

# Modelling the influence of light, turbulence and ontogeny on ingestion rates in larval cod and herring

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## ABSTRACT

Based on existing models of fish vision and turbulence-mediated ingestion rates, we develop a model of ingestion rates in larval fish that combines several physical properties of the environment (turbulence, irradiance, light attenuation) and visual characteristics of predators and prey. The model of visual range was calibrated with observed estimates in larval herring (*Clupea harengus*) and cod (*Gadus morhua*). The improved visual ability with length of larvae was predicted to be the most sensitive part of the model. Both turbulence and light had strong impacts on the ingestion rate of larval fish. The optimal level of turbulence increased with larval length. Also, due to the exponential decay of light with depth, it was predicted that larvae will have higher ingestion rates near the surface, even at high wind velocities. It is also proposed that larvae (particularly the smallest larvae) should concentrate on larger prey in turbulent environments. We suggest that biophysical models of larval growth and survival in field situations should include these factors to account for environmental effects on growth, survival and recruitment processes in the early life stages.

**Key words:** cod larvae, feeding success, herring larvae, ingestion rate, turbulence, visual range, visual resolution

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## INTRODUCTION

Visual predators such as many fish and fish larvae need to recognize their prey by sight (Blaxter, 1968). Thus, prey-encounter rates are expected to depend on variables such as the optical regime of the water column, prey size and contrast, depth and fluctuations in irradiance during the diel cycle (Aksnes and Utne, 1997). The importance of the visual range is implicit in most formulations of encounter rate between predator and prey in the pelagic environment (Eggers, 1977; Clark and Levy, 1988; Aksnes and Giske, 1993). Light has been recognized as a vital factor for the visual range or foraging efficiency of planktivorous fish and fish larvae, not only in the field (Gilbert *et al.*, 1992; Suthers and Sundby, 1996), but in experiments (Chesney, 1989; Miner and Stein, 1993; Utne, 1997) and in theoretical treatments (Duntley, 1962; Eggers, 1977; Clark and Levy, 1988; Aksnes and Utne, 1997). In addition, the importance of the ontogenetic aspects of the visual range has been investigated (Blaxter, 1968; Miller *et al.*, 1988; Wanzenböck and Schiemer, 1989; Walton *et al.*, 1997).

Turbulence enhances the relative velocity between predators and prey, and therefore their contact rates (Rothschild and Osborn, 1988). Depending on the turbulent energy dissipation rate and on the scales of separation, turbulence may cause significant changes in fish foraging success. Field studies have generally indicated that a degree of turbulence is beneficial for foraging success in fish larvae (Sundby and Fossum, 1990; Sundby *et al.*, 1994; Dower *et al.*, 1998). Recently, a number of turbulence models (Rothschild and Osborn, 1988; MacKenzie and Leggett, 1993; MacKenzie *et al.*, 1994; Kiørboe and Saiz, 1995) and experiments (Kiørboe and MacKenzie, 1995; MacKenzie and Kiørboe, 1995) have been described which evaluate the importance of turbulence for larval ingestion rate.

The effects of light, turbulence and ontogeny have not been considered within the same model framework. We have merged existing models of visual range (Aksnes and Utne, 1997) and turbulence-generated ingestion rates (MacKenzie *et al.*, 1994; Kiørboe and Saiz, 1995) with measurements of visual resolution in

larvae of cod (*Gadus morhua*) and of herring (*Clupea harengus*). The main purposes of the present paper are (1) to model the interactions between light, turbulence and ontogeny on ingestion rate in larval fish, and (2) to point out the relative significance of different physical (wind, turbulence, irradiance, optical properties of the water column) and biological (prey and larval characteristics) forces on prey ingestion rates.

## MODELS

### Derivation of visual range

Building on earlier work by Duntley (1962) and Eggers (1977), Aksnes and Giske (1993) and Aksnes and Utne (1997) derived a model of how the visual range of fish depends on environmental properties and the visual specifications of predator and prey. Their equation for visual range  $r$  [m] was given as:

