

VISUAL PREDATORS, ENVIRONMENTAL VARIABLES AND ZOOPLANKTON MORTALITY RISK

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ZOOPLANKTON
MORTALITÉ
LUMIÈRE
MODÈLE

RÉSUMÉ – Plusieurs aspects du risque de mortalité du zooplancton (taille, contraste propre, diminution de la lumière incidente et de la lumière diffuse, profondeur, intensité de la lumière ambiante, sélectivité, satiété du prédateur) sont étudiés à partir d'un modèle de rencontre prédateur-proie dans lequel on suppose que le prédateur se nourrit à vue. Nous mettons en évidence que la pente du gradient vertical de risque décroît avec la taille du zooplancton et qu'il est 3 à 4 fois plus accusé pour les nauplii que pour les formes ayant la taille des Euphausiacés. A petite échelle une distribution verticale en taches se rencontre plutôt chez les petites formes. En raison de différences dans la détection, le risque de mortalité (et le taux de nutrition d'un prédateur non sélectif) dépend très nettement des différences de taille. Une strate turbide, comme par exemple une couche d'eau riche en phytoplancton, superposée à des eaux claires, peut offrir une zone de refuge pour le macroplancton et pour les Poissons de faible taille se nourrissant de plancton. De même, le risque de devenir une cible pour le microzooplancton diminue dans cette strate, mais persiste et s'accroît au-dessous de cette couche. En situation de faible contraste dans des eaux peu turbides, la réduction du contraste inhérent entraîne une meilleure protection.

ZOOPLANKTON
MORTALITY
LIGHT
MODEL

ABSTRACT – Several aspects of zooplankton mortality risk (body size, inherent contrast, beam and diffuse light attenuation, depth, ambient light level, selectivity, predator saturation) is studied from a predator-prey encounter model where the predator is assumed to feed by vision. It is shown that the steepness of the vertical gradient in risk decreases with zooplankton size, being 3-4 times steeper for nauplia than for krill-sized animals. Fine-scale vertical patchiness is thus more likely to be found for smaller forms. Due to differences in detectability, mortality risk (and feeding rate of an unselective predator) will be severely influenced by size differences. A turbid layer, such as a phytoplankton layer, overlying clear water may act as a refuge for macroplankton and small planktivorous fishes. Microzooplankton will also have gradually reduced objective risk in the layer, but even lower risk below the layer than inside it. Increased protection by reduced inherent contrast is only effective for very low contrasts and in water with low turbidity.

INTRODUCTION

Vertical distributions of pelagic animals must be understood in the context of maximizing life time reproductive output (McLaren 1963, Werner & Gilliam 1984, Clark & Levy 1988, Gabriel & Thomas 1988 a, b, Aksnes & Giske 1990). Giske *et al.* (1993) defined phenotypical fitness for an individual as the difference between its own rate of offspring production and the average rate of the population. A measure for these rates is the instantaneous rate of reproduction, r , which can be used both on the individual and the population levels. To describe the rate of individual (semelparous) offspring production over a life time, we may write

$$r = \ln (bS)/G \quad (1)$$

where b is fecundity (offspring per mother) and S is probability of juvenile survival over generation time (G). The term bS thus represents the so-called net reproductive rate (R_0), which is the ratio of individuals separated by one generation. Survival probability (S) can be expressed as the product of mortality risk (Z) and generation time length,

$$S = e^{-GZ} \quad (2)$$

Thus we may rewrite Eq.1 as (Giske *et al.* 1993)

$$r = \ln b / G - Z \quad (3)$$

which is the individual approximation of the continuous population dynamics equation $r = b - d$. uEq. u3 states that a zooplankter will maximize

its fitness by seeking a habitat which allows a high fecundity, a short generation time, and a low mortality risk, and the equation also expresses the relative importance of these three factors on lifetime fitness. For a zooplankton feeding on phytoplankton and preyed upon by visual predators, both feeding rate and mortality risk will generally decrease with increasing depth, so an attempt to increase b will generally also increase Z (and decrease G). While there has been a considerable effort in expressing the influence of environmental variables on fecundity and generation time of zooplankton (e.g. McLaren 1966, 1978, Bottrell *et al.* 1976, Vidal 1980 a, b, Huntley & Boyd 1984, Carlotti & Sciandra 1989, Carlotti & Nival 1992, Huntley & Lopez 1992), there have been considerably fewer attempts to describe local variations in zooplankton predation risk and mortality rate (Aksnes & Magnesen 1983, 1988, Aksnes & Giske 1990), although this is the potentially most important variable in Eq. 3.

