



## The influence of turbidity on growth and survival of fish larvae: a numerical analysis

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### Abstract

Growth and survival through the early larval phase probably limit the production potential of many commercially important fish stocks. Attempts to increase the production of these stocks by restocking of juveniles have generally failed. Here, we analyse how enhanced concentrations of phytoplankton and zooplankton affect the survival of fish larvae during their early life stages. The analysis is developed for larvae feeding on copepod eggs and nauplii, with fish and invertebrates as major predators. A model of feeding and growth of fish larvae is applied to assess the benefit of enhanced phytoplankton and zooplankton abundance. The analysis shows that the shading effect of higher phytoplankton concentration may reduce predation rates on fish larvae substantially. This 'top-down' effect may be more important for the cohort survivorship than the 'bottom-up' mechanism in situations when larval food is sufficiently abundant. However, while increased algal biomass will improve recruitment at high zooplankton concentration, it may also reduce recruitment at low zooplankton concentrations and shallow mixing depths. Both the larvae and their vertebrate predators are dependent on light to detect their prey, and the longer reactive distance of the predators make them more susceptible than the larvae to reduced light levels and increased turbidity. We discuss the implications of reduced predation and increased zooplankton abundance on recruitment and production of fish larvae, and point at environmental conditions where changing algal biomass is likely to affect recruitment success.

### Introduction

The issue of how the production of food from the ocean can be increased has gained interest as the world fish catch has levelled out (Cushing, 1996). Improved management of exploited stocks is an obvious solution to increase yields and avoid recruitment overfishing. Typically, fish are food- or density-regulated at a young age, while carrying capacities of exploited age classes are often above current stock levels. Consequently, the number of recruits that are supplied to the stock frequently limits the production of fish biomass and yield to fisheries. To accommodate this, large-scale rearing of juvenile fish and extensive sea ranching projects have been launched. However, these attempts have frequently failed, as the juveniles are

expensive to produce and seem to have low survival rates after release (Svåsand et al., 2000).

An alternative approach to facilitate the supply of recruits to exploited stocks may be to improve the conditions for growth and survival through critical periods, such as the first feeding and larval stages, when larval fish are particularly vulnerable. The growth (and therefore survival) of fish larvae is often limited by the availability of food organisms (e.g., Ellertsen et al., 1989; Fossum, 1996). The single most important food item for many fish larvae in the North Atlantic is the nauplii of the calanoid copepod *Calanus finmarchicus*. There seems to be at least some correlation between growth and production of these nauplii and the abundance of autotrophs in the sea (e.g., Richardson et al., 1999). According to this reasoning, it may be possible

to increase the number of recruits by artificially enhancing the primary production in the main nursery or other selected areas of these fish stocks.

We acknowledge that this is a question that requires multiple approaches and extensive scientific effort to be answered. More recruits will not increase production of fish if strong density-dependent regulation operates at juvenile or adult stages (Giske & Salvanes, 1999). Neither will nutrient enrichment have any effect on zooplankton and fish unless the ecosystem response to enrichment is such that energy can be transferred to higher trophic levels (Hulot et al., 2000).

We anticipate and analyse three mechanisms by which increased phytoplankton concentration affects growth and survival of fish larvae: positively through (1) the potential for higher food abundance and (2) reduced predation pressure from visually searching predators and negatively by (3) reduced feeding and growth rates due to more turbid water. We use an individual-based model of growth of herring larvae as a function of environmental parameters (Fiksen et al., 1998; Fiksen & Folkvord, 1999). Then we add predation risk and model the effects of prey, predator and chlorophyll concentrations on the recruitment success of the fish larvae cohort.

## The model

### *Feeding and growth of fish larvae*

The individual based model (IBM) of herring larvae is presented by Fiksen & Folkvord (1999). Based on theoretical and experimental studies, they developed a model of prey encounter, prey capture, growth and metabolism for larval herring. All these processes were size-dependent and tied to environmental variables such as temperature, turbulence, light, turbidity, prey concentration and prey size structure. Here, this model is extended to include predation risk from visually searching planktivores such as fish, and the focus will be on how growth, predation risk and starvation of fish larvae are affected by changes in the concentration of phytoplankton.

Both larvae and their predators are modelled as visual, raptorial foragers that detect their prey by sight (Fig. 1). This implies that the optical properties of the water column are important not only for the ability of the larvae to feed, but also for the probability that predators will detect it. The encounter rate between a herring larva and its prey is modelled by the cylinder

equation

$$e = \frac{1}{2} \pi R_l^2 N V, \quad (1)$$

where  $R_l$  is the reactive distance (visual range) of the larvae,  $N$  is prey abundance and  $V$  is the relative velocity (including swimming and small scale turbulent motion) between the larvae and the prey. The reactive distance were calculated by use of a model first derived by Aksnes & Giske (1993) and later elaborated by Aksnes & Utne (1997):

$$R_l^2 \exp(cR_l) = C A_p E' \frac{E_b}{K_e + E_b}. \quad (2)$$

Here,  $E'$  is the size-specific sensitivity of the visual system of the larvae (Fiksen et al., 1998), which specifies the ratio of the weakest and the strongest difference between the reflected light from the prey and the local background irradiance ( $E_b$ ) that can be recognised by the larvae. The satiation parameter ( $K_e$ ) defines how visual range increase with light,  $A_p$  is the area of the prey and  $C$  is the inherent contrast (visibility) of the prey. The local illumination level  $E_b$  at depth  $z$  is a function of surface irradiance  $E_s$  and absorption in the water column:

