Condition, buoyancy and the distribution of larval fish: implications for vertical migration and retention

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Abstract. A Lagrangian time-stepping model driven by water density, daytime larval feeding and swimming, and by condition-related larval buoyancy was used to track the vertical position and condition of individual larval cod (Gadus morhua L.) in a stratified water column. The model results can explain the variety of frequencies, phases and amplitudes of vertical migration (including inverse vertical migrations and increased dispersion at night) observed in field studies. Vertical distributions and conditions of post-yolk-sac larvae, derived from the model during day and night, are also consistent with comparable field observations. When vertical shear is introduced into the model, a simple localized larval retention mechanism, directly related to feeding, condition and buoyancy, is revealed. The model results also demonstrate increased shear dispersion (dilution) of poor-condition larvae relative to good-condition larvae, and may be used to explain the relative paucity of observations of dying or dead larvae in the field. Virtually all of the model results are directly testable in the field and/or laboratory, and we show how the findings may be directly applicable to larvae possessing functional swim bladders and perhaps to freshwater and marine invertebrate zooplankton.

Introduction

Vertical migrations of marine larval fish (Heath et al., 1988; Stephenson and Power, 1988, 1989) and zooplankton (Cushing, 1951; Longhurst, 1976; Zaret and Suffern, 1976; Dodson, 1990; Ohman, 1990; Bollens and Frost, 1991) are well documented. However, after almost a century of investigation, irrefutable evidence for clear and repeated diel vertical migrations is not to be found in the larval fish literature. Many authors reporting on larval fish vertical migration tend to expand on a multitude of explanations of how abiotic and biotic factors are responsible for departures from expected diel patterns, and usually arrive at conclusions which are quantitatively weak (e.g. Seliverstov, 1974; Sameoto and Lewis, 1980; Sameoto, 1984). Further, a number of elaborate complicated schemes have been devised to explain the departures (e.g. Bainbridge, 1961; Hutchinson, 1967). Overall, these explanations have led to additional, and at best, difficult to test hypotheses. The fisheries and zooplankton research community remains at a loss for a mechanism that simply explains the observed temporal variations in vertical distribution and the inferred migration patterns.

Some of the most thorough studies on the vertical migration of larval fish have focused on the Atlantic herring (Clupea harengus L.) and date to the early 1900s (e.g. Johansen, 1925; Russell, 1926, 1928). Recently, it has become possible to
sample discrete depth intervals with high net efficiencies by using opening and closing multiple-net sampling systems such as the BIONESS (Sameoto et al., 1980) and MOCNESS (Wiebe et al., 1976). Stephenson and Power (1988) sampled herring larvae off southwest Nova Scotia in two consecutive years using the BIONESS. In 1987, a clear diel cycle (up during the day and down at night) was observed (Figure 1a). However, Stephenson and Power (1988, 1989) found a semidiel pattern of vertical migration for herring larvae at the same site in 1985 (Figure 1b). Both patterns were repetitive within each study, but clearly demonstrate variability in the frequency of vertical migration. Nichols et al. (1986) show that vertical migration of herring larvae can be the mirror image of that seen by Stephenson and Power (1988) (Figure 1c). Many other examples in the literature show vertical migrations which have no pattern at all. For example, Fossum et al. (1987) found the vertical distribution of herring larvae to be highly variable and without a well-defined frequency (Figure 1d).

In general, our review of the literature (illustrated by more than the few examples of herring larvae above) leads us to conclude that vertical migration patterns are highly variable. Evidence for a clear and repetitive vertical migration pattern within and among larval fish species and regions, based on endogenous rhythms, is not convincing. We recommend Neilson and Perry (1990) for a complete review of marine fish vertical migrations.

Mechanisms and adaptive hypotheses frequently found in the planktonic vertical migration literature include: (i) organisms following preferred light levels which change through time as a result of variations in time of day, cloud cover and moonlight (Woodhead and Woodhead, 1955; Blaxter, 1973; Gliwicz, 1986; Heath et al., 1988); (ii) light-related predator avoidance (Zaret and Suttorp, 1976; Bollens and Frost, 1989); (iii) animals following optimal prey concentrations (Ellers et al., 1977, 1980; Tilseth and Ellersen, 1983; Munk et al., 1989); (iv) animals synchronizing the phase of their migration to the dominant tidal signal (Fortier and Leggett, 1982, 1983); (v) animals migrating to colder water after feeding to lower metabolic rates and conserve energy (McLaren, 1963); (vi) larvae migrating to the warmer surface waters to increase growth (Wurtsbaugh and Neversman, 1988); (vii) abiotic factors such as wind mixing altering the existing migration patterns (Tilseth and Ellersen, 1983; Heath et al., 1988) and finally (viii) changes in larval density/buoyancy resulting from yolk absorption, development and condition (Blaxter and Ehrlich, 1974; Coombs, 1981; Henri et al., 1985; Neilson et al., 1986; Yin and Blaxter, 1987). It is the latter of these hypotheses which we examine here. Throughout this paper, density refers to the mass per unit volume of either the larvae or water. Larval buoyancy is the force acting on a larva that results from the density difference between the larva and the surrounding water.