The optimal trade-off between high fecundity or low mortality as expressed in Eq. 3 is based on the average over the whole life span of the individual. However, age, season and diel variability may impact the actual optimal trade-off between growth and fecundity versus survival: Gilliam (1982) and Werner & Gilliam (1984) showed that juvenile fish should choose the habitat that minimizes the ratio between their mortality risk and growth rate ("minimize μ/g ", in their terminology). Aksnes & Giske (1990) and Giske and Aksnes (1992) showed that adult fish should emphasize survival even more, and minimize $Z/\ln(g)$ in their habitat choice. Such differences between juveniles and adults have also been indicated in experiments with gobies (Utne *et al.* 1993, Utne & Aksnes 1994). Aksnes & Giske (1990) also showed that if generation time is influenced by environmental temperature (Huntley & Lopez 1992), the major trade-off will be between mortality risk and temperature. Furthermore, Giske & Aksnes (1992) and Rosland & Giske (in press) have shown that while risk-willingness of a juvenile mesopelagic fish in winter depends on the average life-history derived trade-off (Z/g) and stomach fullness, the adults seem to employ the strategy of maximizing probability of overwintering survival. Risk-willingness by animals facing the threat of starvation or exhaustion also exceed by far the average expectations from life history models (Stephens 1981, Metcalfe & Furness 1984). Thus the overall importance of avoiding mortality must be found from fitness assessments at the appropriate time scale, while the numerical value of the mortality risk should be assessed by mechanistical models of the predation process.

Two aspects of the environment distinguish the pelagic habitat from all others: 1) compared to air, the transparency of water is low. While visual

range in air is mainly restricted by the horizon, an underwater image is attenuated at scales of millimeters to meters. 2) Also compared to littoral and benthic habitats, the pelagic does not contain obstacles allowing local shelter. Thus visual predation risk in the pelagic habitat may be approximated by underwater light and image transmission (Duntley 1962, Eggers 1977, Aksnes & Giske 1993). The scope of this paper is to analyse some environmental aspects of zooplankton mortality risk caused by visual predators, mainly based on the fish vision model of Aksnes & Giske (1993). Fish visual range depends on the visual ability of the fish, on the size and inherent contrast of its prey, but also on environmental variables as ambient light intensity, attenuation of light beams and attenuation of diffuse light. Fish vision is thus strongly depth dependent, and we will examine some objective aspect of mortality risk, irrespective of local distribution of predators and prey.

MODEL

We assume predators and prey to be randomly distributed on the local horizontal scale. The total number of encounters between predators and their prey over a time period T is then a function of local densities of predators (P) and zooplankton (N), their speed (V) and the ability of the predators to detect their prey (here interpreted as a prey detection area, A):

$$E = TNPAV \quad (4)$$

In the water column, the local rate of encounters (E/T) is strongly influenced by depth distribution of predators and prey. However, as both planktivores and plankton are mobile and can take any position in the vertical, the density-independent aspect of predator-prey contact rates is of fundamental importance, as it describes the objective (i.e. environmental) aspect of predation risk:

$$e = E / (TNP) = AV \quad (5)$$

For a visual predator, the prey detection area A is determined by ambient light (depth), predator eye sensitivity, prey size and contrast, and the speed V is given by the predator and prey. Eq. 5 describes an objective function for food encounters for planktivores, where zooplankton mortality risk is not associated with the current vertical distribution of P . The physical variables underlying A will be crucial for the potential vertical variation in zooplankton predation risk.

Gerritsen & Strickler (1977) showed that the velocity component of contact rates can be described from swimming speeds of both predators and prey, and Rothschild & Osborn (1988) showed that turbulence may increase the contact rates con-

siderably, especially for slow-moving predators. However, for the case of visual predators, predator swimming speed is generally an order of magnitude higher than turbulent velocity and zooplankton swimming speed, and we may write :

$$V \approx v \quad (6)$$

where v is planktivore swimming speed.