$$E_b = E_s \exp(-Kz). \quad (3)$$

The diffuse attenuation (extinction) coefficient  $K$  will normally vary through the water column, but here we assume a homogenous, well-mixed upper layer where  $K$  is constant. We also assume a fixed relationship between  $K$  and the beam attenuation coefficient ( $c$ ), such that  $c = 3K$  (Kirk, 1980). The coefficients  $c$  and  $K$  thus specify the overall turbidity of the water column, and the extinction and scattering of light both before and after reflection from the prey ( $s$  and  $a$  in Fig. 1). The main source of turbidity in oceanic environments is phytoplankton. From Riley (1956), we found the following relationship between  $K$  and chlorophyll  $a$  (Chl $a$ , mg m $^{-3}$ ):

$$K = k_0 + 0.054 \text{Chl}a^{(2/3)} + 0.0088 \text{Chl}a. \quad (4)$$

In the absence of Chl $a$ , the extinction coefficient is  $k_0$  ( $= 0.1 \text{ m}^{-1}$ ). The details of the larval growth and foraging processes are described in Fiksen & Folkvord (1999). The relation between growth and ingestion is taken from Kiørboe et al. (1987), and the prey capture success is modelled as in Heath (1993). Small scale turbulence is accounted for in the encounter rate ( $V$  in Equation (1)) and in the capture success calculation (MacKenzie et al., 1994). The larva starves (dies) if its

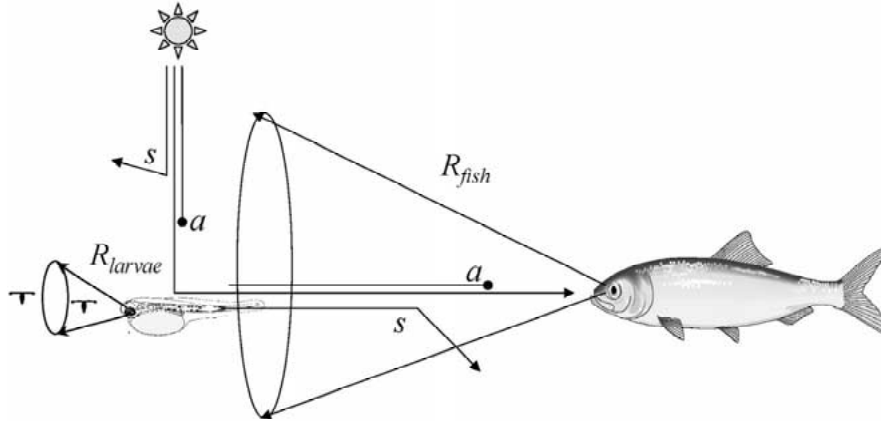


Figure 1. The basic principles of the encounter rate kernel in the model. Light is absorbed ( $a$ ) and scattered ( $s$ ) as it penetrates the water column, depending on the amount and type of particles in the water. Light is reflected (and absorbed) at the surface of prey (copepods or fish larvae), and this reflected light may be absorbed or scattered before reaching the eye of the larvae or the fish. Scattering and absorption depend on the properties of the particles; materials such as clay has a high scattering/absorption ratio; while, e.g., mud absorb rather than scatter light. Due to more sensitive eyes and larger prey, the visual range of the fish ( $R_{fish}$ ) is generally much larger than the visual range of the larvae ( $R_{larvae}$ ). An encounter occurs when the predator is able to separate the prey image from the background irradiance. Modified from Aksnes & Giske (1993).

body mass is less than 80% of the expected body mass at any specific length.

#### Predation risk

Both invertebrates and fish are important predators of larval fish. The vulnerability of the larvae depends on the ability these predators have to detect and capture their prey (Bailey & Houde, 1989). Generally, as the larvae grow, both the encounter rate with predators and the ability to escape an attack increase. For most ambush or entangling invertebrate predators (or filtering fish) the prey encounter rate changes little with prey size, while the capture success drops rapidly as prey gets larger. For visually feeding fish, the encounter rate increases considerably with prey size, and the capture success remains quite high, although it will also decline with prey size (Folkvord & Hunter, 1986; Bailey & Houde, 1989).

The feeding efficiency of fish is highly dependent on reactive distance (Aksnes & Giske, 1993). As in Giske et al. (1994), we assume predation from fish to be proportional to visual range squared:

$$\mu_f \propto (1 - P_e)R_f^2 = k(1 - P_e)R_f^2. \quad (5)$$

Here,  $P_e$  is the probability of escape after an encounter and  $k$  is a constant of proportionality comprising all other factors such as predator density, efficiency and swimming speed. The probability of escaping an encounter with fish is a function of larval size ( $L$ , in mm) and the relative size of the predator and the prey

(Bailey & Houde, 1989). From experiments on adult anchovies feeding on larval anchovies (Folkvord & Hunter, 1986), we let

$$P_e = \frac{0.92}{1 + \exp\left(\frac{L-16.3}{4.13}\right)}. \quad (6)$$

The visual range of the planktivore is calculated as in Equation (2), only replacing  $A_p$  with the area of the larvae ( $0.1 \text{ L}^2$ ) and  $E'$  with a constant ( $10^4$ , Fig. 2). Since the area increases with larval size, the detection distance and encounter rate also increase with the size of the larvae (Fig. 2). On the other hand, the susceptibility to planktivores decreases with length. With the assumptions made above, the vulnerability of herring larvae to fish predation will increase up to about 17 mm, and then decrease. The predation risk as a function of larval size for different values of  $k$  is shown in Figure 3.

