A theoretical model of aquatic visual feeding

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ABSTRACT

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A model for visual feeding by aquatic predators is derived. The predator's visual range, which depends on its visual capability, surface light, water clarity, and size and contrast of the prey, is emphasised. Central to the model is the assumption that a prey may be recognized only if the difference in retinal flux, with and without the prey image, exceeds a threshold. This assumption is equivalent to requiring that the product of apparent contrast at retina, retinal background irradiance and area of prey image must exceed a threshold. Visual range (r) is found from the equation $r^2\exp{(cr + Kz)} = \rho E_0 \mid C_0 \mid \pi\beta^2 \Delta S_e^{-1}$, where c is beam attenuation coefficient, z is depth, K is diffuse attenuation coefficient, ρ is light loss through the surface, E_0 is surface light intensity, C_0 is inherent contrast of prey, β is prey radius and ΔS_e is sensitivity threshold of the eye for detection of changes in irradiance. The model predicts that visual range increases non-linearly with increasing predator size and ambient light. Visual range also increases almost linearly with increasing prey size and decreases non-linearly with increasing turbidity. These predictions are compared with experimental data. It is shown that characteristic fluctuations in light regime may be more important to feeding than characteristic variations in prey abundance in aquatic environments. Due to the direct impact of light on the feeding process of several predators (and thereby on the mortality process of prey), we conclude that light should be considered an important top–down control in aquatic ecosystems in addition to the bottom–up control exerted through primary production. Finally, the model is testable, and should stimulate a stronger interaction between theory and experiments in aquatic feeding ecology of visual predators.

INTRODUCTION

The term "functional response" was developed in studies of predator response to increases in prey population sizes (Holling, 1959, 1966) and is

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commonly used to refer to the shape of the predator's feeding rate curve
with respect to changes in prey density. Prey density, however, need not be
the main limiting factor for feeding rate. Obviously, the light regime and
the predator's visual (or other sense) capability is crucial for feeding and
survival, and this is reflected in the anatomy of deep-water animals (Munz
and McFarland, 1977; Nicol, 1989). Several experiments have also shown
the dependency of feeding rate on lighting (Vinyard and O'Brien, 1976;
Confer et al., 1978; Howick and O'Brien, 1983). Light attenuation in water
is exponential, and vertical migration of fish and plankton is often de-
scribed as an attempt to maintain a constant light regime (Blaxter, 1976;
Forward, 1988). If feeding rate, through the visual range, depends on light
intensity, the animal can adjust both its feeding rate and predation risk by
vertical migration (Bohl, 1980; Clark and Levy, 1988). The visual range is a
complex variable depending on the prey (as size, contrast and mobility) and
predator (as retinal sensitivity and eye size) in question, and on optical
aspects of the environment (as absorption, scattering and light intensity).
An empirical approach, therefore, requires considerable experimentation
in order to relate visual range to all these factors. Meanwhile, a model for
assessing feeding rate of visual-oriented aquatic animals, and mortality risk
of their prey, is lacking.

The problem of describing visual predation may be greatly reduced if a
theoretical model, encompassing several of the variables influencing visual
range, can be developed. Furthermore, quantitative analyses of habitat
selection and vertical migration in the aquatic environment apparently
depend on improved parameterization of the feeding/predation process
(Clark and Levy, 1988; Aksnes and Giske, 1990). Eggers (1977) arrived at
three equations predicting the sighting distance of a predator under three
different sets of combination of prey size, inherent contrast, ambient
illumination and turbidity. We present a model resembling that of Eggers
(1977), but where the visual range is theoretically related to the above
factors in a single equation. The response of the composite model is then
evaluated on the basis of published measurements on visual ranges of
aquatic predators. Our second aim is to evaluate the relative importance of
light and prey abundance in aquatic environments. Here, we suggest that
characteristic fluctuations in light regime (turbidity and cloud cover) may
be more important for a visual predator than characteristic variations in
prey abundance. Finally, we emphasise light as an instantaneous top–down
control affecting processes at the higher levels of the food chain.

THE FUNCTIONAL RESPONSE OF THE FEEDING PROCESS

For the sake of clarity, we deduce the functional response from "first
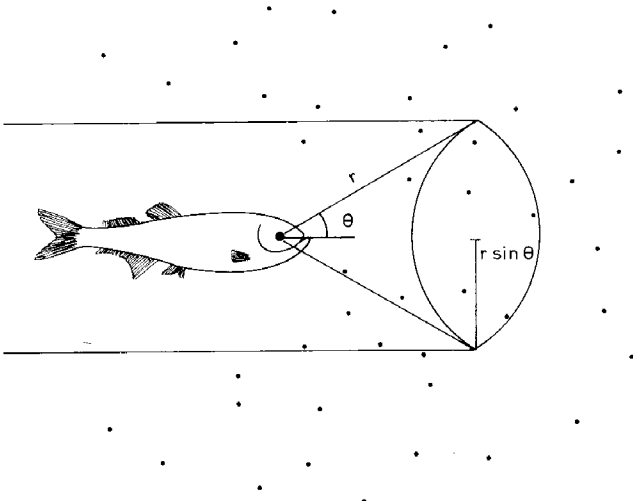principles", and Eqs. (1–5) therefore correspond to the equations given by

Fig. 1. Aspects of prey encounter. Prey encounter rate depends on the visual field angle (θ), visual range (r), prey density (N) and predator swimming speed (v).

