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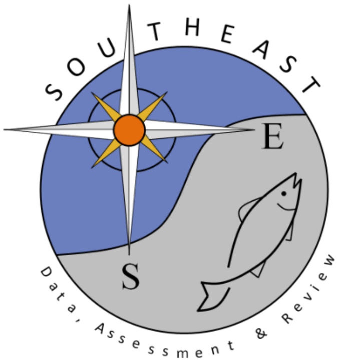

NOTES

Mortality Rate of Fishes in the Pelagic Ecosystem

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A size-dependent equation for mortality rate ($M(w)$) of fish-sized particles is derived using preexisting theory on the distribution of biomass as a function of size (w) in the pelagic marine ecosystem, assuming that mortality is primarily due to predation. The equation $M(w) = ckw^{-x}$ (where c, k, and x are parameters) yields estimates that are close to observed mortality rates.

On dérive une équation dépendante de la taille pour le taux de mortalité ($M(w)$) des poissons, à l'aide d'une théorie élaborée antérieurement et selon laquelle la répartition de la biomasse est fonction de la taille (w) dans un écosystème marin pélagique, en tenant pour acquis que la mortalité est principalement due à la prédation. L'équation $M(w) = ckw^{-x}$ (où c, k et x sont des paramètres) génère des estimations qui s'approchent des taux observés de mortalité.

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Estimation of natural mortality rate for fish populations is critical for the prediction of recruitment and for the optimal management of the recruited stock. As pointed out by Cushing (1974), numbers are reduced by four to seven orders of magnitude between hatching and recruitment. Mortality rate of fish larvae and juveniles is known to decrease with increasing size (Pearcy 1962; Cushing 1974), although the underlying basis for this relationship is not clear. In addition, adult mortality rates for different species decrease with maximum size (Ursin 1967). A general theory for mortality of fishes based on broad marine ecosystem processes may be helpful in understanding these trends.

Organism size has long been used as a scaling factor for such biological processes as growth and metabolism (Fenchel 1974). This has been applied in the development of a theory to explain the distribution of biomass among size-classes in the pelagic marine ecosystem (Kerr 1974; Platt and Denman 1977, 1978; Silvert and Platt 1978, 1980). In one analysis, Silvert and Platt (1980) gave an expression for mortality rate due to predation, but did not evaluate it explicitly.

Their expression (equation (21)) has been used here to derive a size-dependent equation describing mortality rate of fish-sized particles, and the equation is compared with data collected by other workers.

General Equation

The size distribution of organisms in the pelagic food chain can be described by the following time-dependent equation (Silvert and Platt 1980):

$$(1) \quad \frac{\partial \beta}{\partial t} + w\frac{\partial}{\partial w}(\beta G) + \beta M = 0$$

where $\beta(w, t)$ is a biomass density function such that $b(w, t) = \beta(w, t)dw$ is the mass of particles per unit volume in the size interval from w to $w + dw$ at time t. Silvert and Platt (1980) assumed predation scales in a perfectly isometric fashion, i.e. the range of particle sizes acceptable as prey scales as w. Thus, $dw \sim w$.

The function $G(w)$ is the specific growth rate of particles, i.e. $\partial w/\partial t = G(w)\cdot w$. Lastly, the function $M(w)$ is the specific rate of change in numbers of particles due to mortality and reproduction, i.e. $\partial N/\partial t = -M(w)\cdot N$ where $N = \beta/w$.

Silvert and Platt (1980) solved equation (1) after making the following assumptions: (1) the specific rate of change in numbers, $M(w)$, is primarily due to predation, (2) the weight of prey is a constant fraction q of the weight of the predator, and (3) the system is at steady state, i.e. $\partial\beta/\partial t = 0$.

According to the first assumption, production of particles within the spectrum through reproduction must be insignificant. To meet this condition, we will consider the biomass spectrum only above the size corresponding to the size of fish eggs, which is relatively constant between species (Ware 1975). There is a constant influx of material at the lower end of the spectrum.