Estimates of mortality rates in the sea demonstrate a strong reduction with increased body size (Peterson & Wroblewski, 1984; McGurk, 1986; Bailey & Houde, 1989). A number of causes (e.g., developmental malfunction, infections, parasites, and size spectra of predators) could produce this pattern. Since predation risk of small and undeveloped fish larvae may not show strong size-dependence (Leggett & deBlois, 1994), we added a term to include all such effects:

$$\mu_n = aL^b, \quad (7)$$

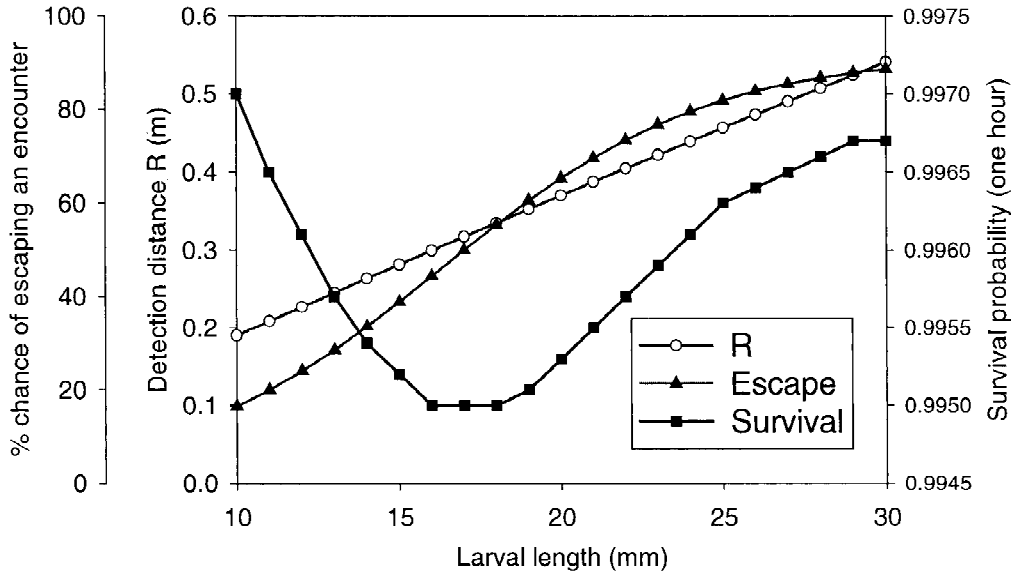


Figure 2. The relationship between the detection distance of the planktivorous predator, the probability of escape, and the probability of survival for a range of larval lengths. In this example, invertebrate predation rate is zero ( $a = 0$ ),  $k = 0.1$ , depth is 10 m and time is midday (irradiance at surface was  $300 \mu\text{mol m}^{-2} \text{s}^{-1}$ ).

where  $a$  and  $b$  are constants (see McGurk (1986) or Bailey & Houde (1989) for reviews of mortality rates in larval fish). At their default values, the parameters  $a = 0.1 \text{ h}^{-1}$  and  $b = -1.3$  will cause visual and invertebrate predation rates to be similar (and reasonable;  $0.01 \text{ h}^{-1}$  or  $\sim 0.2 \text{ d}^{-1}$ ) in environments where fish are efficient (Fig. 3). The survival probability  $P_s$  is then calculated each hour from the exponential probability distribution:

$$P_s = \exp(-\mu_n - \mu_f). \quad (8)$$

If the body mass of the larvae are 80% or less of the expected value at any length, then the larvae starves and  $P_s = 0$ . The probability of  $P_i(\Omega)$  individual  $i$  to have survived  $\Omega$  h after hatching is

$$P_i(\Omega) = \prod_{h=0}^{H=\Omega} P_s. \quad (9)$$

## Results

### Vertical profiles of growth and predation risk

Equipped with these equations and assumptions, we can model the multiple effects of increased chlorophyll  $a$  levels in the water column on growth and predation risk of fish larvae. First, we present some

static, vertical profiles of growth and survival of a 15-mm long larvae (Fig. 4). The profiles show that growth is temperature-limited (food is available in excess) near the surface, while food is increasingly limiting in deeper waters. At higher algal biomass the visual field of the larvae is reduced so that the profitable part of the water column (where growth is positive) is severely reduced. For first-feeding larvae, which is too small to search for benign conditions, this may increase the risk of starvation. At the same time, predation risk from planktivores is also reduced, and depending on food abundance, predation pressure and vertical distribution of the larvae the level of standing stock of algae may be beneficial or detrimental to recruitment. More turbid waters will reduce ambient light at depth, but visibility will be reduced even at similar levels of diffuse light (see Fig. 1). The longer reactive distance of piscivorous predators relative to their larval prey makes them more susceptible to scattering and absorbency within their reactive volume. The volume effectively scanned per unit time by larger fish will therefore drop faster than the volume scanned by fish larvae as turbidity increase (Fig. 5). If, however, the contrast between prey and the background also improve with turbidity (e.g., Utne-Palm, 1999), then the search volume will be less reduced, or even increased, with turbidity under a given ambient light level (Fig. 5).