$$r^2 \exp(cr) = |C|A_p \Delta S_e^{-1} E_{\max} [E_b / (K_e + E_b)] \quad (1)$$

where  $c$  is beam attenuation [ $\text{m}^{-1}$ ],  $C$  is the inherent contrast of the prey [dimensionless; (object brightness – background brightness) / background brightness (Lythgoe, 1966) or in our terminology:  $(E_{\text{prey}} - E_b) / E_b$ ],  $A_p$  is the size of the prey image [ $\text{m}^2$ ], the fraction  $E_{\max}(E_b / (K_e + E_b))$  determines the increase in  $r$  as ambient light  $E_b$  [ $\mu\text{E m}^{-2} \text{s}^{-1}$ ] increases (with half saturation at  $K_e$  [ $\mu\text{E m}^{-2} \text{s}^{-1}$ ], see Aksnes and Utne, 1997) and  $\Delta S_e$  [ $\mu\text{E m}^{-2} \text{s}^{-1}$ ] is a species-specific parameter for the contrast threshold for prey recognition (Aksnes and Giske, 1993). The last parameter ( $\Delta S_e$ ), the maximum level of light that can be processed by the visual system ( $E_{\max}$  [ $\mu\text{E m}^{-2} \text{s}^{-1}$ ]) and the half-saturation coefficient ( $K_e$ ) characterize the visual abilities of the predator, and must be measured for any specific species and ontogenetic stage. If  $\Delta S_e$  and  $E_{\max}$  are combined into a function of length  $E'(l)$  ( $= E_{\max}(l) / \Delta S_e(l)$ ), then from equation 1:

$$E'(l) = \frac{r_l^2 \exp(cr_l)}{|C|A_p \frac{E_b}{K_e + E_b}} \quad (2)$$

Visual range is often found from measurements of visual angle  $a$ , either from direct observations (Wanzenböck and Scheimer, 1989; Walton *et al.*, 1997) or by studying the optomotor response (Neave, 1984; Helvik and Karlsen, 1996). Visual range and visual angle are related by  $r = 0.5H / \tan(0.5a)$  ( $H$  is prey height, Wanzenböck and Schiemer, 1989), thus (in clear water,  $c = 0$ )  $E'(l)$  may also be expressed in terms of  $a$ :

$$E'(l) = \frac{[0.5H / \tan(0.5a_l)]^2}{|C|A_p \frac{E_b}{K_e + E_b}} = (K_e + E_b) \times [0.5 / \tan(0.5a_l)]^2 / (E_b C) \quad (3)$$

Here,  $H$  and  $A_p$  cancel out if the prey image is assumed to be a square (which may be realistic in optomotor studies), while these may be specified separately in direct measurements (using real prey) of visual angle.

We estimated visual angle  $a$  in herring and cod larvae during the first 3 weeks after hatching (using the optomotor response). These measurements (which will be presented in detail by Helvik and others elsewhere) were transformed to  $E'(l)$  by equation 3 and used to find  $E'(l)$  for herring larvae. We assumed attenuation  $c = 0$  (clear water), inherent contrast  $C = 1$  (black prey,  $E_p = 0$ ) and  $E_b = 5.5$  (measured at the surface during the experiments). The parameter  $K_e$  was assigned the same value ( $5 \mu\text{E m}^{-2} \text{s}^{-1}$ ; Aksnes and Utne, 1997) as found earlier for gobies (*Gobiusculus flavescens*), which are adapted to similar light conditions as herring larvae. At this level, the half-saturation coefficient causes light to be a major limiting factor below  $\sim 10 \mu\text{E m}^{-2} \text{s}^{-1}$  ( $\sim 500$  lux), consistent with several other studies on fish larvae (Blaxter, 1986; Chesney, 1989; Miner and Stein, 1993; Fortier *et al.*, 1996).

The fitted functions for  $E'(l)$  (using equation 3), where  $l$  is standard length [mm], are for herring larvae:

$$\text{Log}_{10} E'(l) = \frac{4.88}{1 + \exp(-\frac{l-10.98}{1.34})} \quad R^2 = 0.89, n = 115 \quad (4)$$

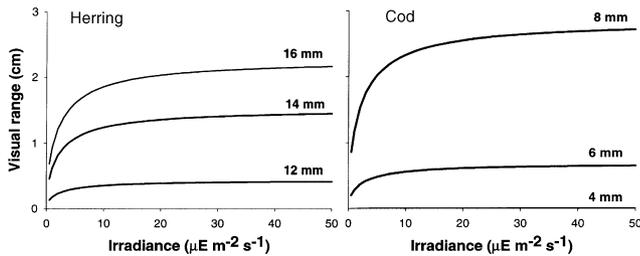
and for cod larvae:

$$\text{Log}_{10} E'(l) = \frac{5.04}{1 + \exp(-\frac{l-5.33}{0.64})} \quad R^2 = 0.97, n = 36. \quad (5)$$

### Visual range and optics

An important factor in the model of visual range (equation 1) is ambient light  $E_b$ . By use of equation 1, visual range can be calculated for increasing background irradiance (Fig. 1). Light is particularly limiting at low levels, and has little effect on visual range beyond 10–20  $\mu\text{E m}^{-2} \text{s}^{-1}$  (Fig. 1). Visual range also improves considerably with larval length.

