessary in using these M values in stock assessment, to make the rather weak assumption that unexploited natural mortality rates also apply in exploited conditions.

In a study of 5 multi-age exploited resources for which 2 or more estimates of M-at-age were available, Caddy (1990) showed that the simplest model that results in a steeply-declining M-at-age vector, to a more or less constant adult M, is:

$$M_t = A + B/t \qquad M_t > 0\,(^*) \qquad (1)$$

There are major problems however in determining the 2 or more values of M-at-age needed to fit this relationship, and another indicative approach appears to be needed, such as a reasonable postulate as to how natural mortality changes with age through the life history.

Whatever the function of M with age, if we know the number of individuals (N) at the beginning of the year, and divide a year into a specific number $i = 1, 2, 3, \ldots, n$ of smaller time intervals Δ_i, then presumably we can write for each:

$$N_{i+1} = N_i \cdot \exp\left[-M_i \cdot \Delta_i\right] \qquad (2)$$

– where M_i is the single value for natural mortality rate that integrates the declining death rate through a short time interval of duration Δ_i. The number N_i at the start of the ith short interval is the number of survivors from the previous interval; (except for the first one, where the optimistic assumption made is that the numbers hatching is equivalent to the mean MLF). This still leaves open the question of how to decide on the appropriate time intervals over which a given mortality rate applies.

Time subdivision

Assuming it is desired to create a series of intervals of increasing duration starting at $t = 0$, given a first time interval $\Delta_1 = t_1$, it is necessary to define subsequent time intervals, Δ_i. This is usually automatically defined by the unit of measure currently used; 1 hour, 1 day or 1 week, for example. The first interval is either a realistic measure of the duration of the first life history stage, or can be defined arbitrarily, as here. Successive gnomonic intervals, $i = 1, 2, 3, \ldots, n$, may be generated by multiplying the time elapsed to the start of each new interval by a constant multiplier, a.

Thus:

$$t_n = \sum_{i=1}^{n} \Delta_i, \qquad \text{where} \quad \Delta_i = a \cdot t_{i-1} \quad (i \geq 2) \quad (3)$$

This strategy of systematic, unequal subdivision of time units was referred to provisionally in Caddy (1990) as 'proportional time allocation', but seems to merit a more specific descriptor. The term 'gnomonic' seem appropriate, as reviving two classical usages:

– Constant linear distances moved by the shadow of the 'gnomon' (Shorter Oxford Dictionary) or sundial, correspond to unequal units of time;

(*) Parameter A is identical to M_A used in Caddy (1990), but has been changed to avoid apparent confusion of this parameter by some readers with the 'constant adult M' value usually quoted in the literature.

– An alternative definition of a gnomon given in geometric terms by D'Arcy Thompson (1917), dates from the early Greek geometers Aristotle and Hero of Alexander, who considered a gnomon as 'Any (geometric) figure which, being added to any figure whatsoever, leaves the resultant figure similar to the original' (Thompson, 1966). Thus, in terms of elapsed time, any two gnomonic intervals in a subdivided life history may be considered equivalent, if they each form the same constant proportion of the time elapsed since birth up to their initiation.

A detailed knowledge of the life history may allow the lifespan to be divided up into biologically realistic subunits of time. In absence of such data, the solution proposed in Caddy (1990) for the reciprocal function, is that the n shorter time intervals into which the year is divided, should increase proportionally in duration with age (Table 4). This non-uniform, but systematic approach to subdivision of a life history is flexible, and has the advantage that after sequential calculations with different numbers of sub-intervals, the number of survivors at the end of the life history is largely independent of the number of intervals (Caddy, 1990).

Table 4. – Division of a year into 4-7 gnomonic intervals.

	Number of intervals			
	4	5	6	7
a: constant value	4.672	2.675	1.833	1.382
Interval No.	Number of days per interval			
1	2.00	2.00	2.00	2.00
2	9.34	5.4	3.67	2.76
3	53.0	19.7	10.39	6.58
4	300.65	72.3	29.42	15.67
5		265.7	83.36	37.33
6			236.16	88.91
7				211.74

The reciprocal model for mortality at age

In comparing the instantaneous mortality rates that apply at times t and $t + \Delta$ since birth, it was shown in Caddy (1991) that if the reciprocal equation for natural mortality rate applies,

$$[M_t - A] \cdot t = [M_{t+\Delta} - A] \cdot (t + \Delta) \qquad (4)$$

where A was referred to as M_a, the 'assymptotic mortality rate', in the earlier paper.