Aksnes & Giske (1993) have derived a simple model for how fish visual range R is influenced by the environment. The visual range depends on depth (z), light regime (air light intensity E_0 , fraction of irradiance lost in the air-water interface ρ , diffuse attenuation coefficient K and beam attenuation coefficient c), the planktivore (sensitivity threshold for eye for detection of changes in irradiance ΔS_e) and the zooplankton (surface area a [$= \pi (L/2)^2$, L = body length] and contrast $|C_0|$:

$$R^2 e^{zK + cR} + \hat{c}R = \rho E_0 |C_0| a \Delta S_e^{-1} \quad (7)$$

The prey detection area of a swimming visual predator is the cross-sectional area of the cylinder determined by its swimming path, its visual search range (R) and the search angle (θ).

$$A = \pi (R \sin\theta)^2 \quad (8)$$

(Luecke & O'Brien 1981, Dunbrack & Dill 1984, Aksnes & Giske 1993). There has been some attempts to measure θ (Hairston *et al.* 1982, Dunbrack & Dill 1984, O'Brien & Evans 1992), and although some of these results indicate that θ is not equal in all directions, we here assume a symmetrical forward oriented visual field. With this assumption, calculations of zooplankton mortality risk is straightforward, and mortality risk for a zooplankter from moving visual planktivores is

proportional to the planktivore's prey detection surface, for which the visual range (given by Eq. 7) is the only environmental variable:

$$Z \propto A \propto R^2 \quad (9)$$

The proportionality factor is influenced by overall abundance of predators (P) and their swimming speed ($V = v$), on the (time or state-dependent) optimal trade-off between survival and other activities (c.f. Eq. 3), and possibly by availability of alternative prey items. Assessments of feeding of mesopelagic planktivores based on Eqs. 7-8 have been performed by Giske & Aksnes (1992) and Rosland & Giske (in press). We will here focus on risk assessment for the zooplankter after Eqs. 7-9.

ANALYSIS AND DISCUSSION

Body size and vertical gradients in mortality risk

For all sizes of plankton, visual based mortality risk will generally be reduced with depth according to a general decrease in ambient light. But the rate of reduction depends strongly on both prey size and actual depth. Generally, the easier a zooplankter is to see, the less change in detection range will be gained after a vertical relocation : the change of detection range of a predator when its prey moves one meter down is higher for smaller than for larger prey, and is also higher in deep water than in shallow water (Fig. 1 A). Consequently, the reduction in visibility with depth is much steeper for microplankton than for macroplankton (Fig. 1 B). Thus, one could predict