Proposing that vertical movement is directly related to egg or larval buoyancy is by no means new (e.g. Blaxter and Ehrlich, 1974; Coombs, 1981; Henri et al., 1985; Neilson et al., 1986; Frank and McRuer, 1989; Page et al., 1989). However, in this paper we investigate the effect of larval condition on larval buoyancy between the stages of yolk-sac absorption and the development of a functional swim bladder. We develop a simple model, based on documented
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Fig. 1. Temporal changes in the depth distribution of larval herring: A and B, averaged maximum larval concentrations (Stephenson and Power, 1988, 1989); C and D, centres of mass (Nichols et al., 1986; Fossum et al., 1987). Black and white bars indicate night and day periods in each study.
behaviour and physiological changes in larval cod (*Gadus morhua* L.), to examine vertical distribution patterns and the inferred vertical migration. Our modelling approach is based on tracking the vertical position of individual larvae and allowing for physiological changes in response to feeding success. We propose a simple and readily testable condition-driven buoyancy hypothesis to explain vertical migration patterns during the early larval stages. This paper places emphasis on larval fish. However, many of the findings may be applicable to zooplankton, as will be outlined below.

**Method**

*The general model*

In its simplest form, the model (Figure 2) consists of a two-layered water column with bottom depth $h_2$, surface ($p_1$) and sub-pycnocline ($p_2$) water densities typical of weakly stratified areas around banks (e.g. Buckley and Lough, 1987; Taggart *et al.*, 1989). Larval food concentration ($F$) is assumed to vary with depth ($z$) according to:

$$F = \exp\left[-\frac{(z - h_1)^2}{2\sigma^2}\right]$$

Note that the food concentration reaches its maximum of unity at the pycnocline.

![Fig. 2](image_url)

*Fig. 2.* The physical and biological components of the condition-driven buoyancy model consisting of a stratified water column with upper depth ($h_1$) and density ($p_1$), and lower depth ($h_2$) and density ($p_2$). The food maximum is distributed around the pycnocline. Open circles represent larval fish and their potential daytime movements, and solid circles represent their potential night-time movement.
(z = h₁) and has a standard deviation of σ about this depth. Food maxima around density gradients are well documented (e.g. Tilseth and Ellertsen, 1983; Buckley and Lough, 1987; Taggart et al., 1989).

The model is Lagrangian in that we track the depth of individual larvae through time and evaluate changes in their condition. Our approach is similar, for example, to that of Woods and Onken (1982) who modelled the diurnal variation of insolation and primary production in the upper ocean using, what they termed, the ‘Lagrangian-ensemble’ method. Woods and Onken’s (1982) model allowed for the integration of phytoplankton physiology (short time scales) at each time step along individual cell trajectories. This Lagrangian method gave rise to different estimates of primary production when compared to models employing the Eulerian frame of reference where developmental variability in individual plankters could not be assessed. In our model, as an individual larva moves through the water column, its depth (z) and the ambient food concentration F(z) will change. Thus, in this Lagrangian frame, F is an implicit function of time.

Larval condition (C) is also a continuous variable with normalized values between 0 and 1. We assume that condition depends on the feeding success of a larva during daylight hours according to:

\[ \frac{dC}{dt} = \frac{1}{T_c} (F - C) \]  

where t is time. This is a ‘fading memory’ model for condition with an e-folding time of \( T_c \); the average food concentration experienced by the larva within \( T_c \), of the present (t) essentially determines its condition. Of course the food concentration experienced by the larva, and hence its condition, will change as it moves through the water column. The finite difference form of equation (2) used in our time-stepping Lagrangian model during the day is:

\[ C(t + \Delta t) = e^{-\frac{\Delta t}{T_c}} C(t) + [1 - e^{-\frac{\Delta t}{T_c}}] F(t) \]  

where \( C(t + \Delta t) \) is the condition at the new time step. We assume that the larva does not feed, and its condition does not change at night. Note that this algorithm for \( C \) ensures that it will always lie between 0 and 1. The density of the larva is assumed to be proportional to its condition, which allows larval buoyancy to be calculated as a function of time.

