NOTE

Natural mortality and size

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ABSTRACT: The relations between size, natural mortality and patchiness proposed by McGurk (1986) are examined critically. It is suggested that the observations are in better agreement with earlier theories of the effect of patchiness if comparisons are considered within taxonomic groups (fish, Crustacea). McGurk's results can be extended to provide size-specific values of natural mortality in exploited fish stocks that may be more realistic, especially for the smaller fish, than the usual assumption of a constant value of natural mortality for all sizes.

In a recent paper McGurk (1986) extends the work of Peterson & Wroblewski (1984) to examine the relation between natural mortality M and size W, and makes 3 points: (1) over an extremely wide range of sizes, from zooplankton to whales, there is a close relation between M and W; (2) the values of M for fish eggs and larvae is larger than would be expected from the general relation; and (3) this deviation can be explained by the patchiness of eggs and larvae. These results are of considerable interest in attempting an understanding of the dynamics of fish populations, but before accepting them some points need further examination.

The theoretical effect of patchiness – to increase M – proposed by McGurk differs from that proposed by other authors (Brock & Riffenburgh 1960), who suggest that if the predator can be satiated, there are advantages for the prey to occur in patches or schools. The details of the benefit depend on several factors including the form of the aggregations. In the simplest case, if the prey occurs in tight clumps of n animals, the clumps being randomly distributed, the mean searching time before a clump is found will be n times that for randomly distributed individuals. Once a patch is found the predator will eat more, and if n prey is less than a full meal, the mean consumption per unit time will the same clumped or unclumped. If, however, the predator is satiated by m prey, where $m < n$, then the mean consumption will be reduced by a fraction m/n.

The mechanism proposed by McGurk whereby patchiness increases M is not clear. The measure used to describe patchiness [$p = 1 + (\sigma^2 \bar{x}^{-1} - 1)\bar{x}^{-1}$] is apparently equal to the number of 'crowders' per personal space, where, according to McGurk, each individual in a randomly distributed population (probably an evenly distributed, over-dispersed, population was meant) is surrounded by its individual space. The model seems similar to the clumped model above. The effect, if there is no satiation, is that each time a predator locates a patch its intake will increase in proportion to the degree of patchiness, as compared with a random distribution of prey, but the searching time between meals will be increased in the same proportion. That is, if increased searching time is taken into account, the impact of patchiness on M due to predation would seem to be small or negative.

It also might be expected that if patchiness affects M for fish eggs and larvae, it will affect M for other organisms. Most of the organisms considered in McGurk's Fig. 1 have patchy distributions, some e.g. pelagic fish and some zooplankton being very patchy. The overall regression line is not one for animals with random distributions, but represents some mean patchiness. If deviations from the line are to explained in terms of patchiness, the quantity that should be examined for its possible relation to the deviation is the difference in the patchiness of the organism from the mean patchiness.

Searching for an explanation for a deviation may in fact be unnecessary. Examination of McGurk's Fig. 1 suggests that while taking all organisms together the relation between size and mortality is best given by a log-log relation of the form $\log M = a - b \log W$ with $b = 0.25$, within a taxonomic group the relation is similar, but with a higher value of b. McGurk himself gives a value of 0.85 for fish eggs and larvae. Pelagic invertebrates, excluding the squid *Illex illecebrosus* (which is the only non-crustacean), have a slope of around 0.6, and all fish, including eggs and larvae, of around 0.5. (More precise values, based on a functional

regression, are given by McGurk 1987.) As plotted the points for fish tend to underestimate the slope because the weight given in the Appendix for the biggest fish, *Galeorhinus australis*, is too high. A dry weight of 110 kg (some half-ton wet weight) probably exceeds the average weight of school shark by at least an order of magnitude.

These 2 within-taxa regressions fit the observations better than the combined regression for all taxa, and the egg and larvae data fall well on the regression for the older and larger fish.

Reasons can be suggested for the within-taxa and between-taxa regressions being different. If a population is to persist it must achieve a balance between mortality on the one hand, and growth and reproduction on the other. Each of these is likely to be a function of size, but the problems involved with differing sizes are likely to vary between taxa. Thus it may be that there is nothing to explain in connection with the mortality of fish eggs and larvae, at least in the sense of there being a difference between expected and observed mortality. Judged by the 'fish' regression, the observed mortality of eggs and larvae is what might be expected of fish of this size.

Nevertheless, 2 important questions remain; what effect does patchiness have on mortality; and how good an estimator is size of the natural mortality of a fish. The second question has been examined several times in relation to commercial fish, and Beverton & Holt (1959) and Pauly (1980) have found good correlations between M and the growth parameters L_∞ and K. McGurk's paper goes further than these studies by recognizing that within a population M is a function of age and size, though different Ms for the same species were only used when several studies were reported, and no attempt was made to distinguish changes in M with size within a single set of observations.

Doing this is far from easy. Even when estimates of numbers at age are available for a good range of ages (and sizes), so that it is possible to look for a departure from linearity in a plot of log numbers against age (i.e. a non-constant M), it may only be possible to obtain a single estimate of M. At the fringes of the distribution, where non-linearity would be most apparent, possible biases in the sampling gear can invalidate any presumptions of varying M (Beverton & Holt 1956). The situation is worse in respect of exploited stocks. For these only total mortality can be estimated directly, and M has to be estimated indirectly, usually as a residual after fishing mortality has been taken into account.