**Figure 1.** Visual range in fish larvae of different sizes as ambient light  $E_b$  increases; the line for the 4 mm cod larvae is along the bottom scale line. The calculations are made with  $A_p = 0.9 \text{ mm}^2$  (copepod nauplius),  $C = 0.1$  (transparent prey),  $c = 0.4$ ,  $K_e = 5$  (estimate for the two-spotted goby, *Gobiusculus flavescens*, by Aksnes and Utne, 1997) and  $E'$  from equations 4 (Herring) and 5 (Cod).

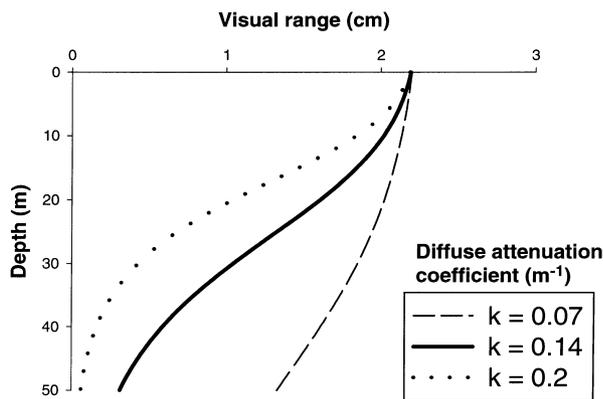


Ambient light decays exponentially with depth; this decay is regulated by the level of diffuse attenuation (turbidity) in the water column. This effect leads to a strong reduction in visual range with depth (Fig. 2). Visual range and prey encounter rate are therefore expected to be highly dynamic variables in time and space, and to fluctuate with the vertical movements (active or passive) of the fish larvae.

*Turbulence*

Following the theory first presented by Rothschild and Osborn (1988), a number of authors have pointed to

**Figure 2.** Visual range for a 16 mm herring larvae, with light above the surface at  $100 \mu\text{E m}^{-2} \text{ s}^{-1}$  and for three levels of turbidity in the water column (diffuse attenuation  $k \text{ [m}^{-1}] = 0.2$ , turbid water, e.g. an algal bloom;  $k = 0.14$ , coastal water;  $k = 0.07$ , clear Atlantic waters). Background irradiance at depth  $z = E_b(0) \exp(-kz)$ , where  $E_b(0)$  is irradiance just below the surface and  $z$  is depth in m. All other parameters are as in Fig. 1. Note that altered surface irradiance will not only shift curves up or down, but will also change the shape of the vertical profile.



the significance of turbulence in the encounter (Sundby and Fossum, 1990; Sundby *et al.*, 1994; Muelbert *et al.*, 1994) and the pursuit processes of planktonic organisms (MacKenzie *et al.*, 1994; Kiørboe and Saiz, 1995). Turbulence enhances the rate of encounter by increasing the relative velocities between prey and predator. For a cruising predator (such as herring larvae), the prey encounter rate  $e \text{ [prey s}^{-1}]$  is described by:

$$e = 0.5\pi r^2 NV, \tag{6}$$

where 0.5 is the fraction of the sphere scanned during search (Rosenthal and Hempel, 1970),  $r$  is the visual range [m],  $N$  is prey density [ $\text{prey m}^{-3}$ ] and  $V$  is the velocity component of the contact rate defined in the initial theory by Rothschild and Osborn (1988). In the present paper, the modified formulation by Evans (1989),  $V = \sqrt{u^2 + v^2 + 2uw}$ , is applied. Here, the velocity  $v \text{ [m s}^{-1}]$  is the prey speed and  $u \text{ [m s}^{-1}]$  is the cruising speed of the predator (fish larvae). The turbulence-generated velocity difference  $w \text{ [m s}^{-1}]$  for two particles separated by a distance  $S$  was formulated by Rothschild and Osborn (1988) as:

$$w = 1.9(\varepsilon S)^{1/3}, \tag{7}$$

where  $\varepsilon$  is the turbulent energy dissipation rate [ $\text{m}^2 \text{ s}^{-3} \text{ kg}^{-3}$ , or  $\text{cm}^2 \text{ s}^{-3}$ ]. We have also made some simulations with  $r$  instead of  $S$  as the spatial scale.

For a pause-travel predator such as a cod larva, the encounter rate kernel changes to (Kiørboe and MacKenzie, 1995; MacKenzie and Kiørboe, 1995):

$$e = \pi r^2 f \left( \frac{2}{3} r + \sqrt{2} \tau w \right) N \tag{8}$$

with  $f (= 0.43 \text{ s}^{-1}$  for a 6 mm cod larva; MacKenzie and Kiørboe, 1995) the pause frequency and  $\tau w = 2 \text{ s}$ ; MacKenzie and Kiørboe, 1995) the pause duration, and all other symbols as outlined above. It is assumed that the larva will move to the outer edge of its reactive distance in each swim event, and that the full volume within the reactive sphere will be scanned while pausing. Note that this behavioural kernel is even more sensitive to visual range than equation 6.