This relationship can be described in words as: 'for any two ages in the lifespan, the product of age, and the difference in instantaneous natural death rate from its final assymptotic value, is a constant'.

It was shown that if the reciprocal model applies, the appropriate value of a steeply declining M-vector to use in calculating natural deaths over a given time interval $t_{i-1} \rightarrow t_i$, is not that at its mid-point, but is given by:

$$M_i = [B/(t_i - t_{i-1})] \cdot [\log_e (t_i/t_{i-1}) + A] \qquad (5)$$

In simulating a life history using the reciprocal model with gnomonic time intervals, the time at the start of each interval is generated first, then the value of M_i for each interval is calculated by equation (5). Given a value for mean fecundity, the number of surviving offspring can then be calculated sequentially to the end of each interval, and onwards to the end of the lifespan. The problem in practice, is that equation (5) is undefined for the first interval, when $t_{i-1} = 0$. The approach to avoiding this problem in Caddy (1991) was to pick a small, positive, non-zero starting point for the life history. Another approach is to make a specific assumption as to the value of $M_i \cdot \Delta_i$ in each gnomonic time interval.

An alternative model: This second approach is the one followed here, and requires that the time division of the life history be such that there is an equal probability of death due to natural causes in each interval. This hypothesis is difficult to test for most species, but it is shown (Fig. 2) that gnomonic intervals for each of which a constant risk of death applies, produces a similar mortality vector to the reciprocal model, but has computational advantages over using the reciprocal relationship directly. This is the procedure followed up in the rest of the paper.

In the 1990 paper I noted that '...the appropriate time intervals in a life history should be ideally chosen such that a constant proportion of the population dies within each interval'. In other words, that it would be convenient to choose intervals such that $M_i \cdot \Delta_i$, the product of instantaneous mortality rate and duration, is constant for each interval Δ_i. *i.e.*:

$$M_i \Delta_i = G \text{ (a constant)} \qquad (6)$$

for all intervals.

This procedure has two advantages over using the reciprocal equation directly to specify natural mortality rates for each interval. The first mentioned already, is that since equation (5) cannot be used for the first interval beginning at $t = 0$, it has to be assumed that the life history initiates after some small positive interval of time. The second applies in the case that parameter A is negative (and this may occur where a rapid decline in numbers is constrained by a short life history). Both are mathematically unsatisfactory and do not arise with the alternative procedure proposed here.

METHODS

Modern spreadsheet programs contain a routine for solving non-linear relationships, (*e.g.* the SOLVER routine of EXCEL) which allows parameter values to be found that satisfy particular mathematical constraints or optima. This mechanism was used to look for values of parameters and/or variables by trial and error that allow, (first) the division of a given life span into a specified number of gnomonic time intervals with the last ending at 1 year of age. Second, SOLVER was used to calculate the decline in numbers in each interval from a mean lifetime fecundity (MLF) such that 2 spawners survive by one year of age.

Modelling M-at-age with the time subdivision strategy

The sequence of calculation is as follows:

1) The duration of the first interval Δ_1 was arbitrarily chosen in the computations reported here, but there might be reasons from field or biological data to set a particular duration or early mortality rate for hatching or larval stages (*e.g.* Sanders, 1995). From a mathematical perspective, the first finite interval after $t = 0$ in a gnomonic time series is inevitably anomalous compared to the following intervals since it includes within it, an infinity of ever smaller gnomonic intervals down to $t = 0$.

An empirical approach was adopted to deciding on a value for Δ_1. Based on trials with annual lifespans, it seems that values of $\Delta_1 < 1$ day lead to unrealistically high values of M_t in the first interval (although what may be regarded as unrealistic may be questioned: *Table* 5 shows that annualized instantaneous rates for the first short interval must be extremely high if population replacement criteria are to be met).