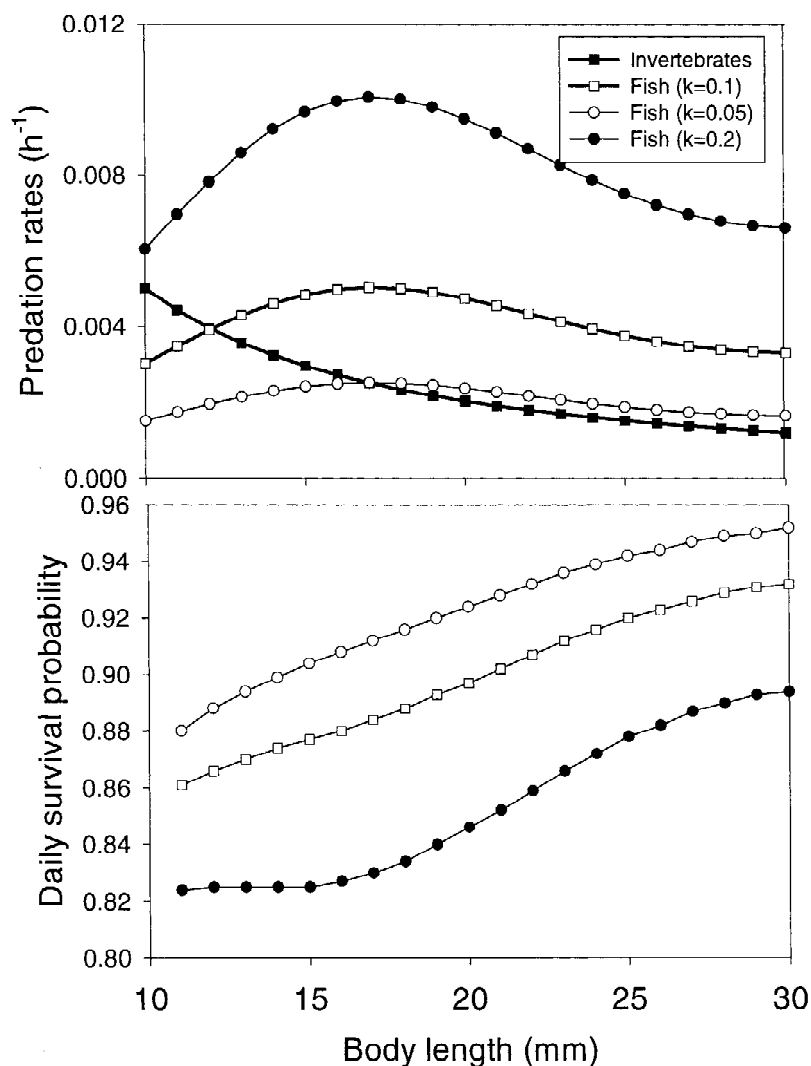


Figure 3. Predation rates at midday when visual predation is at its maximum level (upper panel) and integrated daily survival probabilities (vulnerabilities) under different levels of fish predation pressure and larval sizes (lower panel). Parameters for invertebrate predation rates are:  $a = 0.1$  and  $b = -1.3$ , and depth = 10 m. Surface irradiance fluctuate from near zero at night to  $300 \mu\text{mol m}^{-2} \text{s}^{-1}$  at midday.

The effect on predation risk from a layer of highly turbid water close to the surface is shown in Figure 6. For larger fish, the scattered light in the turbid water creates a refuge with low detection risk. The risk of being detected by predators for smaller fish is less dependent on turbidity. The same reasoning also applies to foraging: large fish searching for large prey will encounter fewer prey in the turbid layer compared to the deeper and clearer water, while small fish will find less food purely as a function of ambient light (Fig. 6). Giske et al. (1994) found the same general pattern using an earlier version of the model for the visual range (Aksnes & Giske, 1993). The revised model of

visual range (Aksnes & Utne, 1997), which includes a term for satiation of the eye as light increases, shows however that the vertical differences in predation risk are less prominent.

#### *Survival of a cohort in different mixing depths*

To assess the combined effects of reduced growth and predation risk in a homogeneous water column under increasing chlorophyll concentrations, we simulated a cohort of 500 newly hatched larvae drifting passively with currents within a surface mixed layer of 10, 20 and 30 m depth (Fig. 7). These larvae are subject to

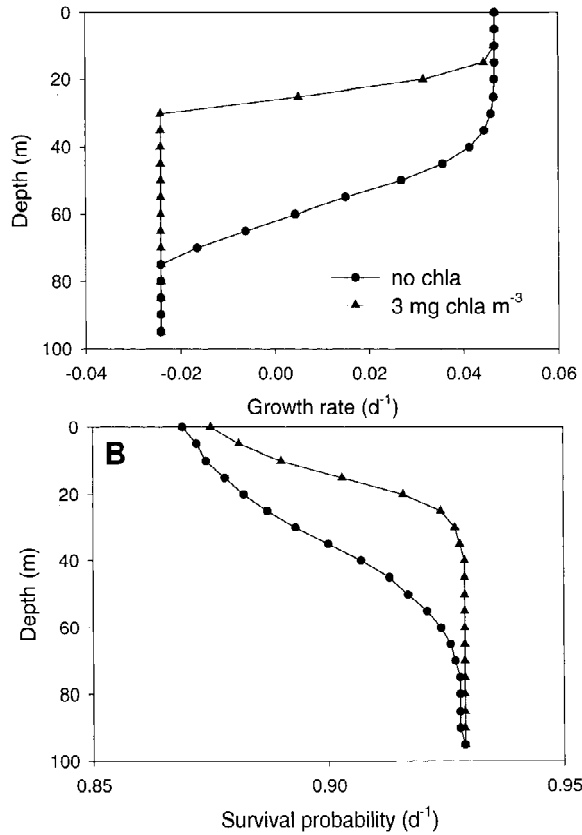


Figure 4. The profiles of (A) growth and (B) survival probability during 1 day for a herring larva (15 mm) staying at different depths in clear (no Chla) and turbid (3 mg Chla m<sup>-3</sup>) water. The simulation use  $N = 5$  mg dry weight nauplii and copepodite prey m<sup>-3</sup> and 10 m s<sup>-1</sup> wind stress at surface (see Fiksen & Folkvord, 1999, for details).