The calculations of pursuit success  $P(sp)$  are based on geometric arguments, and details can be found in MacKenzie *et al.* (1994). Their formulation assumed that the relative turbulent velocity  $w$  was constant within the perception sphere. This constraint has been modified to let  $w$  decrease as prey approaches the predator within the perceptive

sphere (Kjørboe and MacKenzie, 1995; Kjørboe and Saiz, 1995). We have adopted the latter expressions for our analysis (this is the same for cod and herring larvae):

$$PSP = \frac{1}{2}(\rho^3 + 1 - \alpha) + \frac{1}{4}(\alpha^3 - \alpha) - \frac{3}{16} \frac{(\rho^2 - 1 + \alpha^2)^2}{\alpha}, \quad (9)$$

where  $\rho = r/wt$ ,  $\alpha = d/wt$ ,  $PSP$  is the probability of successful pursuit,  $r$  is visual range,  $t$  is time required for pursuit,  $w$  is turbulent velocity (equation 7) and  $d$  is the distance ( $< r$ ) between prey and predator. Then, the expected capture success  $P(sp)$  is:

$$P(sp) = \frac{1}{r} \left[ \int_0^{r-wt} 1 \partial d + \int_{r-wt}^r PSP(d) \partial d \right]. \quad (10)$$

Finally, the successful ingestion rate  $I$  [prey  $s^{-1}$ ]:

$$I = eP(sp) \quad (11)$$

will be a dome-shaped function of increasing small-scale turbulence, as  $P(sp)$  eventually will neutralize the positive effect of higher contact rates. These equations allow us to model ingestion rate as a function of fish length, wind conditions and light intensity.

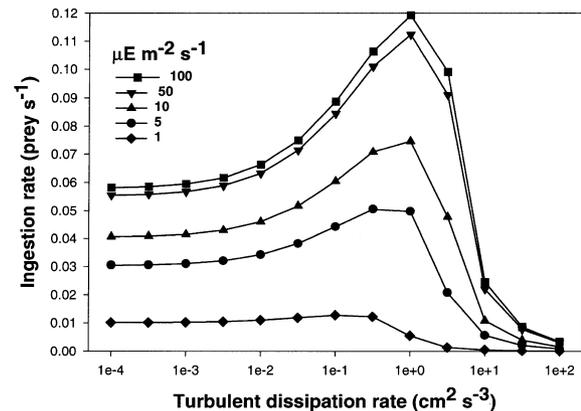
## RESULTS

### Sensitivity analysis

It is clear that the influence of turbulence on (successful) ingestion rate (equation 11) is related to background irradiance (Fig. 3). In terms of absolute values, ingestion is more sensitive to turbulence at high levels of light. At light intensities above  $20 \mu E m^{-2} s^{-1}$ , the increase in ingestion rate is small because the visual system becomes satiated (Figs 1 and 3). Nevertheless, the relative increase in feeding rate is quite constant across all irradiance levels, except at the lowest levels. Lower levels of light (and thus short visual range) make turbulence less beneficial to feeding success (Fig. 3). This change is caused by the increased probability that a prey item will be advected out of the reach of the larva in a smaller reactive volume (Dower *et al.*, 1997, 1998).

When the ingestion rate is expressed as a function of turbulence and irradiance over the full range of possible values (Fig. 4), the interconnection and relative importance of the two forces become even more apparent. At low levels of irradiance (or for small larvae, small prey, or turbid conditions), visual range is short, and prey are more likely to move away from the