At night, we assume that larvae do not swim and that their vertical velocity is simply determined by buoyancy according to Stoke’s terminal velocity (e.g. Batchelor, 1967):

\[ w = 2gr^2 \left( \frac{\rho_w - \rho_l}{9g} \right) \]  

where g is acceleration due to gravity, r is the radius of an equivalent larval spheroid, \( \rho_w \) is the density of the surrounding seawater, \( \rho_l \) is the density of a
larva and \( \nu \) is the coefficient of viscosity of seawater \((1.61 \times 10^{-3} \text{ kg m}^{-1} \text{s}^{-1} \text{ at } 5^\circ \text{C and salinity 35} \text{‰}; \text{Dorsey, 1940})\). During the day, we assume the larva swims toward the food maximum at speed:

\[
|w| = w_{\text{max}} C
\]

where \( w_{\text{max}} \) is the maximum swimming rate and \( C \) is the larval condition. The larval depth \( z(t) \) at each time step is updated during day and night according to:

\[
z(t + \Delta t) = z(t) + w \Delta t + \epsilon
\]

where \( z(t + \Delta t) \) is the new larval depth, \( w \) is the vertical velocity and \( \epsilon \) is a random perturbation added to simulate turbulence. We assume that \( \epsilon \) is normally distributed with zero mean and standard deviation \((2K \Delta t)^{-1/2}\) \(\text{(Page et al., 1989)}\), where \( K \) is the eddy diffusivity. A reflection condition is used at the top and bottom boundaries to ensure that larvae do not ‘leave’ the model \(\text{(Fischer et al., 1979)}\). This is equivalent to a no-flux boundary condition for the equivalent advection–diffusion concentration equation in an Eulerian frame of reference.

In summary, during the day the larva swims towards the food maximum to feed, at a speed determined by its condition. At night there is no swimming; the larva either floats or sinks, depending on its buoyancy, which is determined by its condition and hence feeding success during previous daylight hours. In addition to daytime swimming and night-time floating or sinking, random perturbations have been included to simulate turbulence.

**Biological parameters**

The biological values chosen for the model simulations come from field and experimental data found in the literature. Cod larvae were selected for this simulation because of the availability of buoyancy and behavioural data. The Ellertsen et al. \(\text{(1980)}\) data on cod larval density were used because of the short sampling intervals (1 day). Data from the two separate experiments by Ellertsen et al. \(\text{(1980)}\) were averaged (Figure 3) and the original salinity-based units of density were converted to density \((\text{kg m}^{-3})\) using the UNESCO tables for 5°C water \(\text{(Knauss, 1978)}\). On the basis of these data, larval density at yolk-sac absorption \(\text{(5 days after hatching)}\) was set at 1027.5 \(\text{kg m}^{-3}\) and considered to be typical of a larva in its ‘best’ possible condition \(\text{(Figure 3)}\). Larval density just before moribund \(\text{(15 days post-hatch; Ellertsen et al., 1980)}\) was set at 1024.0 \(\text{kg m}^{-3}\) and considered typical of a starved larva in its ‘poorest’ condition. The decrease in larval density during this 10 day period had an e-folding scale \(\text{(Tc)}\) of \(\sim 3\) days \(\text{(Figure 3)}\). Results from similar studies \(\text{(Neilson et al., 1986; Yin and Blaxter, 1987)}\) for starved cod larvae are consistent with those of Ellertson et al. \(\text{(1980)}\) and show a general decrease in larval density after yolk-sac absorption.

The radius, \( r \), used in equation (4) for the terminal velocity was calculated using:

\[
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\]
assuming that the body of a larval cod (head and gut) is best represented by the equivalent spherical diameter of an oblate spheroid, where \( l_g \) and \( l_h \) are the gut lengths (mouth to anus) and head depth (posterior of the eye), respectively. A 5.75 mm cod larva has an average \( l_g \) of 2.4 × 10^{-3} m and \( l_h \) of 8.0 × 10^{-4} m (T. Miller, personal communication, McGill University, Montreal, PQ, H3A 1B1). For example, assuming a water density \( \rho_w \) of 1026.5 kg m^{-3} and a ‘best’ condition larva with density \( \rho_l \) of 1027.5 kg m^{-3}, the terminal velocity \( (w) \) is 
\[
-1.87 \times 10^{-3} \text{ m s}^{-1}.
\]

Evidence to support feeding of cod larvae only during the day is provided by both laboratory and field experiments. Tilseth and Ellertsen (1984) show that cod, like most marine larval fishes, are visual feeders with more prey captures at high light intensities and fewer prey captures at low light levels. Field evidence from Tilseth and Ellertson (1983) shows more nauplii per larval cod gut during the day relative to night, which is consistent with daytime feeding.

Increased dispersion of the larvae at night (e.g. Heath et al., 1988) supports our assumption of passive floating/sinking at night. More convincing evidence is provided by Ellertsen et al. (1980) where larval cod swimming activity was shown to be higher during the daytime.

The swimming rates of cod larvae are usually determined with the body aligned in the horizontal direction (e.g. Bishai, 1960). However, in our model it is assumed that the swimming rates are equally valid in the vertical direction.
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Burst speeds for a 4–6 mm cod larva can reach 4.5–5.0 × 10⁻³ m s⁻¹ (Blaxter, 1986; Bailey and Houde, 1989), and cruising speeds for a variety of marine larvae in this size range are 5.0 × 10⁻³ m s⁻¹ (Blaxter, 1986). Therefore, it is not unreasonable to assume that a good-condition larva will maintain an average swimming speed of 1.0 × 10⁻³ m s⁻¹ during the day (12 h). The swimming speed of cod larvae was assumed to be proportional to condition. Skiftesvik and Huse (1987) have shown that starved cod larvae quickly lose their swimming and feeding abilities, while feeding larvae readily maintain or increase their swimming activity and prey searching. Frank and Leggett (1982) have shown that starved capelin (Mallotus villosus Müller) larvae typically display sporadic and undirected swimming relative to those which are well fed.