Holling (1959, 1966). All symbols used in the following are defined in Table 1.

Maximal prey encounter rate of a predator is given by

$$E = \pi (r \sin \theta)^2 vN \tag{1}$$

where r, θ, v, N are the predator's visual range, reactive field half angle (Luecke and O'Brien, 1981; Dunbrack and Dill, 1984), swimming speed, and prey abundance respectively (Fig. 1). Of the time devoted to feeding, we distinguish between search time and handling time. If a predator spends time T_1 searching for food, the number of prey encountered is:

$$m = T_1 E = T_1 \pi (r \sin \theta)^2 vN \tag{2}$$

Let h be the handling time for one prey item. Handling time is not a part of search time, but scattered among the search time at all prey encounters. Assuming that all prey encountered are consumed (but see Eq. 6), the time needed to handle the m prey encountered during T_1 is

$$T_2 = hm \tag{3}$$

Maximal feeding rate is found by dividing number of prey encountered by total time spent in searching and handling:

$$f = m/(T_1 + T_2) \tag{4}$$

A more realistic feeding rate could be obtained by including other aspects of the predator's time-budget in Eq. (4). Predator scanning is probably

rather compatible with prey searching, while other vigilant activities, such as predator inspection, are not. However, in the following we will concentrate on the potential or maximal feeding rate as given in Eq. (4). T_1 and T_2 are eliminated by the use of Eqs. 2 and 3, and potential feeding rate may be expressed as:

$$f = \frac{h^{-1}N}{\left(h\pi(r \sin \theta)^2 v\right)^{-1} + N} \qquad (5)$$

This expression corresponds to the Michaelis–Menten, Monod and Holling type II formula, where the "half-saturation constant" is given by $(h\pi(r \sin \theta)^2 v)^{-1}$, and maximum uptake is given by the inverse of handling time, h^{-1}. More realism may be put into the model if handling time is considered as a stochastic parameter reflecting the success of the predation cycle as suggested by Lhotka and Straškraba (1978). In an energy-budget model, Eq. (5) can also be solved for v, to find the optimal swimming speed giving maximal net energetic gain (Ware, 1975; Priede, 1985). For stationary and slow-moving predators, encounter rates are also influenced by the mobility of prey (Gerritsen and Strickler, 1977) and (for planktivores) by small-scale turbulence (Rothschild and Osborn, 1988; Sundby and Fossum, 1990). Prey mobility may also be important for the recognition of prey, and this may be reflected as an increased visual range.

If the predator's gut capacity is approached ($D = D_{max}$), potential feeding rate is limited by the digestive processing rate (d) rather than by handling time, as we prefer not to consider processing as part of prey handling:

$$f_{max} = \begin{cases} \min(d, f), & D = D_{max} \\ f, & D < D_{max} \end{cases} \qquad (6)$$

Several organisms, including fishes with well-developed eyes, are capable of feeding in total darkness (e.g. Pitcher, 1986). Under such circumstances it is reasonable to assume that other stimuli than light are responsible for prey detection. Accordingly, a functional response based on other perceptive cues should be formulated separately. In this paper, only vision-based feeding is considered.

THE VISUAL RANGE

Basic assumption

Munz and McFarland (1977) list two conditions that must be met for an animal to see a target: (1) enough light must come from the target to