It is therefore not surprising that for practical stock assessment work, a single constant value of M is used. However, evidence is accumulating that this is too simple an assumption. For example, that part of natural mortality for several species of North Sea fish that is

due to predation by larger commercial fish, is, for fish that are newly recruited, or just below recruitment size, well in excess of the value of M from all causes that has been generally assumed for the recruited population as a whole (Anon 1986).

The value of M is important in most stock assessment studies, although as Shepherd (1987) points out there are a number of situations in which the results are insensitive to M provided the same value is used consistently. In most cases, e.g. when assessing the effect of protection of young fish, it is the value of M at about the time of recruitment that is important. Using a value that is based on the recruited population as a whole, and which in practice may be based more on the older fish, where problems of partial recruitment are less, may therefore give misleading results. More reliable results might then be obtained by making some hypothesis that allowed for increasing M among the smaller fish.

One such hypothesis would be to accept the relation for fish suggested by McGurk's Fig. 1, i.e. that M can be given by the relation log $M = a - 0.5$log W. To compare with the usual stock assessment situation this can be expressed in terms of the maximum size achieved e.g. the parameters L_∞ and W of the von Bertalanffy equation, and the limiting value, M', approached by the biggest fish, giving

$$\log M = \log M' - 0.5 \log (W/W_\infty), \qquad (1)$$

or in terms of length

$$\log M = \log M' - 1.5 \log (1/L_\infty), \text{ or}$$
$$M = M' (1/L_\infty)^{-1.5} \qquad (2)$$

The effect of a pattern of mortality of this kind is shown in Fig. 1, which shows the changes in M and numbers with age. These were calculated for 30
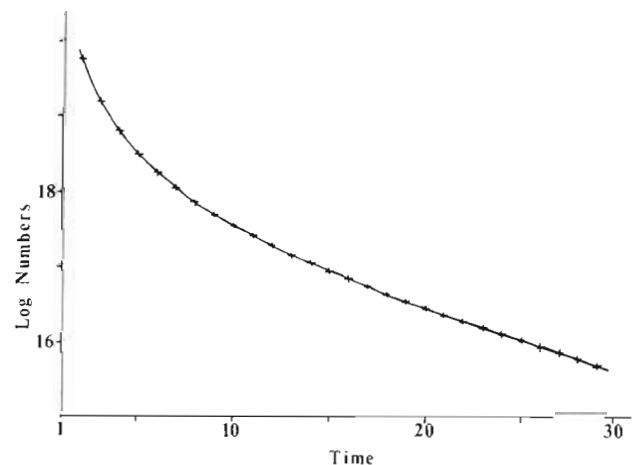

Fig. 1. Decrease in the logarithm (base 10) of the numbers of fish, growing according to the von Bertalanffy equation, and undergoing a natural mortality given by Eqn (1). Note the small apparent departure from a straight line over most of the range

successive 'age-groups', using the transition equation $N_t = N_{t+1}\exp(-M_t)$, and values of $K = 0.1$ and $M' = 0.1$. This may be thought of, using different time units, as 15 yr of a cod stock ($M = 0.2$, $K = 0.2$ in annual units), or 1.25 yr (30 half-months) of a tropical shrimp stock. Taking the data as a whole, the numbers, on a log scale clearly change non-linearly, but from about the 5th age group onwards the difference from a straight line is not apparent, even though there is an appreciable change in M. In any practical situation it would be impossible to detect from data of numbers at age that M was not constant.

It is therefore unlikely that there will enough direct evidence to choose between the 2 hypotheses of M being constant, or varying according to the equation above. The best indirect evidence may come from better estimates of M among the juveniles immediately before recruitment, though there are severe practical difficulties in getting good enough estimates of numbers at age. For the present, the choice of hypotheses must remain subjective, though there are reasons, Occam's razor notwithstanding, that the apparently more complex hypothesis should be preferred; the assessment results will be more conservative; and the hypothesis is in better accord with knowledge of M for the life span as a whole, since assuming constant M for recruited fish implies an abrupt change in M from higher values round about the time of recruitment. The additional computational work can in most cases be readily handled.

The relation between M and patchiness deduced earlier is only valid if predators are searching at random. Usually predators are themselves distributed patchily, and the higher predators may cooperate. If the distributions of predator and prey are positively correlated, then M will be higher than for random distributions. The degree to which this correlation increases with prey abundance is of considerable significance to the dynamics and stability of the prey population. Fishing fleets exploiting highly schooling species, especially purse-seiners, can continue to locate schools even at low fish densities, thus maintaining their catch rates, i.e. for a given nominal fishing effort fishing mortality F increases as fish abundance decreases. This has been one factor in the collapse of several big pelagic fish stocks (Clark 1974, Pope 1980).

For fish eggs and larvae the opposite effect – increasing mortality at higher densities – could be one factor, and possibly the key factor, in explaining why the recruitment in many fish stocks is largely independent of adult numbers i.e. there is strong density depend-

ence somewhere between eggs and recruitment. In discussing this problem Cushing (1987) suggests that aggregation of predators on to patches of high egg or larval density could be a possible mechanism, though he also points out that often the prey densities are low, and that the time taken for any invertebrate predator to aggregate might be long compared to the time for a fish larva to grow through the size range in which it is vulnerable to the predator concerned. The possible role of patchiness in giving some degree of stability to fish stocks remains an unanswered but potentially important question.

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