Model simulations were initiated with the larvae seeded around the pycnocline and the maximum food concentration (h₁). This depth of initialization was chosen because: (i) the average depths of centres of mass for early yolk-sac larvae derived from a number of studies were 30–40 m (Selafani, 1992); (ii) Page et al. (1989) have used a model and field comparisons to show that haddock (Melanogrammus aeglefinus L.) eggs, just prior to hatching, will be concentrated near the pycnocline; (iii) for some species, such as Atlantic mackerel (Scomber scombrus L.), it has been shown that immediately after hatching the relatively high-density yolk-sac larvae are found in the pycnocline region and the zone of maximum food concentration (deLafontaine and Gascon, 1989); and (iv) the larvae of American plaice (Hippoglossoides platessoides), yellowtail flounder (Limanda ferruginea) and witch flounder (Glyptocephalus cynoglossus) are also known to be more concentrated in the region of the pycnocline (Frank et al., 1992).

Larval mortality was not included in the model. If a larva is in poor condition its probability of swimming toward the prey maximum decreases and its condition tends toward zero, resulting in no swimming ability. Size-related changes in larval swimming (e.g. Bailey and Houde, 1989) and sinking velocities (e.g. Hoss et al., 1989) were also not included because of the limited time span for growth in our model (10 days). Average growth between the period of yolk absorption and up to 16 days after hatching is 0.2 mm for starved larvae (Ellertsen et al., 1980) and 0.5 mm for fed larvae (Solberg and Tilseth, 1987), which translates to limited increase in cruising speed (Blaxter, 1986). Thus, growth effects on swimming and sinking rates within the model are negligible, but we recognize that it may play an important role with other species and if longer periods are considered.

Physical parameters

The density of the surface layer (ρ₁) was chosen to be 1026.0 kg m⁻³ and the lower layer density (ρ₂) was set at 1026.5 kg m⁻³. These densities were selected to represent the approximate values of Ellertsen et al. (1980) for larval cod rearing conditions. The model pycnocline was centred at 40 m and bottom (h₂) was set at 100 m. The food concentration was normally distributed at an average depth of 40 m with one standard deviation of 10 m. The size of the random
perturbations included to simulate turbulence from wind mixing was chosen to represent a typical upper ocean eddy diffusivity \(2.0 \times 10^{-1} \text{ m}^2 \text{ s}^{-1}\); Loder et al., 1988). A complete list of parameters and the values used in the simulations is provided in Table 1.

**Model results**

Three simulations, using the parameters in Table 1, are detailed below and illustrate the temporal variations in depth and condition of: (i) two individual cod larvae; (ii) a population of 200 cod larvae; and (iii) a population of 200 cod larvae in a vertically sheared flow. During the simulations, we collapsed the condition into three classes: \(1 > C > 2/3\), good condition; \(2/3 > C > 1/3\), average condition; \(1/3 > C > 0\), poor condition.

The first simulation is provided to simply demonstrate how larval condition and depth change through time. Two larvae were initially introduced at a depth of 20 m. One began in good condition \((C = 0.75)\) and the other in poor condition \((C = 0.25)\). After the first night, it is clear that the larvae are at different depths due to their condition-related buoyancy (Figure 4a). The poor-condition larva is positively buoyant and initially floats towards the surface, while the more dense, good-condition larva sinks out of the surface layer during the night. The high-frequency (tens of minutes) depth variations are due to turbulence.

During the day, both larvae swim toward the food maximum. However, differences in condition result in differences in swimming ability and in feeding success. The poor-condition larva, a relatively weak swimmer, does not reach the food maximum as quickly and eats less. The good-condition larva swims faster, reaches the food maximum more rapidly and eats more. As condition is a function of larval feeding during the day, the condition of the good larva increases slightly, while that of the poor-condition larva decreases (Figure 4a). This becomes more apparent as time progresses, with the poor-condition larva being found progressively higher in the water column, particularly at night. The good-condition larva remains relatively close to the food maximum. The important result is that when repeated over 10 day–night cycles, a bifurcation in larval condition and average depth develops, and the diel vertical migration of the poor-condition larva is consistent with the nocturnal diel vertical migration hypotheses (down at day, up at night), while that of the good-condition larva is consistent with a diurnal vertical migration pattern (Figure 4a).

Different evolutions in larval condition and vertical position can result from larvae which began with the same initial condition and depth. For example, two average-condition \((C = 0.4)\) larvae were introduced at 16 m (Figure 4b). Here, larval condition and depth variation is clearly driven by the larva’s probability of encountering food, which is enhanced or reduced by the simulated turbulence and demonstrates the randomness within the model.