TABLE 1

Definitions of parameters

Symbol	Description	Unit
A	area of retina	m^2
A_{pr}	area of the prey image at retina	m^2
β	prey radius	m
a	absorption coefficient	m^{-1}
b	scattering coefficient	m^{-1}
C_0	inherent contrast of prey	dimensionless
C_r	apparent contrast at retina	dimensionless
C_x	apparent contrast at distance x	dimensionless
c	beam attenuation coefficient	m^{-1}
D	gut content	ind.
d	digestion rate	ind. $ind.^{-1} s^{-1}$
E	prey encounter rate	ind. s^{-1}
E_0	irradiance in the air at the sea surface	$\mu E\ m^{-2}\ s^{-1}$
E_z	irradiance at depth z	$\mu E\ m^{-2}\ s^{-1}$
E_b	background irradiance	$\mu E\ m^{-2}\ s^{-1}$
E_{br}	background irradiance on retina	$\mu E\ m^{-2}\ s^{-1}$
E_{bx}	background irradiance on eye	$\mu E\ m^{-2}\ s^{-1}$
E_{px}	apparent radiance of prey (at distance x) on lens	$\mu E\ m^{-2}\ s^{-1}$
E_{pr}	apparent radiance of prey on retina	$\mu E\ m^{-2}\ s^{-1}$
F_1	radiant flux on retina according to background radiance only (no prey present)	$\mu E\ s^{-1}$
F_2	radiant flux on retina according to background and prey radiance	$\mu E\ s^{-1}$
$\Delta F = F_1 - F_2$	difference in retinal radiant flux in presence and absence of prey in reactive field	$\mu E\ s^{-1}$
f	potential vision-based feeding rate	ind. $ind.^{-1} s^{-1}$
f_1	focal length of eye lens	m
h	handling time of one prey item	s $ind.^{-1}$
K	vertical attenuation coefficient for irradiance	m^{-1}
k	ratio between radiances at retina and lens	dimensionless
m	number of prey encountered during time T	ind.
N	prey density	ind. m^{-3}
r	visual range	m
ρ	fraction of irradiance lost through the air–sea interface	dimensionless
ΔS_e	sensitivity threshold of eye for detection of changes in irradiance	$\mu E\ m^{-2}\ s^{-1}$
ΔS_r	sensitivity threshold for detection of changes in radiant flux on retina	$\mu E\ s^{-1}$
$T = T_1 + T_2$	sum of search time and handling time	s
T_1	total search time during T	s
T_2	total handling time during T	s
v	swimming speed	$m\ s^{-1}$
x	distance between prey and predator eye	m
z	depth	m
θ	reaction field angle	degrees

activate the visual receptors, i.e. the visual system must be sufficiently sensitive; (2) there must be enough visual contrast so that the target can be distinguished from the background against which it is viewed. The amount of photons entering the target-image on the retina depends on both size and irradiance of the image, and the first condition given by Munz and McFarland (1977) should therefore encompass both. Eggers (1977) gave three equations for the sighting distance for different combinations of contrast, prey size, ambient illumination and turbidity. We will arrive at a single equation by simply assuming that the predator may recognize a prey if the difference in number of photons (ΔF) entering retina with (F_1) and without (F_2) a prey image is above a certain threshold (ΔS_r):

$$\Delta F = |F_2 - F_1| \geq \Delta S_r \qquad (7)$$

These quantities have unit $\mu E\ s^{-1}$, and ΔS_r represents the sensitivity threshold for recognition of a prey according to changes in radiant flux on retina, while ΔF is the actual difference between retinal radiant flux in presence and absence of prey. In other words, we assume that the number of photons entering retina has to change with a certain minimum if a prey is to be recognized. It should be noted that we are not assuming a minimum threshold for the rate of change. This may be more realistic, especially if image movement affects prey perception (see Discussion). It should also be noted, however, that with the present model, we do not assume that the prey necessarily is recognized if ΔS_r is exceeded.

With no prey present, number of photons entering retina is a product of the background irradiance on retina (E_{br}) and the area (A) of retina:

$$F_1 = E_{br} A \qquad (8a)$$

With a prey in the reactive field, the number of photons entering retina is the sum of photons entering the retinal image of the prey and those entering the rest of retina:

$$F_2 = E_{pr} A_{pr} + E_{br}(A - A_{pr}) \qquad (8b)$$

where E_{pr} is the irradiance at the area (A_{pr}) of the prey image. Combination of Eqs. (7) and (8) gives:

$$\Delta F = |E_{pr} - E_{br}| A_{pr} \geq \Delta S_r \qquad (9)$$

Defining apparent contrast at retina as $C_r = (E_{pr} - E_{br})/E_{br}$ and inserting into Eq. (9) we obtain:

$$\Delta F = |C_r| E_{br} A_{pr} \geq \Delta S_r \qquad (10)$$

Thus we may rephrase our basic assumption: They prey may be recognized if the product of retinal prey contrast, retinal background irradiance and area of the prey image exceeds a threshold value.

Further elaborations

The irradiance at the retina depends on, but is not equal to, the irradiance at the lens. In the human eye about 90% of the photons are absorbed or scattered in the lens and fluid of the eye (Sternheim and Kane, 1986, p. 599). Furthermore, the ratio between the areas of lens and retina also affects the ratio between the two irradiances. We make no detailed parameterization of losses and magnification in irradiance through the eye, but simply state that there exists an eye-specific ratio (k):

$$k = E_{br}/E_{bx} = E_{pr}/E_{px} \tag{11a}$$

where the subscript x refers to irradiance (and apparent contrast) at the eye lens at distance x from the prey. If we assume a horizontal path of sight relative to the penetrating daylight, the background irradiance (E_{bx}) is independent of x:

$$E_{bx} = E_b \tag{11b}$$

The apparent contrast at the eye lens is related to the inherent contrast (Duntley, 1962):

$$C_x = C_0 \exp(-cx) \tag{11c}$$

where c is the beam attenuation coefficient, and C_0 is the inherent contrast of prey.