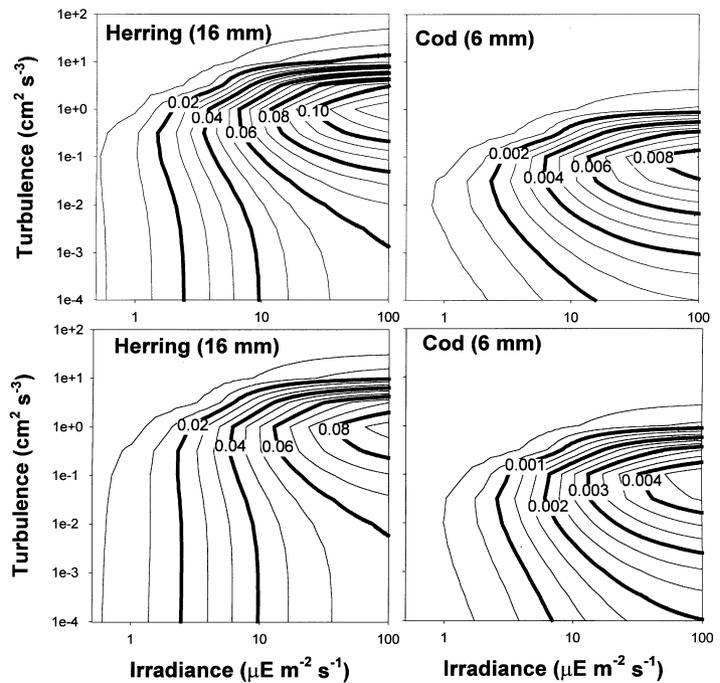
**Figure 3.** Ingestion rate (equation 11) at combinations of irradiance and turbulence for a 16 mm herring larva. Parameters are prey movement  $v = 0.2$  [mm  $s^{-1}$ ], prey density  $N = 5$  litre $^{-1}$ ,  $u = 10^{(1.07 \log(l) - 1.11)}$  ( $R^2 = 0.46$ ,  $n = 93$ ) and  $t = 1.33 \exp(-0.0035 l)$ , with  $l$  in mm,  $u$  in  $cm s^{-1}$  and  $t$  in s (Dower *et al.*, 1997), otherwise as in Fig. 1.



larvae before an attack is made. At higher irradiance and larger larval sizes, this is less probable, and the feeding process is increasingly enhanced by turbulence (up to a certain level). Thus, turbulence will be more beneficial to ingestion rates in well-illuminated areas. Overall, the ingestion rate is higher in all combinations of light and turbulence when the separation distance is used as the turbulent scale (Fig. 4). The exact level of difference will depend upon search mode, prey concentration, light and turbulence. Note that the point where decreasing pursuit success becomes dominant is sensitive to pursuit time. Due to their pause-travel search behaviour, the ingestion rate of cod larvae is more sensitive to turbulence than the ingestion rate in herring larvae (Fig. 4; MacKenzie and Kjørboe, 1995), while the sensitivity to irradiance is closer between the two species.

The major effect of ontogeny is evident when ingestion is depicted as a function of both body length and turbulence (Fig. 5). The model results show that turbulence is detrimental to ingestion for the smallest herring larvae across all energy dissipation rates. Both at high and at low irradiance, ingestion rates in herring are enhanced by turbulence only at body lengths above 12–13 mm, while small cod benefit from turbulence at the lowest dissipation rates. Less light lowers the ingestion rate, but does not seem to affect the shape of the curves (Fig. 5). Thus, a given level of turbulence will reduce ingestion rate for some larvae, but enhance it for others. This is true for a considerable portion of the range of dissipation rates that will

**Figure 4.** Upper panels: range of feasible values of light, turbulence and the corresponding (successful) ingestion rate [prey s<sup>-1</sup>] from equation 11 for larval herring (16 mm, left panels) and cod (6 mm, right panels). Length of cod larvae is set at 6 mm, as in the estimates of pause frequency  $f$  (= 0.43) and pause duration  $\tau$  (2 s) by MacKenzie and Kiørboe (1995). All other parameters are as specified in Figs 1 and 3. Lower panels: using visual range  $r$  instead of prey separation distance as the turbulent scale.



occur in nature (Fig. 5). Additionally, the most influential factor in all cases is larval length, or the sensitivity of the eye. Moving from left to right in each panel in Fig. 5, ingestion rate improves by > 4–5 orders of magnitude. By comparison, the effects of light and turbulence are within one order of magnitude (Fig. 4), if we ignore the lowest levels of light and extremely high dissipation rates.

Dower *et al.* (1998) found larger prey in the stomachs of radiated shanny (*Ulvaria subbifurcata*) in more turbulent environments, and they suggested a possible mechanism for this observation (their fig. 11). Larger prey provide a wider visual range than small prey, so that the probability that large prey will be lost before an attack can be made is reduced. Our model is a detailed quantification of the ‘differential size-based capture success’ concept presented in Dower *et al.* (1998), and we calculated relative ingestion rates in turbulent and calm conditions ( $I_{\epsilon = 0.1}/I_{\epsilon = 0.0}$ ) for a range of prey sizes (Fig. 6). The 12 mm larvae should prefer larger prey in turbulent situations, as small prey seem to be more difficult to catch. This is also true for 16 mm larvae, but the effect of prey size is marginally decreasing, while it is marginally increasing for the 12 mm larvae (at least initially).