Silvert and Platt (1980) showed that one possible solution to equation (1) is

$$(2) \quad \beta(w)G(w) \sim w^{-c}$$

where the exponent c is such that

$$(3) \quad K_1 c = q^{c-1}$$

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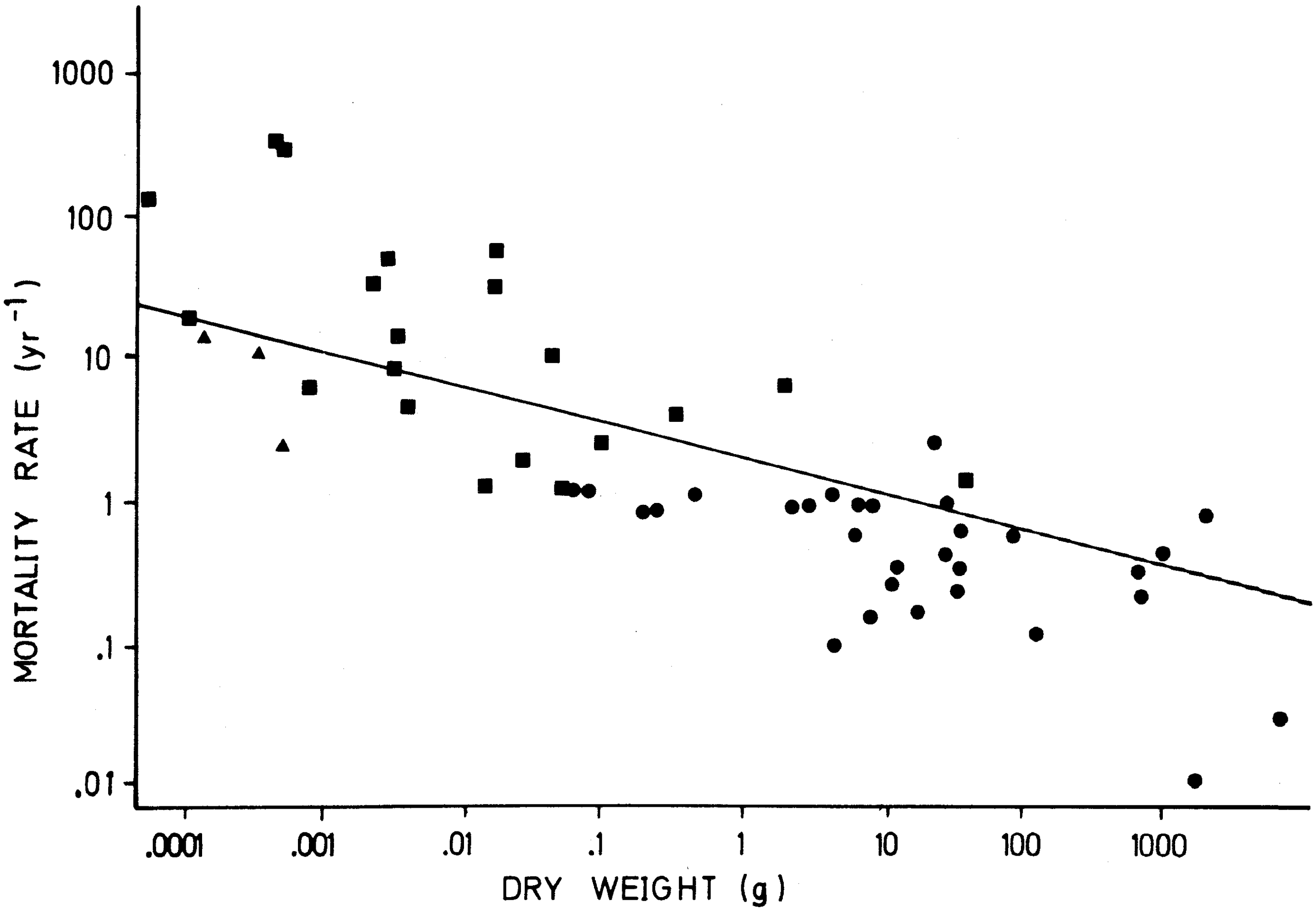