The area of the image of the prey on the retina is related to the real size of (a spherical) prey by:

$$A_{pr} = \pi \beta^2 f_1^2 x^{-2} \tag{11d}$$

where β is prey radius, f_1 is focal length of the lens, and x is the distance between eye and prey. As spherical prey are not general, π may be replaced by a more general prey-shape variable.

By the use of Eqs. (11a–d), Eq. (10) is now rearranged:

$$\Delta F = k\, |C_0|\exp(-cx)E_b\pi\beta^2 f_1^2 x^{-2} \geq \Delta S_r \tag{12}$$

At large depths, colour vision may be more or less neglected (Munz and McFarland, 1977, p. 259) and the background radiance may be considered as identical with the field radiance (Jerlov, 1976, p. 159), which is assumed to depend on surface irradiance (E_0), depth (z) and the vertical attenuation coefficient for irradiance (K):

$$E_b = E_z = \rho E_0 \exp(-Kz) \tag{13}$$

where ρ is fraction of irradiance lost through the air–sea interface. Combination of Eqs. (12) and (13) gives:

$$\Delta F = \rho E_0 \exp(-Kz)\,|C_0|\,\exp(-cx)\pi\beta^2 k f_1^2 x^{-2} \geq \Delta S_r \tag{14}$$

If all parameters, except x, are assigned values and $\Delta F = \Delta S_r$, x is equal to the maximum distance at which a prey may be recognized (r, the visual range):

$$\Delta S_r = \rho E_0 \exp(-Kz)|C_0| \exp(-cr)\pi\beta^2 kf_1^2 r^{-2} \tag{15}$$

In order to omit a detailed parameterization of eye optics, we define $\Delta S_e = \Delta S_r/(kf_1^2)$. Thus, the parameters concerning the eye and the visual system of the predator are lumped together into a single eye-specific sensitivity parameter ΔS_e which has the unit of irradiance (at the eye). Eq. (15) may now be rearranged to express the visual range (r):

$$r^2 \exp(cr + Kz) = \rho E_0 |C_0| \pi\beta^2 \Delta S_e^{-1} \tag{16a}$$

or in logarithmic form:

$$2 \ln r + cr = \ln \rho + \ln E_0 + Kz + \ln|C_0| + \ln \pi + 2 \ln \beta - \ln \Delta S_e \tag{16b}$$

Eq. (16) can be solved by iteration. At large depths, however, visual range may be approximated without iterations by ignoring the term cr, since $cr \ll zK$:

$$r^2 \simeq \rho E_0 \exp(-Kz)|C_0| \pi\beta^2 \Delta S_e^{-1} \tag{17}$$

If, at 50 m depth, $K = 0.1$ m^{-1}, $c = 0.3$ m^{-1} and $r = 0.2$ m, cr is 1.2% of $cr + Kz$, and the error of ignoring cr corresponds to setting $K = 0.1$ instead of $K = 0.1012$ m^{-1}. The validity of Eq. (17) will be discussed later.

DISCUSSION

Eqs. (5), (6) and (16) (or 17) give the potential feeding rate in terms of number of prey eaten per predator per second. It should be emphasized that this rate represents a theoretical maximum as we have neglected time used for other activities than feeding, and that our criterion (stated in Eqs. 7 and 10) says that the prey *may* be recognized. Also, total success in the predation cycle is assumed, i.e. if the prey is recognized, it will be attacked, captured and ingested.

Visual abilities of fishes vary interspecifically (Nicol, 1989) and during development (Blaxter and Jones, 1967; Blaxter, 1986) to an enormous extent, and our assumption about the predator's perception of prey is obviously an oversimplification. Nicol (1989) examines several aspects of the visual capabilities of fishes. Of these, perception of movement, colour vision and adaptation to photoenvironment are perhaps the most important not accounted for in our model. Movement of prey may be important for prey recognition (O'Brien et al., 1976). One could speculate that prey mobility may be incorporated by assuming that the retinal sensitivity

parameter (ΔS_r) should reflect a minimum rate of change in retinal radiant flux rather than a minimum difference (with and without prey). At the present stage, however, we prefer the simpler assumption, and judge how the model predictions of visual range compare with published experimental results on planktivore reactive distances. As the spectral distribution of light is not specifically included in the present model, it is primarily applicable for large depths and in situations where the light can be considered monochromatic. But under the assumption that a fish has one (main) pigment set which is maximally efficient at the dominant wave length at the current depth, we will in the following apply our model also on shallow water and laboratory experiments.