mortality as expressed above and grow according to the amount of food they are able to eat each day. After 50 days, the population is evaluated by the cohort survival index ( $S$ ):

$$S = \frac{1}{N} \sum_{i=1, N} w_i P_i, \quad (10)$$

where  $w_i$  is the body mass ( $\mu\text{g}$ ) and  $P_i$  is the survival probability (zero if starvation occurs) of individual  $i$  after 50 days. This index will return high values when growth and survival are high. An additional penalty is put on slowly growing individuals, since they also suffer higher risk of predation (Fig. 3).

The results show that at prey densities of 5 mg dw m<sup>-3</sup> increased turbidity will cause lower recruitment ( $S$ ) for all mixing depths (Fig. 7A). At this resource level, the larvae will be food limited during their first feeding period, and at deep mixing depths many lar-

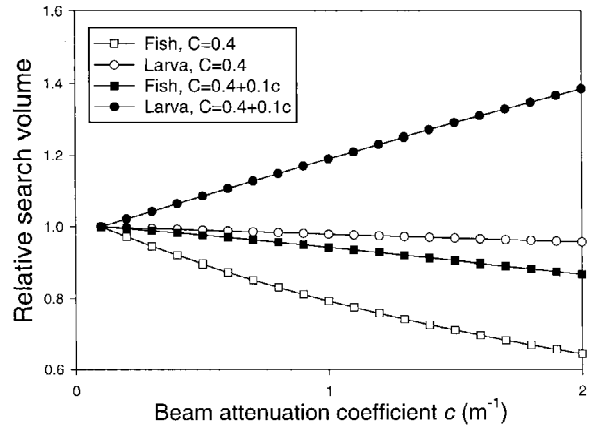


Figure 5. The effect of the beam attenuation coefficient  $c$  (turbidity) on the search volume of a herring larva (15 mm) eating nauplii and a fish eating the larva. When contrast  $C$  is not affected by turbidity (open symbols), both predator and prey experience reduced feeding abilities, although the impact is mainly on the predator. If the contrast is only slightly improved (assuming there is a statistical relation between  $C$  and  $c$  so that  $C = 0.4 + 0.1c$ ) as turbidity increase (black symbols), the larvae will improve its search volume, while the predator's search volume is still reduced by turbidity.

vae starve when turbidity is high. As food availability increase to 7.5 (Fig. 7B) and 10 (Fig. 7C) mg dw m<sup>-3</sup>, the effect of lowered predation rates from fish (due to higher turbidity) becomes more important to the survivorship index. At these prey concentrations, higher turbidity (from the increased chlorophyll content) is predicted to be beneficial to recruitment provided the mixing depth does not exceed  $\sim 20$  m (as long as the larvae cannot search for the optimal depth). Some combinations of prey and mixing depth seems to give maximum  $S$  at intermediate levels of turbidity. The actual change in  $S$  as a function of turbidity will depend in part on the intensity of visual predation on the cohort (Fig. 8). The relative change in larval growth and survival may be quite opposite in high and low predation regimes.

The latter prediction is made under the assumption that no extra zooplankton biomass is produced from the enhanced algal concentration. However, a striking feature of Figure 9 is that increasing prey abundance from 5 to 10 mg dw m<sup>-3</sup> may increase  $S$  with about an order of magnitude. At high chlorophyll  $a$  levels (4 mg m<sup>-3</sup>), the expected effect of satiation with increasing prey concentration is prevented (Fig. 9). The vertical aspects of prey encounter rate in the pelagic can explain this feature (Fig. 4). In clear water, the larvae in the bottom part of the mixed layer will still be encountering prey at reasonable rates, but under more turbid

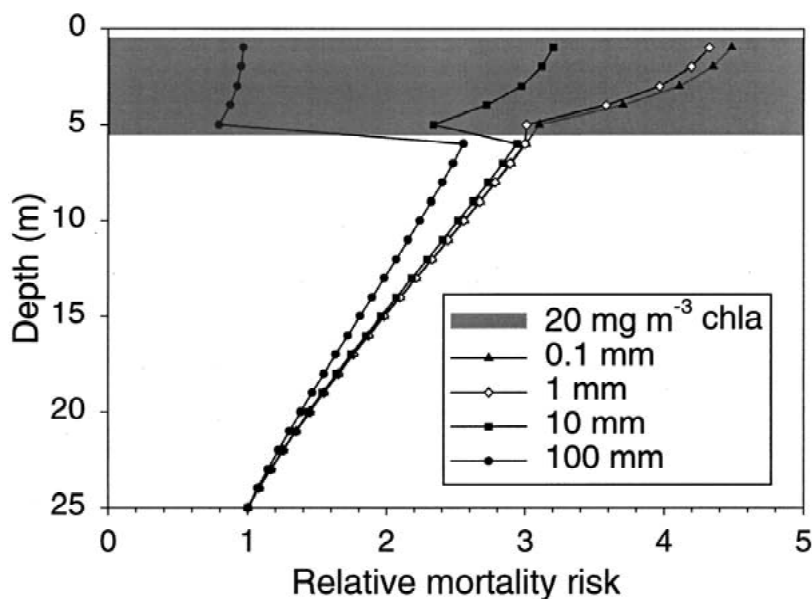


Figure 6. Chlorophyll as a refugium. Recalculation of Figure 6 in Giske et al. (1994) using the revised model of visual range (Aksnes & Utne 1997). The general picture is the same as the original, but the profiles are considerably less sensitive to depth (diffuse light).