Long durations for Δ_1 are problematical, since they may result in SOLVER solutions where $a < 1$, and as a consequence of the procedure proposed in equation (6), $M_2 > M_1$ which is clearly unrealistic. As a suggestion, a value of around $\Delta_1 = 2/365$ (48 h) appears to provide reasonable solutions, but this could be adjusted to fit independent estimates of hatching/larval mortality on duration if these exist.

2) Next, decide on the number n of intervals into which the life history will be divided. The n intervals are generated by sequential procedure 3) above such that the nth sub-interval finishes 1 year after hatching. Unlike the earlier paper, which gave a method of calculating the multiplier a that corresponds to an exact division of the life span into n gnomonic intervals, this was achieved here using the EXCEL SOLVER routine.

3) Estimate the value of G in equation (6) by iteration using SOLVER, that corresponds to $N = 2$ survivors at the end of the last time interval. For each of the n successive time intervals Δ_i calculated, a vector of natural mortality rates is then generated from $M_i = G \cdot \Delta_i$.

RESULTS

Simulation of various M vectors for fecund, and less fecund species

Two sets of calculations are presented here for annual life spans; the first assumes a high-fecundity r-type recruitment strategy (*e.g.* Pianka, 1970) with mean lifetime fecundities of around 200 000 eggs (such as a generalised penaeid shrimp, but from recent evidence, this also applies fairly well to *Illex* squid; *e.g.* Laptikhovsky and Nigmatullin, 1993. The second assumes either a degree of parental care or other mechanisms to increase survival chances of eggs in an uncertain environment, and can be referred to as a K-selection strategy. Here it is assumed to correspond to a fecundity of around 135 eggs; (*Rossia macrosoma*: Table 1, can perhaps be used as an example). The fecundity values used are of course arbitrary, but illustrate the results towards two fairly extreme ends of the scale of fecundities.

Highly-fecund r-strategy mortality vectors

The values generated for fecundities of the order of those published for penaeid shrimp and *Illex* squid, suggest that for MLF to be reduced to 2 by the end of 1 year, we have to admit the possibility of initial annual mortality rates on eggs and larvae corresponding to annual rates of $M > 300$: equivalent to 55-75%/day (Tables 5*a*, 6). The vectors of mortality rates and survivors for the calculation using 7 gnomonic intervals are given in Figures 2 and 4. The pre-adult mortality rates found (Table 6) are of the order of $M = 2.8$-3.5 for the last time interval, over durations 0.58-0.82 y (7-10 months) respectively; depending on the number of time intervals used.

Although the high rates of 'wastage' implied by the M values for the post-hatching interval might be considered excessive, they seem inevitable if annual rates of natural mortality are to remain below 5.0 for pre-spawning ages. This high wastage appears inevitable with the fecundity data available, and must be almost independent of the model used; since we can hardly envisage a more rapid decline in early life history M, unless we assume an instantaneous drop in numbers at an early age is typical of this type of life history (Such a phenomenon, if occurring consistently, would seem in contrast to Darwinian principles, since it would presumably imply a massive, unselective mortality die-off at a particular life history stage). An alternative justification for such high rates mentioned earlier, is that published fecundity estimates do not allow for unviable eggs, which would then be included in the high mortality in the first interval.

Table 5. – Some natural mortality vectors satisfying the axiom of population stability (*see* text) for 2 annual species, with Mean Lifetime Fecundities of 200 000 and 350 eggs respectively (under gnomonic subdivision of 1 year).