Validity of the model

A main problem in comparing model predictions of visual range to experimental findings is associated with the specification of the light environment in experiments compared to that required by the model. Most often, artificial light has been used, and measurements are given in calories or lux. It is unclear to what extent an increase in such quantities are relevant to the visual system of the actual predator. The spectral composition of the light is crucial for the visual system, and our model should be evaluated against data where an increase in the total intensity of the light source results in the same relative increase in the wave lengths relevant for the visual system. Furthermore, in experiments optical properties of the water are often given in turbidity units (JTU or NTU), while our model require data on beam attenuation (c) and extinction of diffuse light (K). Despite the non-compatibilities between our model assumptions and experimental conditions, we make a qualitative analysis on how model predictions compare to experimental results.

Influence of predator size. Schmidt and O'Brien (1982), Breck and Gitter (1983) and Wanzenbock and Schiemer (1989) found that reactive distance increased with the size of the predator (*Thymallus arcticus* and *Lepomis macrochirus*). The results of Breck and Gitter (1983) indicated that the increase was non-linear, being smaller for large fish. This is also reflected in the model-predicted relationship (Fig. 2A) where it is assumed that the eye lens diameter increases linearly with fish size. Breck and Gitter (1983) concluded that increased eye size was responsible for the improved vision in larger fish, but that decreased cone density may, to some extend, have counteracted this improvement. Reduced cone density should be reflected as a higher ΔS_r parameter in our model.
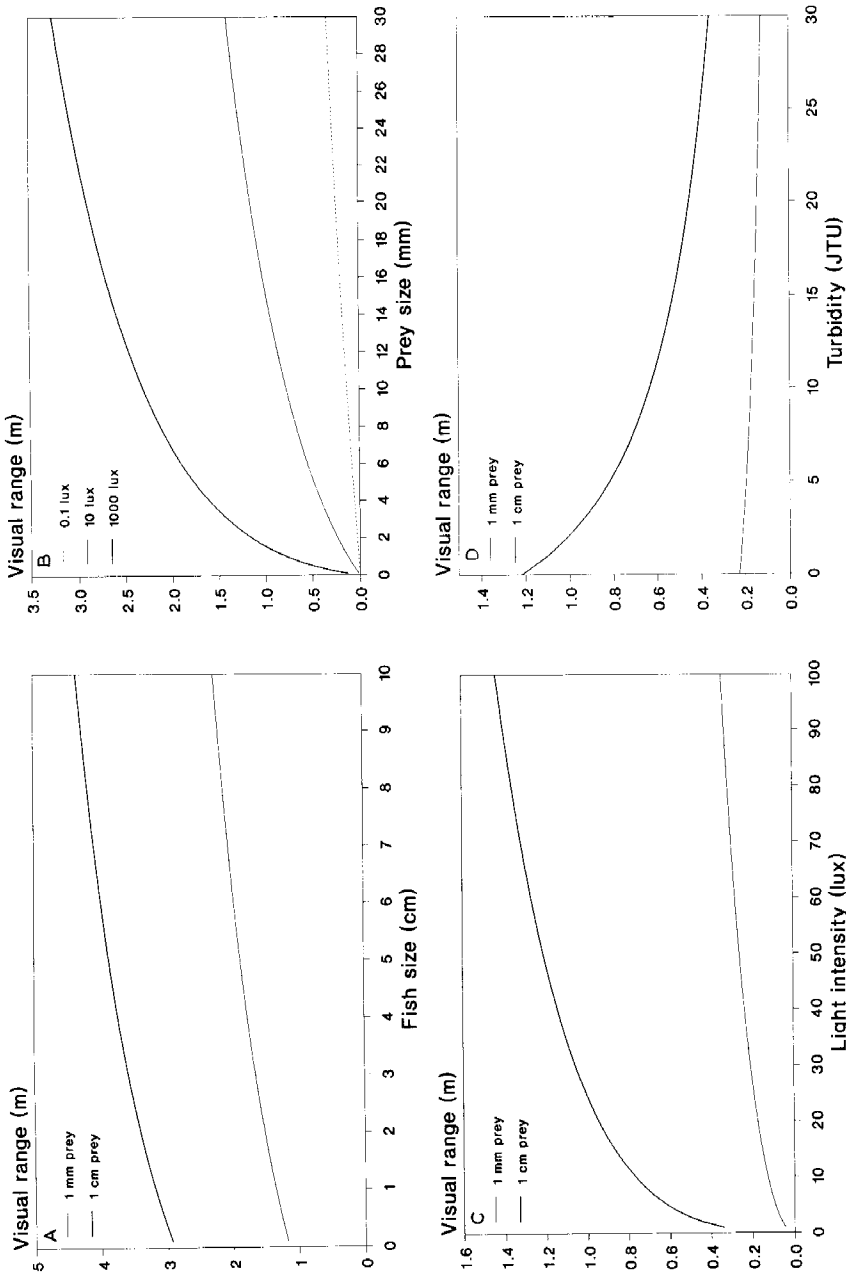
Fig. 2. Model-predicted visual range (Eq.17). Visual range is given as a function of predator size (A), prey size (B), light intensity (C), and turbidity (D). Units commonly used in feeding experiments are used for light intensity and turbidity, and the following parameter values were used (when not depicted on the plot): $C_0 = 0.5$, $E_0 = 100$ lux, $K = 1.14$ m^{-1}, $c = 1.57$ m^{-1} (corresponding to JTU $= 1$, see below) $\Delta S_e = 8.9 \cdot 10^{-5}$ lux, $\rho = 0.5$ and $z = 0.1$ m. In the simulations of predator size (BL, cm), $\Delta S_e = 1.41 \cdot 10^{-6}/(0.8 + 0.03 \text{ BL})^2$. In the turbidity simulations, $c = 0.313$ JTU $+ 1.26$, $K = 0.0616$ JTU $+ 1.08$ and $E_0 = 35$ lux.