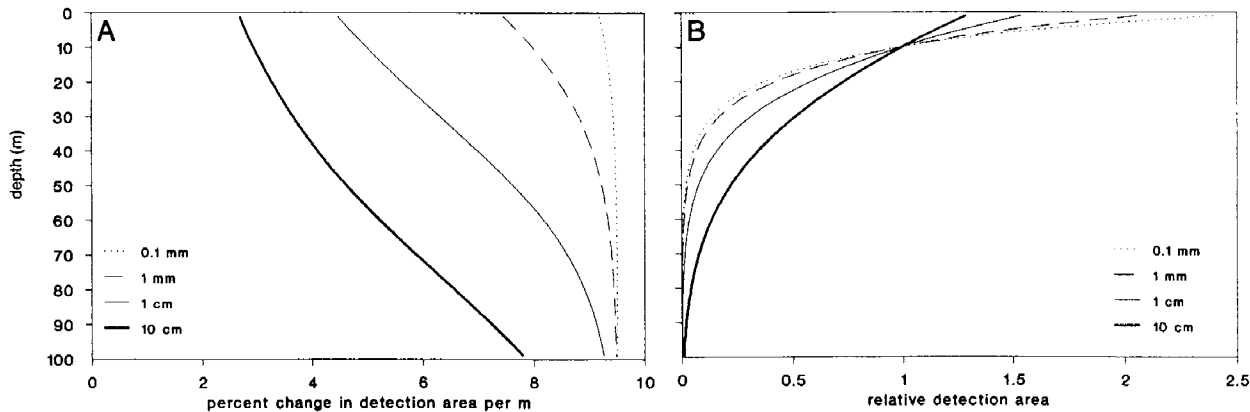


Fig. 1. – Effects of depth for detection risk of zooplankton. A, Relative vertical change in detection area. B, Detection area relative to area at 10 m depth. The parameter values in Eq.7 have the following standard values, if not varied in a simulation : E_0 : $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$, $\rho = 0.5$, $z = 1 \text{ m}$, $K = 0.1 \text{ m}^{-1}$, $c = 0.3 \text{ m}^{-1}$, $C_0 = 0.5$, $\theta = 30^\circ$, $L = 0.1 \text{ cm}$, $\Delta S_e = 2.5 \cdot 10^{-5} \mu\text{mol m}^{-2} \text{s}^{-1}$. Zooplankton is assumed spherical, so that its surface area $a = \pi (0.5L)^2$, where L is body length. Zooplankton wet weight is $W = 4/3 \pi (0.5L)^3$, where L is length in cm (thus assuming a spheric zooplankter ; $1 \text{ g wet weight} = 1 \text{ cm}^3$).

a more pronounced fine-scale vertical distribution of microzooplankton than of macrozooplankton. The benefit in terms of increased survival by adopting a narrow vertical range must eventually be balanced by costs of maintaining this vertical position, as small-sized individuals have higher swimming costs (Vlymen 1970).

Prey selectivity and size: relative visibility and body size

There has been a debate on whether planktivorous fish select their prey items on basis of energetic content (according to the optimal foraging theory) or visibility (Werner & Hall 1974, Confer & Blades 1975, Eggers 1982, Li *et al.* 1985, Wetterer & Bishop 1985, O'Brien & Evans 1992). Frequently, the term "selectivity" is used when the size - (or species-) composition of zooplankton in fish stomachs differs from zooplankton samples, irrespective of whether the difference is caused by detection limitations, zooplankton behaviour or the planktivore's food choice.

The range R at which an individual can be detected by a visual planktivore increases with zooplankton size and decreases with depth. At large depth, the detection range of the planktivore is proportional to L^2 , since (when R is small and $cR \ll zK$ so that $cR + Kz \approx Kz$) $R^2 \propto a \propto L^2$ (Eq. 7, Fig. 1). However, this proportionality does not hold for the largest plankton (i.e. when cR is of same magnitude as Kz), and the deviation

from $R^2 \propto L^2$ appears first in shallow water (Fig. 2). This is because when R is large, $R^2 \propto L^2 e^{-cR - zK}$ (Eq. 7). Thus, while a high representation of larger individuals in fish stomachs from shallow water may be explained by active prey selection, the same pattern in stomach composition at larger depth (or more generally at low irradiance levels) would be expected for encounter-based feeding. However, we should here remind that our prey is assumed passive and stationary, and quite different results could be obtained if prey swimming speed is of importance (e.g. Jakobsen & Johnsen 1988).

Inherent contrast and ambient light level

Transparent forms of zooplankton occur both in marine and limnetic habitats. Generally, the forms with higher inherent contrast experience higher mortality risk from visual predators (Nilsson 1960, Merret & Roe 1974, Mellors 1975) or are confined to habitats void of such predators (Fox 1948, Hobeak & Wolf 1991). The fitness cost associated with high fecundity and growth (many eggs or full gut) or extended habitat utilization (e.g. by UV protective pigments or red haemoglobin) depends on the water quality of the habitat and the size and position of the zooplankton. The benefit of reduced contrast is strongly dependent on the overall visibility of the animal. In decreasing order of importance, the dependency of contrast for mortality risk is influenced by overall