*Vertical profiles*

The model can easily be applied to natural situations, such as a water column in which light and

turbulent energy decay from the surface (Fig. 7). The ingestion rate in fish larvae as modelled here (with no effect of tide or density gradients) will be a highly non-linear function of depth. Because light decays exponentially with depth, visual range declines throughout the water column. Near the surface, ingestion rate may be reduced by wind conditions, but generally wind is beneficial throughout the column. Again, wind is most beneficial during the daytime owing to the larger visual volumes at this time. Light is the primary forcing variable below depths of  $\approx 30$  m, while wind conditions have a quite significant influence above this, particularly for cod larvae (note that a thermocline or halocline could cause abrupt changes in the vertical profiles). Strong winds lead to a lower decline of ingestion rate in near-surface waters compared with the model of MacKenzie *et al.* (1994). Environmental factors such as cloud cover, seasonal variations in irradiance, and turbidity due to freshwater run-off or algal blooms (Gilbert *et al.*, 1992; Giske *et al.*, 1994; Fortier *et al.*, 1996) will modify the shape of the vertical profiles (Fig. 2).

**DISCUSSION**

*Model*

Our model includes mechanistic formulations not only of the encounter process, based on characteristics of

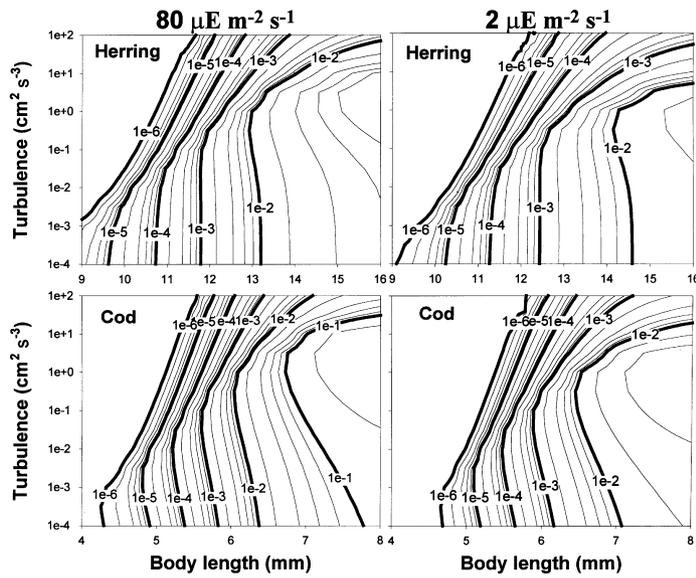
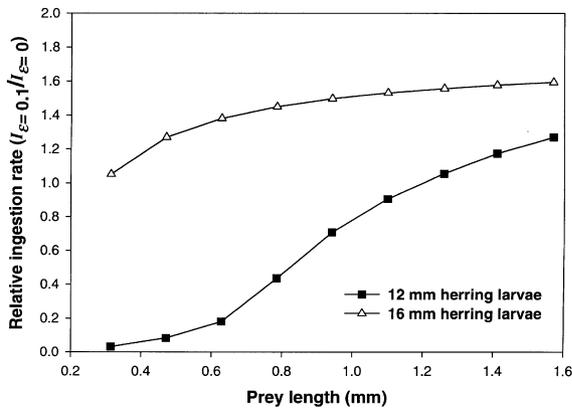


Figure 5. Ingestion rate (log scale) at  $80 \mu\text{E m}^{-2} \text{s}^{-1}$  (left panels) and  $2 \mu\text{E m}^{-2} \text{s}^{-1}$  (right panels) at all body lengths and turbulence levels for herring (upper panels) and cod larvae (bottom panels).

Figure 6. Relative prey ingestion rates ( $I$  at  $\epsilon = 0.1$  divided by  $I$  at  $\epsilon = 0$ ; dimensionless) at various prey sizes, all parameters as in previous figures. The smallest larvae gain more than larger larvae by switching to larger prey in turbulent situations.



prey, prey density, optics, visual abilities of the larvae (Aksnes and Utne, 1997), and swimming- and turbulent- velocities, but also of the pursuit process (as described earlier by MacKenzie *et al.*, 1994 and Kjørboe and Saiz, 1995). The species-specific elements of the model are the visual ability, search mode and prey characteristics.