Influence of prey size. Several experiments have revealed a linear relationship between reactive distance and prey length (Vinyard and O'Brien, 1976; Confer et al., 1978; Schmidt and O'Brien, 1982; Howick and O'Brien, 1983; Wright and O'Brien, 1984). Our model does not predict a linear relationship over large increases in prey size, but over the characteristic experimental prey size variations (1–4 mm), the model prediction may in practice be considered as linear (Fig. 2B). Experimental support of non-linearity over larger prey size variations (2–16 mm) are given by the data presented by Confer et al. (1978, their fig. 1d) originally derived by Ware (1973).

Influence of light intensity. Vinyard and O'Brien (1976) and Confer et al. (1978) found that increased light intensity resulted in increased reactive distance, but at a slower rate as light intensity increased. Our model for visual range is consistent with these findings (Fig. 2C). Vinyard and O'Brien (1976) also observed that the relative change in reactive distance with increased light intensity was more pronounced for large than for small prey. This is also predicted by the model, but here this is a trivial result as the curves for all prey sizes are necessarily intercepting origin. Schmidt and O'Brien (1982) found that for arctic grayling reactive distance increased moderately with light up to 748 lux, above which there was a marked increase in the reactive distance. At higher intensities, however, the increase in reactive distance dropped again as also reflected in Fig. 3C. According to Schmidt and O'Brien (1982) arctic grayling may have a weak selection for low light intensities as this fish is feeding under conditions of continuous daylight and very clear water, which in our terminology should be reflected as a high ΔS_e.

Influence of turbidity. Using the results of Zaneveld et al. (1979), Witherspoon et al. (1988) established relationships between the beam and diffuse attenuation coefficients on one hand and turbidity units (JTU) at the other. Using these relationships (fig. 3 in the paper of Witherspoon et al., 1988), we substituted c and K in our model with their turbidity measure, and could then plot visual range against turbidity (Fig. 2D). The experimental results of Vinyard and O'Brien (1976) indicate inverse relationship between reactive distance and turbidity. They also observed that the relative change in reactive distance with altered turbidity levels was much greater for large prey than for small prey. Both these relationships are reflected by the model (Fig. 2D). Confer et al. (1978) and Wright and O'Brien (1984) confirmed the findings of Vinyard and O'Brien (1976) and suggested that the relationship between reactive distance and turbidity was hyperbolic.

Depth

A

Eq. 16   Eq. 17

Visual range (m)

Ratio

B

100   50   25   10   5   1
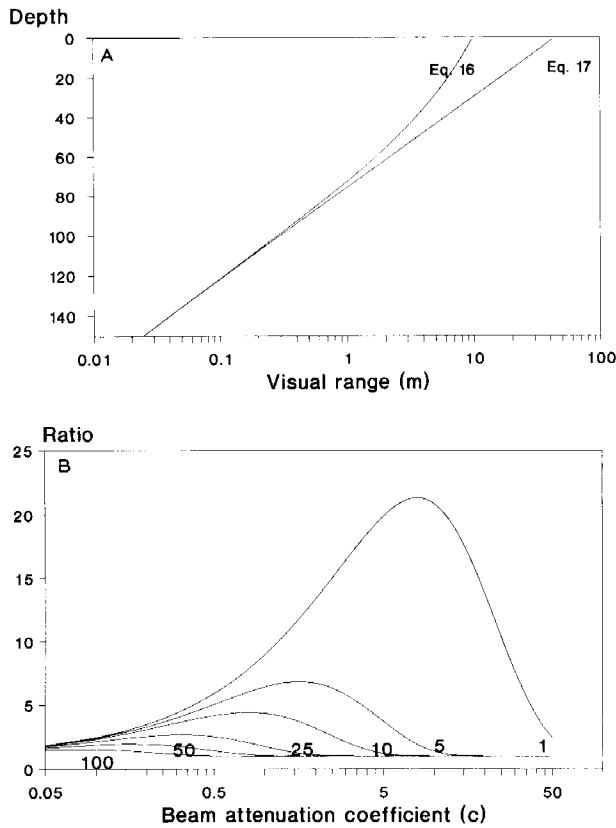
Beam attenuation coefficient (c)