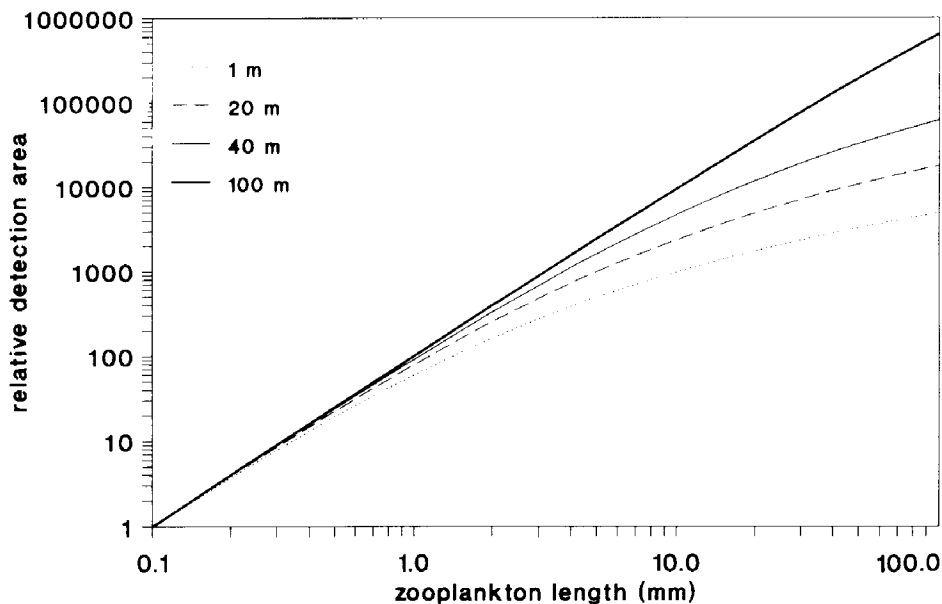


Fig. 2. – Effects of size for detection risk of zooplankton. Detection areas relative to 0.1 mm animal. Constant parameter values in Eq. 7 as in Fig. 1.

ambient light intensity, zooplankton size and water clarity. At low light intensities, change in mortality risk is proportional to change in contrast, while changes in contrast does not affect mortality risk so much in brightly illuminated water (Fig. 3 A). While minute zooplankters will gain a pronounced reduced predation risk by reduced inherent contrast, this will not influence risk of large-bodied individuals (Fig. 3 B). Changes in turbidity operate the same way a light intensity; contrast is of minor importance in highly turbid water, but will gradually increase in importance as water clarity increases (Fig. 3 C). An isoline for depths and inherent contrasts giving equal visibility and predation risk is shown in Fig. 4. This curve is independent of prey size and shows the potential increase in surface habitat exploitation for truly hyaline animals. The shape of the curve is also independent of absolute level of contrast, so that starting with less hyaline animals close to the surface will only shift the whole line to the right.

For the smaller size classes, reducing contrast is beneficial (Fig. 3 c), while migration may be relatively more costly (Vlymen 1970, Morris *et al.* 1985) due to drag coefficient and Reynolds number. An alternative strategy to diel vertical migration may then be diel variation in contrast, due to a diel pattern in feeding (Frost 1988, Haney 1988). There are several reports in the literature