conditions the growth of these larvae will be limited by prey encounter. Therefore, more phytoplankton or turbidity will augment the effect of higher food concentrations (Fig. 9). More zooplankton will ensure that the larvae grow more rapidly through the critical first feeding stages and the turbidity will provide shelter against predators as they grow larger. However, this effect will only have significant impact on recruitment success at quite high prey concentrations ( $> 8 \text{ mg m}^{-3}$ ).

## Discussion

### *Some limitations of the model*

The model presented here is a simplified representation of the foraging process of fish larvae and their fish predators. We have analysed how growth and survival of a cohort of fish larvae (herring) respond to nutrient enrichment and stimulated production by autotrophs. In contrast to traditional food-web analyses, our attention was on how the altered optical properties of the water column modified predator-prey relationships. This is obviously an important aspect of the interaction between visually searching foragers such as fish larvae and planktivorous (or piscivorous) fish and their prey. The model is not intended to explore the trophic nutrients-phytoplankton-zooplankton-fish larvae dy-

namics. The model does suggest, however, that fish larvae with developing brain and nervous system will benefit from increasing food concentration during the first feeding phase (Figs 7 and 9, Fiksen & Folkvord, 1999). This is due to the low prey encounter and capture rates during the first feeding stages, and the effect of more food would persist even at quite high concentrations (Fig. 9). Larger larvae will become satiated at far lower prey densities, as they are more efficient both in finding and capturing prey.

Another limitation of the model is the lack of behavioural responses, and diel vertical migration in particular. The simulations shown in Figure 7 assume that the fish larvae drift passively with convection in the mixed layer. If the larvae were allowed to select their optimal position in the vertical, they would stay nearer the surface as turbidity increased, and deeper as they grew older. This behaviour would greatly offset the negative influence of the deeper mixed layer, and also reduce the probability of encountering planktivorous fish during daytime. On the other hand, only the slightest diel vertical migration of prey organisms (nauplii) or variation in prey contrast over the day (diel feeding patterns) would greatly reduce food availability of the larvae (Giske et al., 1994). In a model including optimal diel vertical migration of zooplankton, Fiksen & Giske (1995) found that increased resource levels would reduce the exposure of zooplankton to predat-