Fig. 3. Comparison of the non-linear (Eq. 16) and linear (Eq. 17) equations for calculation of visual range. A: Depth dependence of visual range. B: Ratio of the visual ranges obtained by Eqs. 17 and 16 for different beam attenuations (c) and different depths (z). The diffuse attenuation coefficient K depends on c, $K = c/4$. Other variables are kept constant: $E_0 = 100 \ \mu\mathrm{E} \ \mathrm{m}^{-2} \ \mathrm{s}^{-1}$, $\rho = 0.5$, $C_0 = 0.5$, $\beta = 5\cdot10^{-4}$ m, $\Delta S_\mathrm{e} = 10^{-8} \ \mu\mathrm{E} \ \mathrm{m}^{-2} \ \mathrm{s}^{-1}$.

The above comparison of model predictions and observations can hardly serve as a test of the model. It does indicate, however, that the model, qualitatively, behaves in accordance with experimental findings. A more strict quantative test of the model requires that the beam (c) and diffuse attenuation (K) coefficients are measured rather than turbidity. Furthermore, as also stated above, a doubling in light intensity should also result in a doubling in the intensity of those wavelengths relevant for the visual system. The parameters k and C_0 may be measured, but may also be lumped together with ΔS_e (in Eq. 16) if it is reasonable to assume them

constant within an experiment. If visual ranges (or another measure related to this variable) are then measured under different light and optical conditions, the model predicts that the different ΔS_e-estimates (or the estimates of a lumped version) obtained by Eq. (16) should have the same value.

Influence of beam attenuation versus extinction of diffuse light

Both light extinction variables K and c depend on the absorption (a) and scattering coefficients (b), and empirically they have been expressed as functions of each other (Phillips and Kirk, 1984). (This dependency of both c and K on a and b could lead to an alternative expression of the visual range, where beam attenuation and diffuse attenuation are replaced by absorption and scattering.) The beam attenuation (c) is simply the sum $a + b$, while the diffuse attenuation (K) is more complexly related to a and b. Such, in a field study of 27 New Zealand lakes, Vant and Davies-Colley (1984) used the relationship of Kirk (1981) where K is described as a/μ, where μ (mean = 0.6) defines the average component of the vector light field in the vertical direction. Beam attenuation (c) is often 2–4 times larger than K in waters with low turbidity. Eq. (17) then approximates Eq. (16) when $Kz \gg 4Kr$, or $z \gg 4r$. Thus $c = 4K$ is assumed in Fig. 3. Here, we see that the solutions of Eq. (16) and (17) converge at large depths, and due to the covariation in c and K, also at high and low values of c. We may conclude that the error of ignoring c (using Eq. 17) is at maximum in shallow water at some intermediate beam attenuation coefficient.

Sensitivity to the different parameters

Despite the obvious simplifications of the present approach, the model may also be criticized for its complexity and the many parameters already involved, although these may be lumped. Most ecological models dealing with aquatic predation emphasize effects of variations in prey abundance. The other parameters of the functional response are often lumped together into an empirical derived "half-saturation" constant. The parameters of the present model are not empirical. They have a physical or a biological meaning, and should not be neglected unless there is a physical or biological reason for omitting them (i.e. assigning them a constant value). The parameters in the present model, however, do not have equal impact on the feeding rate. Below, we will discuss the relative significance of the different parameters on the basis of Eq. (17). This discussion is therefore valid when the depth is much larger than the visual range of the fish.

From Eq. (17) we see that the influence of water clarity (K) is exponential. The potential importance of this parameter is illustrated by considering an increase in the light attenuation coefficient from $K = 0.04$ m^{-1} (clear ocean water) to $K = 0.2$ (turbid coastal water). This reduction in water clarity decreases the visual range by a factor of 53 at a depth of 50 m, and a factor of more than 3000 at 100 m. This may most efficiently be compensated by upward migrations as depth is also part of the exponent. A 10% increase in the extinction coefficient may be compensated by a 10% decrease in depth.

At large depths the visual range is proportional to the size of the prey (β) and the focal length of the predator's eye $(f_1$, Eq. 15). A doubling of prey size or predator focal length leads to a doubling of the visual range. The significance of alterations in inherent contrast of the prey (C_0), sensitivity of the eye of the predator (ΔS_e), the surface light (E_0) and finally the air–sea light transmission coefficient (ρ) is depressed by the square-root operator. The visual range is therefore least sensitive to changes in these parameters. In nature, however, the range of variability of the parameters differ, and the true impact on visual range and feeding rate cannot be assessed unless this natural variability is considered (next paragraph).

Ecological implications

Feeding rates may be calculated, for different sets of parameter values, by using Eqs. (5) and (17). The parameters may be organized into three groups; three prey characteristics $(N, C_0$ and $\beta)$, four predator characteristics $(h, \theta, v,$ and $\Delta S_e)$, and four environmental characteristics $(E_0, \rho, z$ and $K)$. For one predator and one prey species, $C_0, \beta, h, \theta, \Delta S_e$ (and sometimes v) can be regarded as constant. On the evolutionary time scale, however, they may be treated as variables in an "arms race" between prey and predator. Here we will emphasize the ecological time scale where prey abundances, radiation and light extinction are the main fluctuating variables.