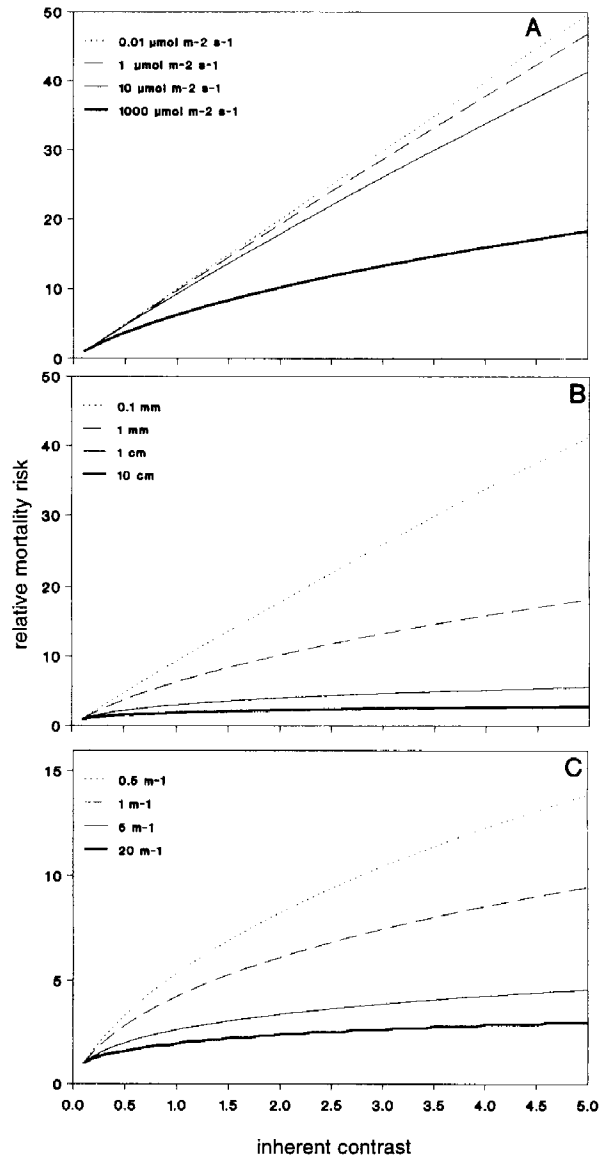


Fig. 3. - Effects of inherent contrast for detection risk of zooplankton. A, Relative detection areas under different light intensities. B, Relative detection areas under different body sizes. C, Relative detection areas under different beam attenuation coefficients. Constant parameter values for Eq. 7 as in Fig. 1.

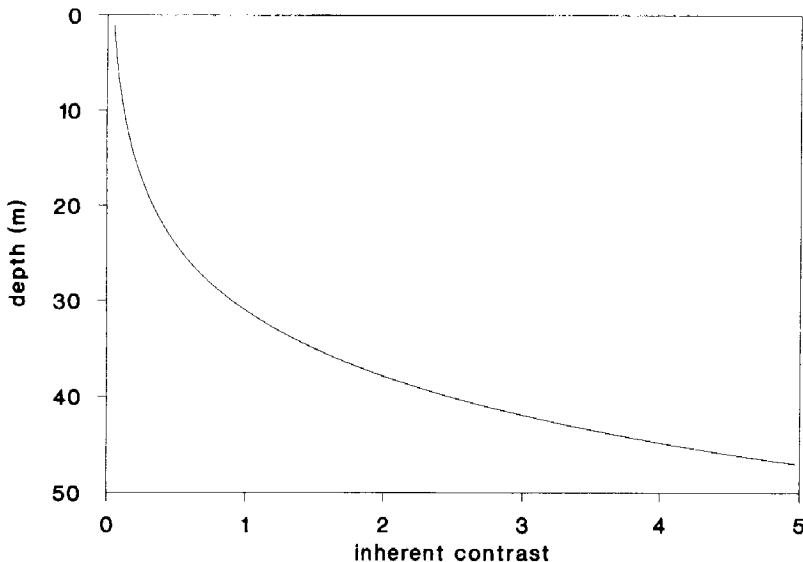


Fig. 4. - Isoline for equal visibility under varying inherent contrasts and depths. Constant parameter values in Eq. 7 as in Fig. 1.

of a diel rhythm in copepod feeding, independent of vertical migration (Mackas & Bohrer 1976, Hayward 1980, Head *et al.* 1985, Daro 1988, Włodarczyk *et al.* 1992). By feeding in darkness, small zooplankters may adjust their contrast during day to a minimum. This gain in survival thus has a cost in growth, and several field studies have shown that diel feeding rhythms are reduced under low food availability (Boyd *et al.* 1980, Dagg 1985, Daro 1988).

Chl. a maximum and beam attenuation: can maximizing gain be equal to minimizing risk ?

The underwater light regime is strongly influenced by absorption and scattering processes. A collision between a light beam and a particle will result in a change in direction of the light beam (scattering) or an absorption of the beam by the particle (i.e. an algae or an eye). Due to scattering, light at large depths will generally be diffuse. Scattering does, however, not reduce the overall light intensity, as absorption does. However, the transport of an image is damaged by both scattering and absorption. Parts of the image will be scattered out of the straight line between the object and an eye, and diffuse light will be scattered into the same path, both corrupting the image. From Eq. 7 we see that the attenuation coefficients (c and K) are exponents, and have therefore a potential high impact on objective predation risk. There is no general relationship between c and K , as this depends on the type of material [e.g. algae (mainly absorbing) or clay (mainly scattering)] causing attenuation. The diffuse attenuation coefficient at a depth (K_z) can be estimated from local chlorophyll concentration (C , mg m^{-3}) and extinction caused by non-chlorophyll particles (k_0 , m^{-1}):

$$K_z = k_0 + 0.054 C^{2/3} + 0.0088 C \quad (10)$$

(Riley 1956). Beam attenuation at depth z is commonly 2-4 times the local diffuse attenuation (Kirk 1980), and we assume here