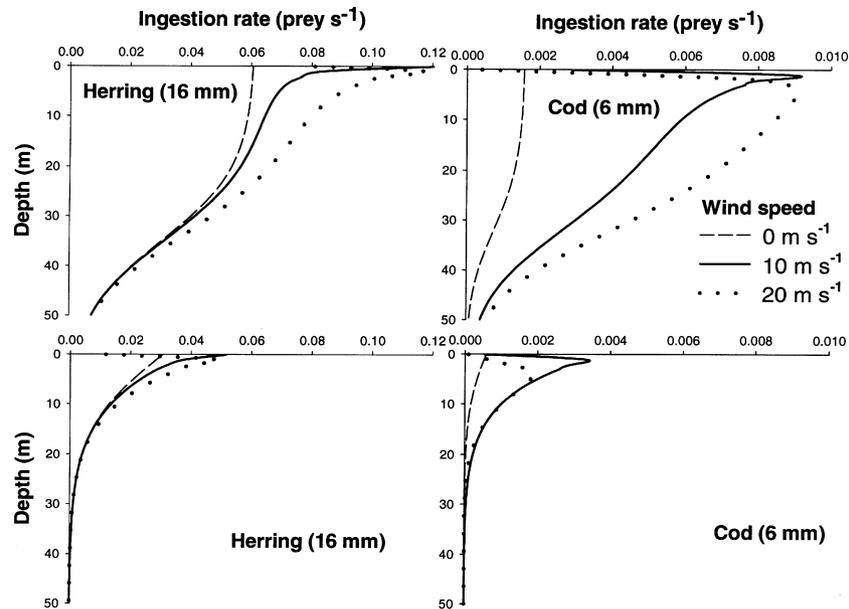
Light is less acknowledged than turbulence in the quantitative literature on larval feeding success. It is generally accepted that fish larvae do not feed during the night, and that there is a lower light threshold for initiation of feeding (Blaxter, 1986). However, light and optical properties of the water column, the prey

and the visual system of the fish larva itself will generate a continuous influence of light on ingestion rates. Based on observed values of visual range in larvae, we predict that light and ontogeny of visual abilities potentially have controlling effects on ingestion rates. A short visual range will lower the optimum level of turbulence; in contrast, a long visual range allows more time to prepare an attack, so the pursuit success will be less affected by strong turbulence (MacKenzie *et al.*, 1994; Dower *et al.*, 1997, 1998).

Visual ability in cod larvae seems to be similar to that of herring at the same age, although the cod larvae were only half the body length of the herring larvae. This difference points to the problems of using multispecies data in generating length-specific relations of processes that depend on ontogeny rather than length. While cod larvae seem to have a well-developed visual system at 8 mm length, herring of 10 mm will have a functionally undeveloped visual ability. Factors such as cruise speed and prey size will also differ between the two species, reinforcing the conclusion that feeding rates are size-dependent. The measurements of visual angle (equations 4 and 5) suggest that visual ability (in terms of visual range) in larval herring and cod improves by orders of magnitude during the first 3 weeks. This improvement is also consistent with the histological development of the retina and brain. However, we have not considered other sensory organs (e.g. organs detecting pressure waves, movements and/or olfaction), which may play an important role in the response to prey.

Field measurements on first-feeding cod larvae show that wind-induced turbulence increases the

**Figure 7.** Vertical profiles of foraging success in daylight ( $500 \mu\text{E m}^{-2} \text{s}^{-1}$ , upper panels) and in twilight ( $5 \mu\text{E m}^{-2} \text{s}^{-1}$ , lower panels) with speeds of  $0 \text{ m s}^{-1}$  (dashed line),  $10 \text{ m s}^{-1}$  (continuous line) and  $20 \text{ m s}^{-1}$  (dotted line) for cod larvae (right panels) and herring larvae (left panels). Other parameters are as in earlier simulations, and energy dissipation is purely wind generated:  $\epsilon = 5.82 \times 10^{-9} W^3 / z$ , where  $W$  is wind at the surface [ $\text{m s}^{-1}$ ] and  $z$  is depth [m] (MacKenzie and Leggett, 1993).



feeding rate by a factor of 7 when wind speed increases from near 0 to  $10 \text{ m s}^{-1}$  (Sundby and Fossum, 1990; Sundby *et al.*, 1994). The model predicts a similar increase in feeding rate as wind increases from 0 to  $10 \text{ m s}^{-1}$  in 6 mm cod larvae (Fig. 7). However, smaller larvae (4 mm) would not find much food by visual searching if they had the eye sensitivity as described by equation 5 (Fig. 1).

Kjørboe and Saiz (1995) stated that negative effects of turbulence would not be important for most predators at realistic intensities of turbulence. This conclusion was founded on fixed perceptive volumes and pursuit times. When pursuit time is fixed (or increases with size as shown in fig. 11 of Dower *et al.*, 1997) and perceptive volume varies with light and ontogeny, then turbulence will have negative effects on less-developed individuals over a considerable range of the turbulent scale (Fig. 5). This conclusion relies solely on the model of pursuit success (equation 10), because the encounter rate will continue to increase for higher turbulence.