Giske and Aksnes (1992) have applied the present model to the mesopelagic fish *Maurolicus muelleri* in Masfjorden, a fjord of western Norway. During winter *M. muelleri* performs vertical migrations and preys upon non-migrating zooplankton during the day (Giske et al., 1990). The migrations correspond to the classical pattern described for sound-scattering layers, where the organisms follow an isolume (Blaxter, 1976; Forward, 1988). The day-depth is about 100–150 m, depending on the incident radiation. Advection of the watermasses above the sill depth (70 m) supplies the fjord with prey for the fjord-resident planktivores like *M.*

TABLE 2

Feeding rates for a visual predator at 125 m depth under different light extinction (K), surface radiation (E_0) and prey abundances. The extremes were selected to encompass the variability in the winter environment for *Maurolicus muelleri* in Masfjorden, western Norway (see text). The other parameters of the functional response were chosen as: $\rho = 0.5$, $\beta = 0.002$ m, $C_0 = 0.5$, $h = 2$ s, $\theta = 30°$, $v = 0.04$ m s^{-1} and $\Delta S_c = 7 \cdot 10^{-5}$ μE m^{-2} s^{-1} (Giske and Aksnes, 1992). Feeding rates were calculated by Eqs. (5) and (17) and are given as 10^{-5} ind. ind.$^{-1}$ s^{-1}

Water extinction (K, m^{-1})	Surface radiation (E_0, μE m^{-2} s^{-1})	Prey abundance (N, ind. m^{-3})	
		10	40
0.07	10	2.2	8.9
	200	45.0	178.0
0.11	10	0.015	0.06
	200	0.3	1.2

muelleri (Aksnes et al., 1989). Prey abundance in the upper 70 m during winter is therefore a result of predation and advection as prey (mainly *Calanus finmarchicus*) does not reproduce at that time of the year.

To study the relative impacts of variations in light regime and prey concentrations on the feeding process of *M. muelleri*, we calculated visual range and feeding rate (by tuning a value of ΔS_c to field data) for different values of the light attenuation coefficient, surface radiation and prey abundance (Table 2). The vertical attenuation coefficient in fjords and coastal waters varies according to the water mass characteristics, which are governed by local runoff and wind pattern along the coast of western Norway. A variation in K on the interval 0.07–0.11 m^{-1} for the upper water masses is therefore not unlikely. In winter, prey abundances in the upper 100 m typically varies between 10–40 ind. m^{-3} (Giske et al., 1990), and the midday surface radiation may fluctuate between 10 (heavy cloud cover) and 200 μE m^{-2} s^{-1}.

The significance of vertical attenuation is again emphasized by the fact that a decrease in K from 0.11 to 0.07 m^{-1} may increase the feeding rate at 125 m depth by a factor of 150 (Table 2). A characteristic increase in prey abundance (from 10 to 40 ind. m^{-3}) may increase the feeding rate maximally by a factor of 4, while a typical increase in the surface radiation (from 10 to 200 μE m^{-2} s^{-1}) may increase the feeding rate by a factor of 20. The combined effect of an increase in both radiation and water clarity (i.e. decreased K) may lead to an increase in feeding rate at 125 m depth by a factor of 3000 (from 0.015 to 178 in Table 2) without any alteration in prey abundance! Covariation between radiation and water clarity is to be

expected on the west coast of Norway. Normally, southerly winds lead to cloudy weather (reduced surface irradiance), increased precipitation and local freshwater runoff which decreases the water clarity, and to a thicker layer of coastal water (Sætre et al., 1988) which also tends to decrease water clarity. Northerly winds, during winter, will generally lead to coastal upwelling of water with low light extinction, clear weather and reduced land runoff.

Light as a top–down control

In aquatic systems light has mainly been linked to primary production and bottom–up control, and impact of light variations is generally believed to be damped out through the sequence of energy flow up the food chain. Predation is an important top–down control in the aquatic environment. We have shown that this process (in the case of visual predation) may be severely influenced by the light regime (including E_0, ρ, c and K). Ambient light at any depth may vary several orders of magnitude, not only over the died cycle, but over several time scales. Meteorological conditions give rise to clouds and cloudiness that may last from minutes to months. Furthermore, both freshwater discharge and increased algal biomass due to eutrophication may alter the water clarity significantly and have dramatic influence on opportunities for visual predation (K may be much higher than the values given in Table 2). This is likely to influence vertical migrational patterns (Clark and Levy, 1988). Hence light should be considered as top–down, as well as bottom–up, control through its direct impact on the feeding process (and thereby through the mortality process of prey) of aquatic predators.

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