A. High fecundity category:

[$n = 7$; $\Delta_1 = 2/365$ year; $a = 1.382$; Eggs = 200 000; $M_t \Delta_t = 1.645$]

Interval No.	Age (year)	No. survivors	Interval duration (Δ_t)	M_t
	0.000	200 000		
1			0.005	300.16
	0.005	38 614		
2			0.008	217.25
	0.013	7 455		
3			0.018	91.27
	0.031	1 439		
4			0.043	38.30
	0.074	278		
5			0.102	16.08
	0.176	54		
6			0.244	6.75
	0.420	10		
7			**0.580**	**2.84**
	1.000	2		

B. Low fecundity category:

[$n = 7$; $\Delta_1 = 2/365$ year; $a = 1.382$; Eggs = 135; $M_t \Delta_t = 0.602$]

Interval No.	Age (year)	No. survivors	Interval duration (Δ_t)	M_t
	0.000	135		
1			0.005	109.82
	0.005	74		
2			0.008	79.48
	0.013	41		
3			0.018	33.37
	0.031	22		
4			0.043	14.01
	0.074	12		
5			0.102	5.88
	0.176	7		
6			0.244	2.47
	0.420	4		
7			**0.580**	**1.04**
	1.000	2		

Low fecundity K-strategy mortality vectors

For the *Rossia* example which seems characteristic of cephalopods in sheltered, relatively constant environments or where parental protection or 'nesting' behaviour applies, the values resulting from experimentation with SOLVER correspond to more steadily declining M_t vectors with age. With fecundities of the order of 350 eggs/female, predicted annual mortality rates on eggs and larvae are much lower than for high fecundity species, but still of the order of $M_t = 100$-200, or 25-40% per day for the first 2 days. Pre-adult mortality rates are predicted to be in the range 1.0-1.3 (Table 6, Fig. 3). Again, lower egg and larval mortalities would require higher adult mortalities than these for population replacement (Fig. 3).

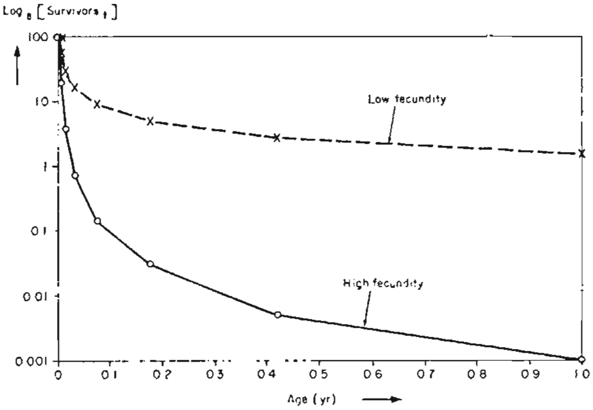

Figure 3. – Change in the log arithm of the number of survivors at the end of 7 gnomonic intervals for low and high fecundity species (Tables 5*A*, *B*).

The decision then, is whether to accept a higher larval and a lower adult *M*, or *vice versa*; and clearly, ancillary biological information will be needed to support such a judgement in specific assessments. Information on the mortality rate in the juvenile stage then becomes invaluable in choosing a more or less unique life-history vector (Fig. 2).

DISCUSSION

The problem of arriving at realistic estimates for adult natural mortality rates for short-lived species is an acute one, and a high proportion of existing natural mortality estimates currently used in stock assessments are largely empirical, and apply for an unspecified part of the life history. This paper attempts to provide indicative values for natural mortality vectors with age and the time periods over which they apply, under specified assumptions as to how death rate declines with age towards the age at maturity: assumptions that could be wrong in particular cases, but at least are explicit! Evidently, for semelparous species like many squids, there is an almost instantaneous increase in adult death rate shortly following spawning, but the fate of adults, post-spawning, is considered extraneous to population replacement. The post-spawning mortality rate, which subsequently increases steeply, is not modelled in this paper. If these post-spawning adults survive long enough to be of importance from a fisheries perspective, the 'adult' rate of natural mortality used in assessments must of course be higher than predicted here for the last interval.

No specific allowance is made for special factors such as cannibalism, which may be important for squid

Table 6. – Investigation of the effects of changing the number of time intervals in an annual life span for low and high fecundity annual species.

	[MLF = 200 000 eggs]				[MLF = 135 eggs]			
n	$G = M_t\,\Delta_t$	M_1 and % dying/day	M_n	Δ_n (y)	$G = M_t\,\Delta_t$	M_1 and % dying/day	M_n	Δ_n (y)
4	2.878	525 (76%/day)	3.494	0.824	1.053	192 (41%/day)	1.278	0.824
5	2.303	420 (68%/day)	3.163	0.728	0.842	154 (34%/day)	1.157	0.728
6	1.919	350 (61%/day)	2.966	0.647	0.702	128 (30%/day)	1.085	0.647
7	1.645	300 (56%/day)	2.835	0.580	0.602	110 (26%/day)	1.037	0.580

(although to the authors knowledge, there is no reason to suppose that the size-specific risk of cannibalism in squids differs greatly from that due to other types of predation).