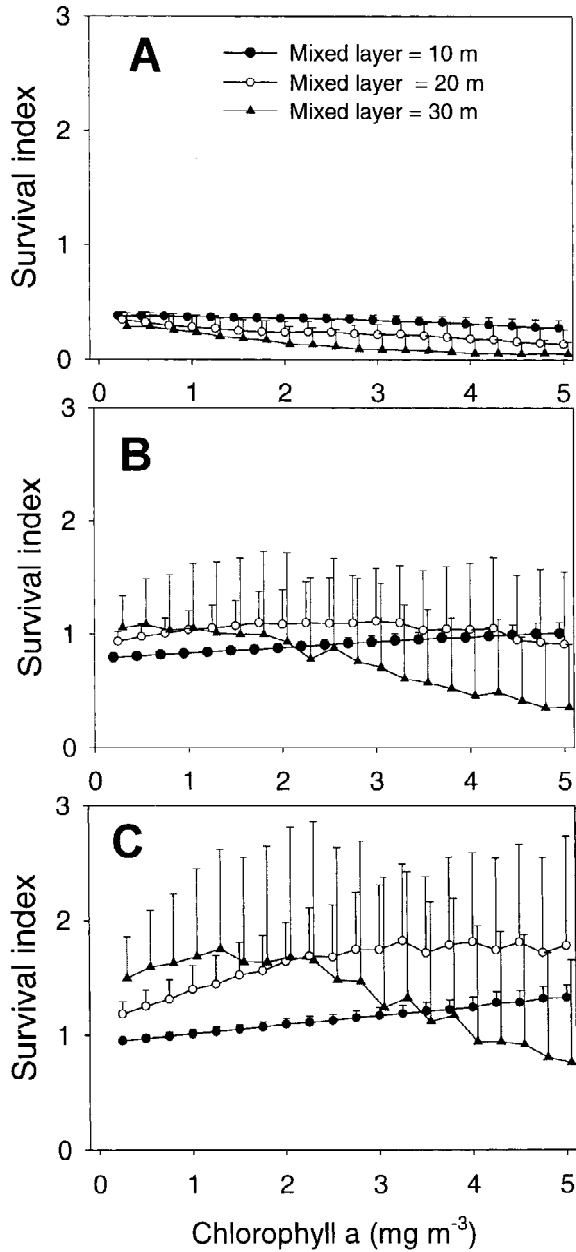


Figure 7. The effect of increasing chlorophyll levels on survival index  $S$  (Equation (10)) at (A) 5, (B) 7.5 and (C) 10 mg dry mass of prey  $m^{-3}$  for three different mixed layer depths, other parameters are as in the previous simulations. A concentration of 1 mg dry mass of prey  $m^{-3}$  would correspond to about one *Calanus* nauplii (stage 4) per l, and in the nursery areas of Norwegian spring spawning herring the density of nauplii would typically vary between 0 and  $\sim 10$  per l at the time of first feeding (Fossum, 1996). The simulation is initiated with 500 identical, newly hatched larvae that are tracked for 50 days. Their position in the mixed layer is assumed to be governed by convection, and is modelled as a purely stochastic process. The survival index  $S$  is the average body mass ( $\mu g$ , dry) of all 500 individuals multiplied by the corresponding survival probability (see Equation (10)). The error bars represent 1 SD.

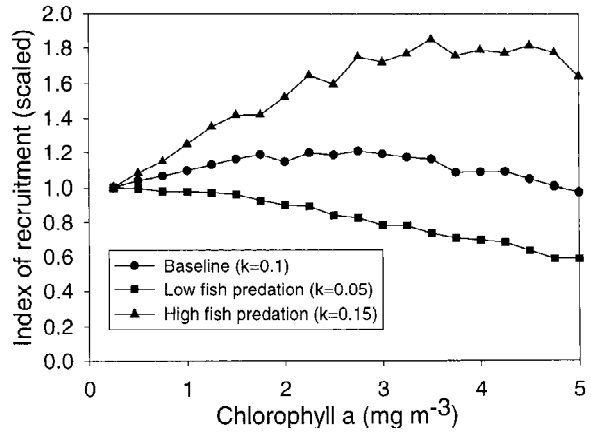


Figure 8. The relative recruitment success (scaled to its lowest value) at increasing phytoplankton densities and three scenarios of fish predation. The simulation is similar to Figure 7, with 7.5 mg prey  $dw m^{-3}$  and a mixing depth of 20 m (no wind).

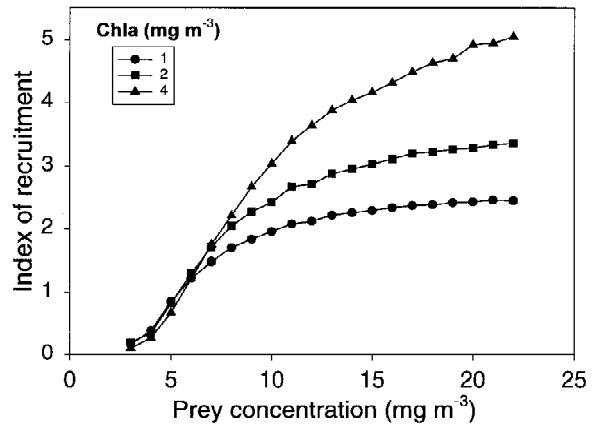


Figure 9. Recruitment success scheduled as a function of prey and chlorophyll concentration. All other parameters are as in Figures 7 and 8.

ors. The copepods can then stay in deeper and darker waters and still maintain high growth rates, but at lower risk of predation from fish. Also the predation risk estimation is sensitive to behaviour, as small pelagic fish and macroplankton are of the sizes that would most benefit by remaining in the turbid layer (Fig. 6). In a study of optimal vertical migration in mesopelagic fish, Rosland & Giske (1994) found that the fish would benefit by remaining in the turbid surface water for prolonged feeding during dusk and dawn.

Our model does not include behaviour, but we outline general mechanisms of how turbidity will modify growth and survival in larval fish. Although flexible behaviour can modify our conclusions, the direction of the predictions should persist even if behaviour



were included. The role of behavioural flexibility in both prey and predators is obviously a topic that deserves further attention in aquatic ecology (Verity & Smetacek, 1996).

Mechanisms other than those included in the model may operate on the success of larvae at high phytoplankton concentrations. Some fish larvae can feed on phytoplankton directly (van der Meeren, 1991), but this is not evaluated in the model presented here.

#### *Turbidity in laboratory and field studies*

A range of experiments have been conducted to assess the role of turbidity on foraging of fish (e.g., Vinyard & O'Brien, 1976; Boehlert & Morgan, 1985; Chesney, 1989; Miner & Stein, 1993; Utne, 1997; Utne-Palm, 1999). These studies have shown various relations between turbidity and foraging success. Surprisingly, fish seems to have higher feeding rates at intermediate levels of turbidity (Boehlert & Morgan, 1985; Bristow & Summerfelt, 1994; Bristow et al., 1996; Utne, 1997; Utne-Palm, 1999), at least at high ambient light conditions. At low light, the turbidity reduces ingestion success (Miner & Stein, 1993). One mechanism put forward to explain these observations is that the contrast between the background and the prey is increased in water with more particles (Hinchshaw, 1985; Utne-Palm, 1999). At low light levels, the detection of prey may instead be limited by absolute light levels rather than contrast. Miner & Stein (1993) found that more turbidity caused larval bluegill to select smaller prey (at high light levels), and Vinyard & O'Brien (1976) and Reid et al. (1999) observed that the reactive distance of large prey was severely reduced as turbidity increased. Utne (1997) and Utne-Palm (1999) also found that gobies had longer reactive distance under slightly turbid conditions, but at higher turbidity the reactive distance dropped. These results conform well to predictions from the model of visual range used here (Aksnes & Giske, 1993; Aksnes & Utne, 1997), where larger prey will be less frequently encountered in turbid water relative to smaller prey (Equation (2)).