FIG. 1. Natural mortality rate vs. dry weight. The straight line is described by equation (8). ●, adult fish (Ursin 1967); ■, larval and juvenile fish (Ahlstrom 1954; Cushing 1974; Farris 1961; Graham and Chenoweth 1971, 1973; Pearcy 1962; Poulsen 1931; Sette 1943); ▲, chaetognaths (Sameoto 1971).

and parameter K_1 is the growth efficiency, i.e. growth divided by ingestion. Specific growth rate can be expressed as

$$(4) \quad G(w) = kw^{-x}$$

where k and x are constants (Kerr 1974), so that from equation (2),

$$(5) \quad \beta(w) \sim w^{x-c}.$$

Using equations (20) and (21) from Silvert and Platt (1980),

$$M(w) = \frac{G(w/q)}{K_1 q}\,\frac{\beta(w/q)}{\beta(w)}$$

and from equations (4) and (5) above,

$$(6) \quad M(w) = \frac{k}{K_1} q^{c-1} w^{-x} = ckw^{-x}.$$

To estimate parameter c in equation (3), we need to know the growth efficiency, K_1. Somatic growth represents the difference between assimilated ration and losses due to metabolism and reproduction. Metabolism is found to take the form αw^{γ} where $\gamma \simeq 1 - x$ (Kerr 1974). As will be shown below, reproductive losses are small relative to metabolic losses and therefore can be ignored. Thus, if I is the ingestion rate and p is the assimilation efficiency,

$$\frac{dw}{dt} = pI - \alpha w^{1-x} = G(w)\cdot w = kw^{1-x} \quad \text{for all } w.$$

Clearly, then,

$$I = \frac{k + \alpha}{p} w^{1-x}$$

and growth efficiency,

$$(7) \quad K_1 = \frac{p}{\alpha/k + 1}.$$

Calculation of Biomass and Mortality Rate Parameter Values

The following values are used to solve for the growth efficiency, K_1. The weight coefficient for metabolic rate α is taken to be $2 \times 10^{-7}\cdot s^{-1}$ (Fenchel 1974). The weight coefficient for growth rate k is set at $5 \times 10^{-8}\cdot s^{-1}$, which is the geometric mean of values given in Ware (1980). Finally, Kerr (1974) gave a value of 0.7 for the assimilation efficiency p. Substituting these values of α, k, and p into equation (7), we obtain a growth efficiency K_1 of 0.14.

To solve for c, the prey predator size ratio q is taken to be 3.45×10^{-4}, assuming that prey are 7% of the predator's length (Ware 1978) and that weight is proportional to the cube of the length. There is some indication that q decreases with increasing size (Silvert and Platt 1980), but this will be ignored. Therefore, from equation (3), $c \simeq 1.22$.

Finally, to solve for natural mortality rate, we need a value for the weight exponent x for growth and metabolic rate. According to D. M. Ware (Pacific Biological Station, Nanaimo, B.C.,

TABLE 1. Results of the sensitivity analysis as percentage change in the mortality rate for perturbation in individual parameters.