Assuming a 1:1 sex ratio, male and female mortality rates are assumed the same, and it is supposed that the survival to spawning of one female fulfills the requirement for population replacement, but implies one male survives also. An alternative approach using the same methodology, would be to consider the survival of half of the lifetime egg production (assuming 50% sex ratio) to a single spawning female, and from this, estimate the male mortality rate per interval from the sex ratio at age, if available.

It may be argued that no single continuous function will correctly represent the change in natural death rate with age, and would anyway vary from year to year. The present approach may be however a reasonable point of departure for an investigation of M-at-age in short-lived motile animals, and has the considerable advantage, in absence of other information, of allowing experimental verification, and provides a standard of comparison with field results.

This procedure also allows one to raise useful research hypotheses, such as on the relative importance of parental care on survival to maturity, or the effects of cannibalism on natural mortality of older juveniles. Alternatively, the possibility could be tested that fecundity estimates are inflated due to egg parasitism or incomplete fertilization, and therefore that larval, juvenile and/or adult mortality rates are lower than predicted. The intention of the present paper is simply to draw attention to the likely order of magnitude of mortality rates and their biological relevance if population replacement is to be effected; realizing for example, that natural mortality rates of heavily exploited stocks may differ from those of virgin populations, but probably the rate of change in the vector of M with age may be less affected.

In contrast to current stock assessment practice, where much vital biological information cannot be used by existing methods, life history information can be used here in distinguishing between 'high larval mortality plus lower adult M', and 'low larval mortality plus higher adult M' strategies, and a more restricted range of possible mortality vectors may result. For highly fecund species, especially those that are iteroparous, this approach predicts egg and larval mortalities could reach values as high as M (annual) of 100-300 y^{-1} (equivalent to roughly 25-75% of the population predated per day). This may not be unreasonable for penaeid shrimp where predation on juveniles moving into nursery lagoons could be high, or for *Illex* squid (Bakun and Csirke, in press), where larvae may be carried passively for long distances to return to feeding and spawning areas. A question raised here relates to the different time units employed in expressing mortality rates in nature: it is obviously not very practical to express instantaneous rates on an annual basis for very short-lived or microscopic species, but doing so, at least focusses attention on the issue of standardization of units; as on the unit time frame employed.

There seems no reason to suppose that relevant time spans and mortality rates of planktonic larvae differ greatly from those for adult organisms of the same size. Mortality rates for zooplankton are rarely quoted as such, but in Sommer (1989) a graph from Threkeld (1979) showed that during the mid-summer die off of cladocerans, populations of *Daphnia galatea* dropped from 10 to 1 individual per litre over a period of roughly 3 days. It is probable that such a rapid decline in numbers exceeds those typical of normal zooplanktonic survival rates, but in this case the rate of mortality must have been of the order of $M = 280$ expressed on an annual basis. It is not usual to consider that egg laying or hatching is followed by a rapidly attenuating burst of mortality, but this would be consonant with the model presented here.

The indicative values arrived at for 'adult M' in this paper are independent of existing estimates, but appear to fall within the range of published values. It appears unlikely for annual species, even those with relatively low fecundity and parental care, that adult M values as low as M ('prespawning') = 0.2-0.5 are feasible, since this would imply extremely high egg and larval death rates. For penaeid shrimp and *Illex* squid living at least one year, values of adult M greater than 5.0 for species spawning at around 1 year of age, again, seem broadly incompatible with presumably high egg and larval mortalities, despite high fecundities. With respect to squids, it may be that more recent research (*e.g.* Laptikhovsky and Nigmatullin, 1993) showing batch spawning in *Illex* sp., will change the current impression that most squids are 'lower fecundity' spawners than penaeid shrimp.