The model of pursuit success (MacKenzie *et al.*, 1994; Dower *et al.*, 1997) also implies that turbulence is mainly negative for small larvae (Figs 5 and 6), although this may be compensated slightly by switching to larger prey (Fig. 6). However, this implication is not consistent with the observation by Dower *et al.* (1998), where the smallest larvae had comparatively

higher stomach fullness. Smaller larvae (low swim speed) benefit from turbulence in terms of encounter rate but this advantage does not compensate for the effect of shorter visual range and lower  $P(sp)$ . Alternative mechanisms may be needed to explain the increased ingestion rates in small larvae at high levels of turbulence, such as the lower escape ability of prey under turbulent conditions. If copepods are less vigilant – or less responsive – in turbulent habitats, they may become more vulnerable, particularly to the smallest larvae, which are less efficient predators.

#### Applications

Recent individual-based models of larval trophodynamics have incorporated many mechanistic aspects of prey encounter. By coupling the spatial prey field and a prey-encounter-rate model including turbulence generated by tide and wind, Werner *et al.* (1996) developed a state-of-the-art biophysical model of larval growth and distribution. However, the model ignored light, except for the day/night variability in feeding rate. The absence of a specific account of light in the foraging process led to the conclusion that contact rate would increase by a factor of 2–5 near the sea bed, as a result of turbulent shear from the tidal cycle. But if light is limiting feeding rates during the night (as assumed in their model), it is also likely to be limiting at 40–90 m depth. Many field studies have pointed to the

importance of the light field and optical properties of the water column in larval growth and foraging success. In south-eastern Hudson Bay (Quebec, Canada), studies have demonstrated the integrated effect on larval growth from light and prey density (Gilbert *et al.*, 1992; Fortier *et al.*, 1996). Under the ice, variability in river run-off affected the irradiance below the freshwater plume, and thereby the prey availability to the larvae. In a similar study in the Greenland Sea, Michaud *et al.* (1996) found no correlation between feeding success of Arctic cod (*Boreogadus saida*) larvae and variability in wind or irradiance. This was not surprising, because the larvae were probably not food limited (their fig. 10a). Further, the attenuation coefficient in the latter study was in the range of 0.09–0.53 [ $\text{m}^{-1}$ ], while in Hudson Bay it was between 1 and 3 [ $\text{m}^{-1}$ ]. Short-term variability in growth of otoliths in herring larvae was also found by Gallego *et al.* (1996) in the Orkney–Shetland area. They found a significant positive correlation between otolith growth and increased irradiance, they also found the predicted dome-shaped relationship with increasing turbulence.

The results for the influence of light on ingestion rate might explain interannual variations in early-life-stage growth patterns for higher-latitude fish stocks, as well as latitudinal difference in larval and early juvenile growth. Suthers and Sundby (1996) compared the growth rate of early juvenile cod from the Arcto–Norwegian and Nova Scotian stocks. They found that the growth rate during the summer period was about twice as high for the Arcto–Norwegian cod. Furthermore, the growth rate was considerably more variable for the Arcto–Norwegian cod stock, and the daily ring structure of the otoliths was more complex. Because other important environmental parameters influencing the ingestion rate were quite similar (temperature, wind conditions, copepod concentration), they proposed that the difference in length of the day, 16 vs. 24 h, caused the differences in growth rate. The complex and variable ring structure in the Arcto–Norwegian cod otoliths might be caused by large variations in light conditions during the day: in Arctic regions where the altitude of the sun is low, variations in cloud cover might cause lower light intensities at midday than at midnight.

The peak ingestion rate does not occur at depth in our model, as it would do in any purely turbulence- (wind-) forced model (MacKenzie *et al.*, 1994). Instead, the most profitable habitats in terms of feeding are predicted to be near the surface, at all levels of wind and irradiance (Fig. 7). It is important to keep in mind that the risk of predation also will vary with

light. Fish at all stages of development are major predators on fish larvae, and because they are visual predators, they also will be less efficient in darker habitats. Factors such as primary production, fresh-water run-off and particle density will also change the light environment. Giske *et al.* (1994) and Fiksen and Giske (1995) found that increased turbidity may benefit fish larvae if they are subject to visual predation risk, as their risk of predation is likely to be more reduced than their food intake. This finding is due to the difference in beam attenuation for long and short reactive distances (equation 1). However, the overall cost or benefit of reduced visibility depends on the relative contribution of visual predators and other sources of mortality such as non-visual predators, risk of starvation, and the cost of prolonging the vulnerable juvenile stages.

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