The second simulation shows how the condition and depth distribution of a population of cod larvae evolves. The simulation was initialized with a population of 200 cod larvae having a randomly distributed condition of between
Table 1. Summary of variables, parameters and values used in the condition-driven buoyancy model simulations

<table>
<thead>
<tr>
<th>Variable</th>
<th>Symbol</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larval density: 'best' condition</td>
<td>( \rho_b )</td>
<td>1027.5 kg m(^{-3})</td>
<td>Ellertsen et al., 1980</td>
</tr>
<tr>
<td>Larval density: 'poorest' condition</td>
<td>( \rho_p )</td>
<td>1024.0 kg m(^{-3})</td>
<td>Ellertsen et al., 1980</td>
</tr>
<tr>
<td>Surface layer water density</td>
<td>( \rho_s )</td>
<td>1026.0 kg m(^{-3})</td>
<td>Ellertsen et al., 1980</td>
</tr>
<tr>
<td>Sub-pycnocline water density</td>
<td></td>
<td>1026.5 kg m(^{-3})</td>
<td>Ellertsen et al., 1980</td>
</tr>
<tr>
<td>Bottom depth</td>
<td>( h_b )</td>
<td>100 m</td>
<td>Valentine and Lough, 1991</td>
</tr>
<tr>
<td>Pycnocline and food maximum mean depth</td>
<td>( h_f )</td>
<td>40 m</td>
<td>Buckley and Lough, 1987</td>
</tr>
<tr>
<td>Food maximum standard deviation</td>
<td>( \sigma )</td>
<td>10 m</td>
<td>Buckley and Lough, 1987</td>
</tr>
<tr>
<td>Maximum daytime swimming speed</td>
<td>( w_{max} )</td>
<td>10 (^{-2}) m s(^{-1})</td>
<td>Bjaxter, 1986</td>
</tr>
<tr>
<td>Larval density e-folding scale</td>
<td>( T_e )</td>
<td>3 days</td>
<td>Ellertsen et al., 1980</td>
</tr>
<tr>
<td>Eddy diffusivity coefficient</td>
<td>( K_e )</td>
<td>(2.0 \times 10^{-3}) m(^{2}) s(^{-1})</td>
<td>Loder et al., 1988</td>
</tr>
</tbody>
</table>
Fig. 4. The 10 day evolution of depth and condition of (A) a good-condition (dashed) and poor-condition (solid) cod larvae initialized at the same depth, and (B) two neutral-condition cod larvae initialized at the same depth. Black and white stippling indicate night and day periods in each study.
A sequence of instantaneous vertical samples taken every 12 h (midday and midnight) reveals the population’s depth and condition changes through time. The initial population begins to form two distinct populations differing in average condition. The overall depth distribution also reveals which samples were taken during the day or night (Figure 5). During the day, the larvae are more concentrated around the food maximum and at night there is greater vertical dispersion. Some of the average-condition larvae switch between good (midwater) and poor (near-surface) condition depending on their day-to-day encounters with food, and by the end of 10 days the initial population has separated into relatively good- and poor-condition sub-populations. This is important because it demonstrates how population average condition evolves through time. The results further show how typical inverse vertical migration patterns based on population centre of mass can evolve simply through differences in larval condition and buoyancy.

As most ocean plankton are found in advective environments, a simple vertically sheared current simulating wind stress on the water surface was added to the model. The surface current was $1.5 \times 10^{-2}$ m s$^{-1}$ and decayed with an e-folding scale of 15 m. This makes the Lagrangian model two-dimensional. The model was initialized as in the previous simulation, with the initial horizontal position ($x$) equal to zero, and samples were taken every 12 h over a 4 day period (Figure 6). After the first night separation of the good- and poor-condition larvae results, as well as a reaggregation near the food maximum during the following day. The poor-condition larvae near the surface are advected away from the initialization point by the higher current velocities there, and at the end of 4 days the increased horizontal dispersion (relative to the good-condition larvae) is evidence of shear dispersion (Figure 6). The deeper, good-condition larvae are ‘retained’ near the initialization point due to lower current velocities and reduced shear and dispersion. At the end of 4 days, two populations are apparent with the poor-condition larvae separated from the good-condition larvae by a maximum of 40 km.

Vertical distributions of larval concentration

Vertical profiles of larval concentration, representative of samples taken at 10 m intervals, were calculated from the model results with the parameters given in Table I to further examine the vertical distributions as a function of larval condition. The distribution of the total population of larvae shows greater vertical dispersion and a slight upward movement at night (10 m), and less vertical dispersion around the food maximum during the day (Figure 7a). When the total population is stratified by condition, the good-condition larvae are aggregated around the food maximum during the day and show a slight increase in dispersion at night (Figure 7b). The poor-condition larvae, however, show maximum concentrations near the surface during both day and night with a slight downward migration occurring during the day (Figure 7c). Therefore, stratifying larval samples by condition, which the ‘Lagrangian ensemble’ method permits, provides a new view of vertical distribution and inferred migration patterns. This
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Fig. 5. Sequential vertical profiles of a larval cod population showing the depth and condition distribution over a 10 day period at 12 h intervals representing midday and midnight (crosses represent individual larvae in good condition, dots are average condition and circles are poor condition).