$$c_z = 3 K_z \quad (11)$$

The diffuse attenuation coefficient in Eq. 7 is, however, the average of the water column from the surface to depth z , and is thus found from the local attenuation coefficient at depth and the average of the column above:

$$K = K_{0-z} = [(z-1) K_{0-(z-1)} + K_z] / z \quad (12)$$

The overall importance of the beam attenuation coefficient in surface water ($z = 1 \text{ m}$) depends on prey size and overall light intensity (Fig. 5). While mortality risk of small prey is falling

rapidly with increased attenuation in the whole range $0.2 - 20 \text{ m}^{-1}$, large prey will gain much more by an increase in c from 0.2 to 2 m^{-1} than from 2 to 20 m^{-1} . The overall light intensity is also of importance: the lines for the large 1 and 10 cm prey at $0.1 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (civil twilight, Fig. 5 A) are identical to the lines for the small 0.1 and 1 mm prey at $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (sunny summer day, Fig. 5 B), respectively.

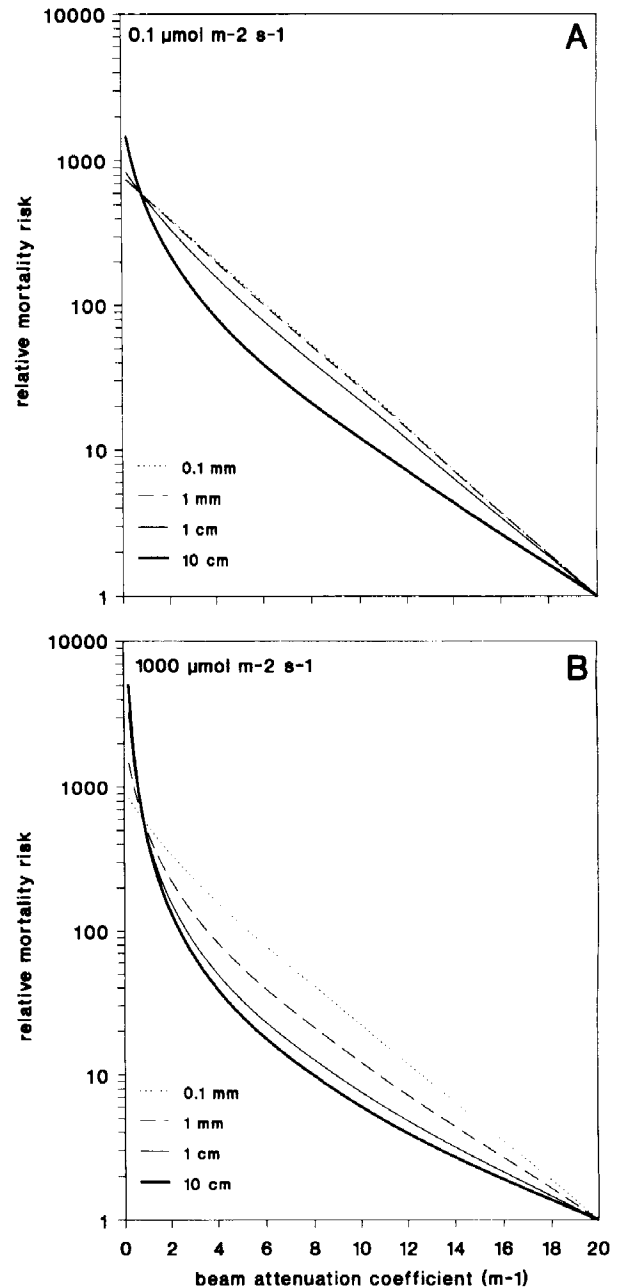


Fig. 5. - Effect of turbidity, prey size and light intensity on detection risk of zooplankton. Diffuse attenuation coefficient is $K = c / 3$. A, Civil twilight, $E_0 = 0.1 \mu\text{mol m}^{-2} \text{ s}^{-1}$. B, Sunny summer day $E_0 = 1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$. Constant parameter values for Eq. 7 as in Fig. 1.