A fairly small improvement of contrast with turbidity is required to reverse the negative effect of turbidity at a given light intensity (Fig. 5). However, from the empirical studies listed above, it does not seem likely that the effect of turbidity on prey contrast will persist at high turbidity, as assumed in the simulations presented in Figure 5. It is likely that the benefit of contrast

levels off at increasing turbidity (Utne-Palm, 1999), and that the reduced visibility eventually becomes the dominant factor.

In the cultivation of fish larvae, it has been shown that larva walleye in turbid tanks feed and grow at rates superior to larvae in clear water (Bristow & Summerfelt, 1994; Bristow et al., 1996). If the water is clear, their larvae showed a tendency to cling to the walls (where light is reflected) of the tank and have low feeding success. The more diffuse light in turbid tanks may have prevented light reflection from the walls and thus the phototactic behaviour of clinging to the walls, and at the same time provided improved contrast to the food particles (Bristow & Summerfelt, 1994; Bristow et al., 1996). Bristow et al. (1996) compared the effect of a dye (Aquashade, absorbing light at wavelengths required for photosynthesis) with clear and turbid (from adding clay) water on growth and survival of larval walleye (*Stizostedion vitreum*). It turned out that the dye reduced performance of the larvae, while clay was beneficial. The cones of perch (*Perca fluviatilis*) absorb light at wavelengths similar to those of Aquashade, and therefore may block out visual stimuli (Bristow et al., 1996). It is difficult to speculate on whether different types of algae may produce similar results. Given the potential importance of algae in generating turbidity, there are surprisingly few studies reported on their effect on the reaction distance, growth and survival of fish. These mechanisms are not included in the model, but then they may also be 'tank-effects' that do not apply to natural settings.

The role of estuaries, river plumes and fronts in the recruitment success of fish has been examined at several locations (e.g., Fox et al., 1999; Grimes & Finucane, 1991; Grimes & Kingsford, 1996; Sirois & Dodson, 2000). Such areas are characterised by high productivity and are often more turbid and turbid than other oceanic sites. Fox et al. (1999) found that tidally induced turbidity probably reduced the fraction of the water column suitable for feeding of herring larvae in the Blackwater Estuary (Essex, England). However, no reduction in feeding incidence was recorded over the tidal cycle, and feeding seemed more correlated to surface irradiance. Similarly, Sirois & Dodson (2000) did not find significant differences in feeding rate among larval rainbow smelt (*Osmerus mordax*) from a turbid and a less turbid region of the St. Lawrence estuary. Laboratory experiments confirmed this, and showed that larvae in turbid water grew better although feeding rates were similar. Larvae in turbid tanks probably had a lower activity

level and allocated a higher proportion of ingested energy to somatic growth (Sirois & Dodson, 2000). Grimes & Finucane (1991) found higher chlorophyll and zooplankton concentrations and growth rates of ichthyoplankton in frontal areas compared to adjacent waters. Grimes & Kingsford (1996) reviewed the literature of the effects of river discharge plumes on larval fish, and their conclusion was unequivocal. Apparently, some species seem to be more adapted to take advantage of enhanced food production than others, therefore various species may respond differently to fronts.

In relation to our model, these observations emphasise the potential of individual behaviour in modifying the consequences of environmental factors such as turbidity. In clear water, the risk of being detected by predators increases, and the behavioural response may be to reduce the level of activity or to descend in the water column. At intermediate turbidity, the larvae will be less susceptible to visual predators, and thus less vigilant and more efficient in searching for food or in transforming ingested food into growth. At some point, however, turbidity will certainly reduce both feeding and growth rates.

#### *Nutrient enrichment and recruitment to fish stocks*

Hjort (1914) suggested that the variations in year class strength of major fish stocks could be caused by lack of food during the first feeding period. Fossum (1996) found clear evidence that the survival of first feeding Norwegian spring-spawning herring larvae were correlated to the temporal overlap with prey, and Ellertsen et al. (1989) found similar results for Arcto-Norwegian cod. Additionally, the model developed by Fiksen & Folkvord (1999) supported the 'critical period' concept, since first feeding larvae have short reactive distance, low prey capture success and limited foraging abilities. Although there is a general consensus that fish larvae are food-limited (Cushing, 1996), the stage at which food is most limiting is not clear. Cushing (1996) reviewed this issue, and concluded that the late larval stage was the best candidate to predict recruitment. This would imply that as the larva grows, its food demand would increase more than its ability to find and capture prey. Naturally, density-dependent survival at older stages would impede the effects of enhanced survival during the early larval phase.

In conclusion, the model predicts higher phytoplankton concentrations to be favourable to recruit-

ment. The most prominent effect of higher algal biomass is obtained when both predation risk from visual predators and the food availability (zooplankton) is high. If there is linear food-chain dynamics, so that more nutrients are converted into phytoplankton and zooplankton biomass, then nutrient enrichment is likely to augment the recruitment success of fish. Whether the food-web response is likely to be linear is, however, not obvious (e.g., Hulot et al., 2000). Several studies have looked at how egg production of *Calanus finmarchicus* relates to primary production, and there seems to be a positive correlation when corrected for the effect of lipid reserves (Richardson et al., 1999). Therefore, higher primary production and growth or egg production of zooplankton in the first feeding areas of larval fish probably enhance the survival of larvae and recruitment to fish stocks.

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