Fig. 6. Sequential vertical profiles of a larval cod population simulation showing the depth and condition distribution over a 4.5 day period at 12 h intervals representing midday and midnight with a vertically sheared surface current of $1.5 \times 10^{-1}$ m s$^{-1}$ (crosses represent individual larvae in good condition, dots are average condition and circles are poor condition). The maximum horizontal separation between the good- (pycnocline region) and poor-condition (surface) larvae in the final profile is $-40$ km.
Fig. 7. The vertical distribution of condition-based larval cod concentrations collected at 10 m intervals during the day (dotted line) and night (solid line). The left panels (a,b,c) represent model results without vertical shear. The right panels (d,e) are redrawn from field data for haddock (*Melanogrammus aeglefinus* L.) larvae collected by Frank and McRuer (1989) off southwestern Nova Scotia where the larvae were indexed for condition using Fulton’s *K*.

implies that vertical distribution and migration patterns derived from field collections without a consideration of variations in condition of the larvae may be considerably biased.

Comparison with field data

Field data on larval haddock, also a gadoid species, collected off southwest Nova Scotia by Frank and McRuer (1989) were used for a comparison with the results provided by our models. Frank and McRuer (1989) classified the larvae into ‘better than average’ and ‘less than average’ condition on the basis of Fulton’s *K*...
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(weight/standard length$^3$) condition index (LeCren, 1951). The larvae were sampled in well-mixed and stratified water masses, as Frank and McRuer's (1989) model predicted that poor-condition larvae would be found in well-mixed waters having characteristic low production and good-condition larvae would be found in the more productive stratified regions.

Frank and McRuer's (1989) data were extracted and redrawn as frequency distributions of good- and poor-condition larvae during day and night. Three stations were sampled during the daytime and the station data for both the good- and poor-condition larvae were averaged. The resulting distributions show that the good-condition larvae remained concentrated at mid-depth during the day with a slight increase in dispersion at night (Figure 7d). The poor-condition larvae are more concentrated at the surface during the day and night, with increased dispersion at night (Figure 7c). Our model predictions (Figure 7b and c) are consistent with these profiles. It is, however, unrealistic to make a quantitative comparison between our model results and Frank and McRuer's (1989) field observations because their larval data came from different hydrographic regions and our model was not fit to the water mass characteristics encountered in the field. Nevertheless, the distributional similarities are compelling.

Discussion

The Lagrangian vertical migration model shows that condition-driven buoyancy can explain most vertical migration patterns and distributions of larval fish observed in the field. This has important implications to the fisheries research communities as it represents a simple and testable explanation of vertical distributions. The condition-driven buoyancy model also has important implications for the vertical distribution and horizontal dispersion of zooplankton and ichthyoplankton, and possibly to recruitment estimates.

Our model results suggest that larval condition and buoyancy between the period of yolk-sac absorption and development of a functional swim bladder can explain most patterns of vertical migrations observed in the field. If a sampler is repeatedly towed through a patch consisting only of poor-condition larvae (e.g. Figure 7c), a vertical migration in the surface layer is predicted. Poor-condition larvae would also exhibit the classical nocturnal diel vertical
migration of up at night and down during the day. When repeatedly sampling a patch consisting of good-condition larvae (e.g. Figure 7b), our model predicts diel vertical movement around the food maximum (pycnocline), with a slight increase in dispersion at night. Good-condition cod larvae would, however, exhibit an inverse diel pattern relative to the poor-condition larvae. When sampling a mixed population consisting of both good- and poor-condition larvae, more complicated patterns would be expected, consisting of mixed phases and amplitudes, as often described in the literature (e.g. Fossum et al., 1987; Stephenson and Power, 1988, 1989).

It is important to note that our model results are sensitive to the selected surface and sub-pycnocline water densities ($\rho_1$ and $\rho_f$). Our values were selected to represent the density of water during the larval cod rearing conditions seen in Ellertsen et al. (1980). The vertical distributions of the larvae would be very different for other values of water density. For example, using the same values of larval cod density ($\rho_r$) and sub-pycnocline water density ($\rho_f$) as in the previous model simulations, and changing the surface layer water density ($\rho_1$) such that it was less dense than the weakest-condition larva, would result in all of the larvae (good and poor condition) being distributed near the pycnocline region, or deeper. Even the poorest-condition larvae would not float to the surface. This situation may explain the interannual and short-term (days) and regional variations in migration patterns that may result from interannual and short-term regional variations in water mass structure.