Mortality risk at a depth depends on ambient light ($E_z = E_0 \rho e^{-Kz}$) and the local attenuation coefficients (K_z and c_z). As shown in Fig. 1 A, the decrease in mortality risk does with increasing depth is low for large prey in shallow water, while they are quite sensitive to changes in the beam attenuation coefficient in water of low or moderate turbidity (Fig. 5). Thus a situation may arise where mortality risk increases downwards. This may happen if attenuation in a distinct vertical layer is high (e.g. a layer of brackish water or a sharp chlorophyll peak). Such a situation is sketched in Fig. 6 A. Due to a subsurface chlorophyll maximum, beam attenuation c_z is high at 1 - 5 m and low at surface and below 5 m and average diffuse attenuation coefficient increases through the turbid layer. The objective effect of this layer of high turbidity on the vertical predation risk profile is highly size-dependent, reflecting the different size-dependent impact of K and c (Fig. 6 B). For minute zooplankters, a layer of high turbidity acts to reduce overall light intensity below, and mortality risk below this layer is much less than above. For macrozooplankton, the layer works as thick fog where they can hide. In the graphical example, mortality risk is 10-30 times higher below the layer than inside it, while risk is not much less below than above the layer. Thus macrozooplankton benefit from the high c_z in the layer, while microzooplankton gain from the increase in K_{0-z} through the layer.

The turbid layer may be a very beneficial habitat for macroplankton, especially if they feed on the abundant turbidity-generating particles (such as phytoplankton). If macroplankton and small pelagic fishes feed on microplankton, the turbid layer may act as a high risk area for microplankton, as their predators may gain protection by

staying there without reduction in their prey encounter rates. This was observed by Miner & Stein (1993), who found predation intensity of larval bluegill sunfish on crustacean zooplankton to increase in situations with high turbidity and high light intensity.

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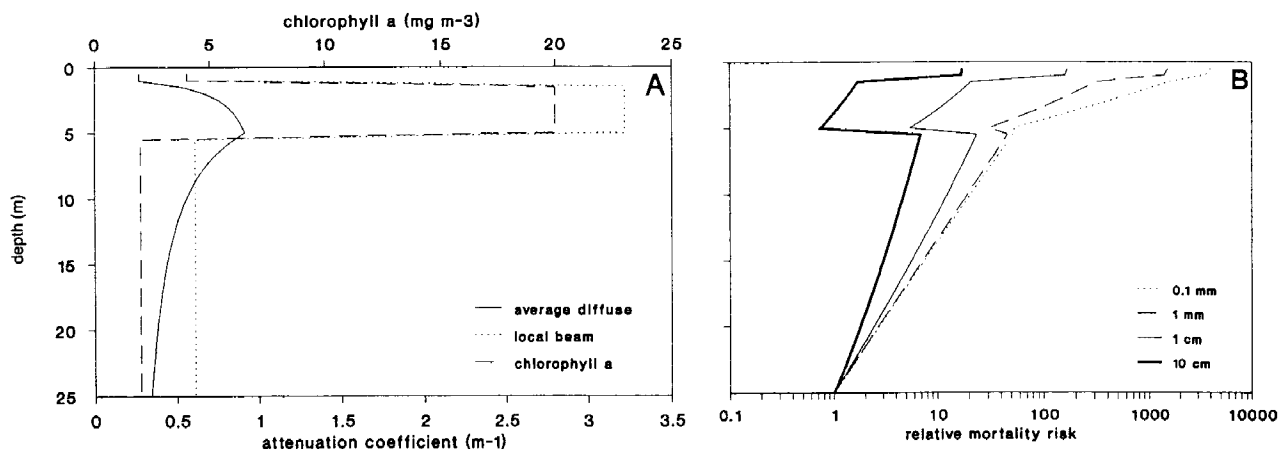


Fig. 6. – Effect of turbidity on vertical distribution of mortality risk. A, Vertical profile of attenuation coefficients. The local beam attenuation coefficient c_z and the average diffuse attenuation coefficient K_{0-z} are calculated from chlorophyll concentration and non-chlorophyll extinction after Eqs. 10-12. Non-chlorophyll extinction k_0 is sat at 0.5 m^{-1} in the turbid layer and 0.1 m^{-1} above and below. B, Size-dependent relative detection risk for zooplankton. Constant parameter values for Eq. 7 as in Fig. 1.

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