It is interesting to consider the practical significance of the last time interval in the gnomonic time series. With division into up to 7 time intervals, this last interval is equivalent to more than 50% of the lifespan. By varying the initial interval and the total number of intervals, this last interval can be readily adjusted to the duration of the exploited phase, and the M value for the last interval used in conventional stock assessment methods as a constant; the duration and rates for earlier unexploited stages being of less practical interest. Figure 4 shows that although the duration of this interval is not critical, for low and high fecundity species increasing the number of intervals, and hence the duration of the last interval gradually increases the terminal M_t value.

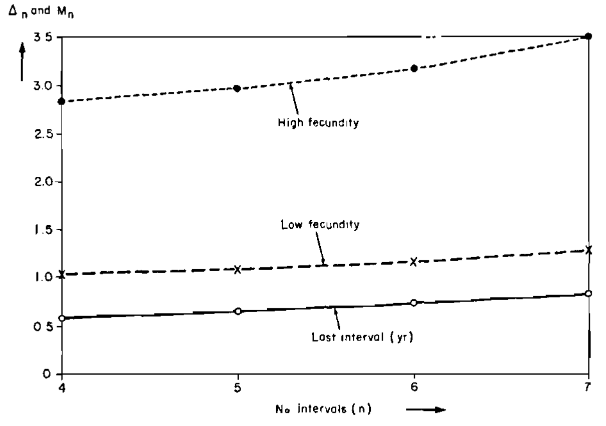

Figure 4. – Effect of changes in number of intervals on the natural mortality rate M_n in the last interval, (2 upper lines), and its duration Δ_n: (bottom line).

The strategy followed here of subdividing the lifespan into proportionally increasing sub-intervals, (e.g. Fig. 2) has the inconvenience of not fitting well with the equal weekly or monthly time intervals commercial fishing statistics are usually divided into, but other effectively gnomonic strategies for dividing the life history are widely used: for example, in length-based methods increasing time intervals corresponding to fixed increments in average size are implied. Other possible applications of a gnomonic time interval could be explored, such as the feasibility of using linear growth functions with a gnomonic time subdivision. A similar approach was used for moult-based modelling in crustaceans (Caddy, 1985; Caddy and Cobb, 1989) and moulting schedules of crustaceans often seem to correspond to an empirical gnomonic time scale.

In the author's opinion, the present strategy of time division is therefore not arbitrary, but may have some biological justification, if expressed verbally as:

'Any 2 or more intervals of time in the life history that are a constant proportion of the preceding life duration, are likely to be comparable in terms of the risk of natural death during those intervals'.

An even broader view follows from that quoted at the start of this paper from Toffler (1971).

'Any 2 time periods may be regarded as biologically equivalent, if during them, an organism accumulates the same proportional increment of interractions or other biologically meaningful events with respect to those experienced previously in the life history'.

The formulation of gnomonic intervals proposed in this paper corresponds to this conception.

REFERENCES

Au D. 1975. Considerations on squid (*Loligo* and *Illex*) population dynamics and recommendations for rational exploitation. ICNAF Res. Doc. 75/61, 10 p.

Bakun A., J. Csirke (in press). Squid recruitment dynamics. Environmental processes and recruitment variability. *In*: P.G. Rodhouse, E.G. Dawe, R.K. O'Dor. FAO Tech. Pap. (in press).

Caddy J. F. 1990. Death rates and time intervals: an alternative to the constant M axiom for fish stock assessment. *Rev. Fish Biol. Fish.* **1**, 109-138.

Caddy J. F., J. S. Cobb 1989. The population biology of decapods, 327-374. *In*: Marine Invertebrate Fisheries. J.F. Caddy ed. John Wiley 752 p.

COPACE (Comité des pêches pour l'Atlantique Centre-Est) 1987. Rapport du troisième groupe du travail *ad hoc* sur l'évaluation des stocks de Céphalopodes dans la région nord du COPACE. COPACE/PACE *Ser.* 86/4, 101 p.

Csirke J. 1987. The Patagonian fishery resources and the offshore fisheries in the South-West Atlantic. FAO Fish. Tech. Pap. **286**, 75 p.