The model results also reveal an increase in variance at night, relative to day, for both good- and poor-condition larvae. This variance pattern is commonly observed in the field (e.g. Heath et al., 1988).

Our demonstration of how vertical shear can separate an initial population into two separate populations of good- and poor-condition larvae is also a significant result. In the model, the good-condition larvae remain deep in the region having lower current velocities, while the poor-condition larvae are found near the surface where they are subject to greater advection and shear dispersion. It is, however, important to recognize that the good-condition larvae remained aggregated, through a "retention" mechanism that requires limited innate behaviour (i.e. 'directed' daytime swimming). This simple two-dimensional model clearly demonstrates how populations can develop spatially and temporally as a result of differential condition and current velocities with depth.

The comparisons with Frank and McRuer's (1989) field data were compelling, as our model results are consistent with their observations of larval haddock vertical distributions stratified by condition. Owing to the nature of the sampling scheme (stratified versus well-mixed water), further quantitative comparisons between larval condition during the day and night are not possible. If, however, we consider the case where good- and poor-condition larvae are separated by depth-varying currents, one can speculate that poor-condition larvae should be advected to other regions, possibly leading to the different larval condition found on and off banks (e.g. Buckley and Lough, 1987; Frank and McRuer, 1989).
In addition, Shelbourne (1957) found temporally and spatially separated concentrations of good- and poor-condition plaice (*Pleuronectes platessa* L.) in the North Sea. Shelbourne (1957) also showed a strong correlation between larval condition and prey concentration. Interestingly, we have calculated from Shelbourne's (1957) data that the poor-condition larvae were in relatively low concentration in low-density water (1027.6 kg m\(^{-3}\)) compared to that of the good-condition larvae that were in higher concentration in higher density water (1027.8 kg m\(^{-3}\)). Unfortunately, no vertical distribution data were available, but again our model results are consistent with these observations.

**Buoyancy as a predictor of larval condition and implications for recruitment estimates and patch studies**

Frank and McRuer (1989) speculate that it may be possible to assess the condition of a larval population through vertical distribution data alone. Our model predictions, Frank and McRuer's (1989) field data, and the Neilson et al. (1986) laboratory data are consistent with this suggestion, at least for larval gadoids. It is expected that larval condition will be different near the surface of a water column (stratified or well mixed) relative to greater depths, and it is possible to examine condition-based depth differences directly in the field to test this hypothesis. If such differences are found in the field, then fisheries researchers must consider larval condition when making predictions of year-class strength estimates from larval surveys (assuming survival probability is a function of condition). The general pattern of temporal variation in the vertical distribution of a whole larval population may prove a suitable proxy measure of the overall condition and, therefore, survival probability of the population, as suggested by Frank and McRuer (1989).

The results from the vertically sheared simulation also raise the question of whether we can actually follow the same population of larvae for any given period with fixed-depth drifters. It is clear in Figure 6 that the poor-condition larvae separated from the good-condition larvae. Therefore, a drifter which is drogued at a particular depth would only follow one of the two groups (or a limited part of both). The simulations show that poor-condition larvae are quickly advected and dispersed in the surface layer. If one were to sample at a fixed location, a lower concentration of poor-condition larvae would be observed relative to the good-condition larvae which remain aggregated deeper in the water column. Further, increased predation in the well-lit surface waters is to be expected (Neilson et al., 1986). These results may help to explain the relatively low frequency of observations of dead or dying larvae in the field.

**Condition-driven buoyancy and larger fish**

We suggest that it is not unreasonable to apply the concepts particular to our model to stages beyond the development of a functional swim bladder. Hoss *et al.* (1989) have shown that larval menhaden (*Brevoortia tyrannus*) migrate to the air-water interface at night to inflate the swim bladder and subsequently descend during the day as the swim bladder deflates. The same authors suggest
that the diel vertical migration of the larval menhaden is not an endogenous rhythm as the larvae did not maintain periodicity in vertical movement in the absence of a change in light cue. Hunter and Sanchez (1976) also provide evidence that larval anchovy (Engraulis mordax) migrate to the surface at night to inflate the swim bladder and subsequently descend. Blaxter and Ehrlich (1974) have shown that changes in the protein, lipid and water content result in differential buoyancy forces acting on the larvae through ontogeny. We speculate that differential condition will affect the vertical distributions of larvae having functional swim bladders, particularly as inflation of the swim bladder does not necessarily overcome negative buoyancy (Hoss et al., 1989). Thus, it may be instructive to assess larval condition in conjunction with swim bladder volume when interpreting the vertical distribution of larger fish.