Parameter	Perturbation			
	−25%	−5%	+5%	+25%
α	−1.6	0.0	0.8	1.6
k	−23.2	−4.2	5.0	23.0
q	−0.8	0.0	0.0	0.8
p	2.5	0.8	0.0	−1.6

pers. comm.), x varies between 0.1 and 0.4, so that an average value of 0.25 is used here. A value of 0.25 agrees with Fenchel's (1974) value for the weight exponent of metabolism. Thus, equation (6) becomes

$$M(w) = (6.1 \times 10^{-8} \cdot \mathrm{s}^{-1}) w^{-0.25} \quad \text{or} \, (1.92 \cdot \mathrm{yr}^{-1}) w^{-0.25}. \tag{8}$$

Note that from equation (5), $\beta(w) \sim w^{x-c} \sim w^{-0.97}$ as shown by Silvert and Platt (1980). Since $b(w) = \beta(w)dw$ and $dw \sim w$, then $b(w) \sim w^{0.03}$. As the exponent of w is very small, the biomass is virtually the same in all size-classes, in accordance with observations by Sheldon et al. (1972, 1973).

It was stated earlier that reproductive losses are small relative to metabolic losses and can therefore be ignored. This can be shown in the following way. Using values of α, k, and x given above, an animal of 125 g would have respired 198 g over the preceding year, while an animal of 1000 g would have respired 1010 g. Since egg production averages about 16% of the weight of the animal for various fish stocks (Gunderson 1980), metabolic rate is 6–10 times higher than reproductive losses for animals between 125 and 1000 g.

A sensitivity analysis was performed to assess the effects of perturbations of the parameter values for α, k, q, and p on the mortality rate (Table 1). Clearly, mortality rate is relatively insensitive to all parameter values except that of the growth rate, k.

Comparison with Data

The relationship between mortality rate and dry weight given by equation (8) is compared with data from various sources (Fig. 1). Body wet weight was calculated from Ursin's (1967) formula giving the mean size $\hat{w}$ of fish from which mortality estimates were made. A dry weight to wet weight ratio of 0.2 was assumed. Although the preceding analysis refers to pelagic ecosystems, no attempt was made to identify and exclude data from demersal fishes. Data for chaetognaths are also included, since chaetognaths are of the size being considered here.

On the whole, the relationship given by equation (8) agrees well with the observations except for very small and very large w. For fish larvae, field estimates of mortality rate may be too large in some cases because of patch diffusion and increasing net avoidance with age. For very large w, mortality rate of the adult fish is lower than that predicted by equation (8) because of the lack of predation above a certain size.

Discussion

The theory described in Silvert and Platt (1980) and applied here to fish-sized particles involves several assumptions. First, it is assumed that mortality is primarily due to predation. This is probably reasonable in the case of small organisms, for although disease and senility are present, the proximal cause of mortality is usually predation (Cushing 1974). However, in the case of the largest organisms, mortality is obviously controlled by other factors. Second, it is assumed that there is a constant influx of material at the lower end of the spectrum, when in fact the influx varies seasonally. Finally, no provision is made for food energy gained from the benthic ecosystem.

The relationship between mortality rate and size (equation (8)) can only be viewed as a central tendency for organisms in an ecosystem as a whole and may not be applicable to individual species. In any size-class, certain species will be particularly vulnerable to predation and will therefore have a higher mortality rate. In addition, mortality rate for individual species appears to increase after sexual maturity is reached (Cushing 1975).

It appears from Fig. 1 that the magnitude of larval fish mortality is consistent with the hypothesis that predation is the primary source of mortality. This is of interest in light of recent attention given to food availability as a major factor affecting larval survival, particularly at the end of the yolk sac stage (see May 1974). Presumably, though, the condition of individual larvae affects their vulnerability to predation.

In critique, the general expression for fish mortality as a function of size, $M(w) = ckw^{-x}$, yields values that are encouragingly close to observed mortalities. Parameters k and x are well founded in bioenergetics, while c can be calculated. It is easier to measure these parameters in the laboratory than to estimate the mortality rate of fishes directly in the field. However, this expression does not offer a practical alternative to the traditional methods of mortality estimation. Its application is limited by the assumptions and approximations made in formalizing the theory from which it is derived. Nevertheless, the expression does serve to relate many observations simply and to increase our understanding.

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