Ehrhardt *et al.* 1983. On the fishery and biology of the Giant Squid Dosidicus gigas in the Gulf of California, Mexico, 306-340. *In*: Advances in assessment of world cephalopod resources. J. F. Caddy ed. FAO Fish Tech. Pap. **231**, 452 p.

Garcia S., L. Le Reste 1981. Life cycles, dynamics, exploitation and management of coastal penaeid shrimp stocks. FAO Fish Tech. Pap. **203**, 215 p.

Hatanaka H., S. Kawahara, Y. Uozumi, S. Kasahara 1984. A comparative description of five Ommastrephid Squids fished by Japan: *Todarodes pacificus, Illex illecebrosus, Illex argentinus, Nototodarus sloani sloani* and *Nototodarus sloani gouldi*. NAFO SCR Doc. 84/IX/99 (Mimeo) 19 p.

Juanico M. Squid maturity scales for population analysis, p. 341-378. *In*: Advances in assessment of world cephalopod resources. J. F Caddy. FAO Fish. Tech. Pap. **231**, 452 p.

Lange A. M. T., M. P. Sissenwine 1983. Squid resources of the Northwest Atlantic, p. 21-54. *In*: Advances in assessment of world cephalopod resources. J. F. Caddy ed. FAO Fish. Tech. Pap. **231**, 452 p.

Laptikhovsky V. V., C. M. Nigmatullin 1993. Egg size, fecundity, and spawning in females of the genus *Illex* (Cephalopoda: Ommastrephidae). *ICES J. Mar. Sci.* 50, 393-403.

Mesnil B. 1977. Growth and life cycle of squid, *Loligo pealei* and *Illex illecebrosus* (LeSueur) from the Northwest Atlantic. *ICNAF. Select. Pap.* **2**, 55-69.

Osako M., M. Murata 1983. Stock assessment of cephalopod resources in the Northwestern Pacific, p. 55-144. *In*: Advances in assessment of world cephalopod resources. J. F. Caddy ed. FAO Fish. Tech. Pap. **231**, 452 p.

Pascual M. A., O. O. Iribarne 1993. How good are empirical predictions of natural mortality? *Fish. Res.* **16**, 17-24.

Pianka E. R. 1970. On r-selection and K-selection. *Am. Nat.* 592-597.

Rodhouse P. G., R. C. Swinfen, A. W. A. Murray 1988. Life cycle, demography and reproductive investment in the myopsid squid *Alloteuthis subulata*. *Mar. Ecol. Prog. Ser.* 45, 245-253.

Rodhouse P. G., E. M. C. Hatfield 1990. Dynamics of growth and maturation in the cephalopod *Illex argentinus* de Castellanos, 1960 (Teuthoidea: Ommastrephidae). *Phil. Trans. R. Soc. Lond.*, 229-241.

Roper C. F. E, M. J. Sweeney, C. E. Nauen 1984. FAO Species Catalogue. Vol 3 Cephalopods of the World. FAO Fish. Synopsis **125**, 3, 227 p.

Rothschild B. J., S. L. Brunenmeister 1984. The dynamics and management of shrimp in the Northern Gulf of Mexico. In: Penaeid shrimps – their biology and management. Gulland J.A., B.J. Rothschild eds. Fishing News Books Ltd, 303 p.

Sanders M. J. 1995. Introduction to Thompson and Bell yield analysis using EXCEL spreadsheets. FAO Fish. circ. 895, 21 p.

Sommer U. 1989. Plankton ecology. Brock/Springer series in contemporary bioscience, 369 p.

Summers W. C. 1985. Comparative life history adaptations for some Myopsid and Sepiolid squids. ICNAF Sci. Counc. Stud. 9, 139-142.

Thompson D'A. W. 1966. On growth and form. An abridged addition edited by J. T. Bonner. Cambridge University Press, 346 p.

Threlkeld S. T. 1981. The recolonization of Lake Tahoe by *Bosmina longirostris*: Evaluating the importance of reduced *Mysis relicta* population. *Limnol. Oceanogr.* 26, 433-444.

Toffler A. 1971. Future Shock. Bantam Books, 561 p.