Applicability of model results to zooplankton

The condition-driven buoyancy hypothesis may be applicable to freshwater and marine zooplankton. Vertical migration patterns of zooplankton also reveal variable frequency, phase and amplitude which are cued to light (e.g. Hutchinson, 1967; Raymont, 1983). Endogenous rhythms are believed to be primarily responsible for the observed patterns (e.g. Hutchinson, 1967; Longhurst, 1976). However, evolutionary hypotheses such as predator avoidance (e.g. Zaret and Suffern, 1976; Bollens and Frost, 1989) and energetic benefits (e.g. McLaren, 1963; Ohman, 1990) are commonly considered. Developmental stages (ontogeny) also play an important role in determining the different amplitudes of diel vertical migration in zooplankton (Ohman, 1990; Uye et al., 1990). For example, some adult copepods exhibit large diel vertical migrations, whereas some copepodite stages exhibit little or no vertical movement (Uye et al., 1990). These patterns may simply result from buoyancy difference between the adults and the copepodites. Adult copepods are known to have oil globules (Raymont, 1983) which can change in lipid content. Therefore, condition differences in the adults may give rise to diel and ontogenetic vertical migrations as in our model of larval fish, whereas the copepodite stages, which have a less developed oil globule, will appear non-migratory.

Bollens and Frost (1991) show that non-ovigerous adult female copepods (Euthectea elongata) display a strong diel vertical migration. On the other hand, ovigerous adult females were non-migratory or 'weakly' migratory and found in deeper water. The same authors use an adaptive argument to conclude that the ovigerous females remain at depth both day and night to avoid visual predators. A simpler and testable explanation is that buoyancy differences between ovigerous and non-ovigerous females give rise to the observed patterns. Ovigerous females are very likely to be in good condition, as feeding constraints limit egg production. If in good condition and laden with eggs, it is also likely that the eggs will increase the density of the adult copepod, bringing them deeper in the water column to a level of neutral buoyancy. After the eggs are released, another change in density, inverse relative to the ovigerous stage,
would act to bring the copepod towards the surface again. This would represent an ontogenetic vertical migration on a seasonal scale. It is also expected that the ovigerous females, as a result of their condition status, would display limited vertical movements once they have reached a depth of neutral buoyancy. If the non-ovigerous females consisted of a mix of conditions, the individuals would adjust to a depth of neutral buoyancy on a relatively short (possibly diel) time scale and appear to actively migrate.

Further support for density changes which depend on sexual maturity of the individual organism is provided in Kapp (1991). The author discusses the function of a gelatinous matrix in the lateral fins of chaetognaths as a mechanism to reduce their density and balance the increase in weight from the maturing gonads. The density increase during the maturation process is species specific and other plankton organisms such as salps and medusae are also believed to use jelly as a buoyancy regulator. In addition to length- and gonad-dependent differences in density, we speculate that condition-driven buoyancy will also affect the chaetognath's vertical position in the water column.

Stirling et al. (1990) concluded that changes in the diel vertical migration of *Daphnia galeata mendotae* were a direct response to changes in planktivore density. Changes in the residence time of *Daphnia* in the epilimnion and changes in amplitude of vertical migration were correlated with an increase in the planktivorous fish biomass. The authors were not able to reject Zaret and Suffern’s (1976) predator avoidance hypothesis where vertical migration amplitudes were observed to increase with predators. We suggest that the interannual variations in the depth and size distributions may simply have been the result of passive ascension/descention at night due to differences in buoyancy. Further, Stirling et al. (1990) state that the numbers of *Daphnia* caught at midnight were always greater than at midday. The limited amplitudes (2–6 m) of vertical migration observed and the consistent midnight ascensions may be most easily explained through differential sampler avoidance (Scalfani, 1992).

The condition-driven buoyancy model results provide a simple and testable means of explaining the various vertical distributions and migration behaviours of larval fish and zooplankton typically observed in the field. The particle tracking model is clearly simplistic and does not include all of the biological or physical processes, but it can easily be extended to represent any species of larval fish or zooplankton and their surrounding water mass characteristics and subsequently tested. As each larval fish species displays different density changes during starvation (see Blaxter and Ehrlich, 1974; Yin and Blaxter, 1987), it is possible that the various observations of vertical distributions and migration patterns could be explained through differential buoyancy forces acting on the individuals.

The Lagrangian time-stepping model makes predictions that can be readily tested in both the laboratory and field. Eggs and larval densities can be measured in density columns (e.g. Coombs, 1981) or derived from measurements of weight on microbalances (e.g. Power et al., 1991), and condition indices can be developed from morphometric (e.g. Neilson et al., 1986) and/or
biochemical (e.g. Fraser, 1989; Hakanson, 1989; Ouellet et al., 1992) measurements. Our model has displayed the variables to which it was sensitive and we believe that further tests of the hypothesis should be examined through direct measurements of these variables. A re-examination of historical vertical distribution data complemented with morphometric measures and water mass characteristics may also be used for tests.

We argue that the combination of physical and biological models used to address transport- and recruitment-related questions may be limited due to improper representation of the biological components. Describing vertical migration patterns as 'well behaved' particles may lead to erroneous estimates. Laboratory and field tests of the condition-driven buoyancy hypothesis are warranted for both ichthyoplankton and zooplankton.

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