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 Suffern, 1976; Bollens and Frost, 1989); (iii) animals following optimal prey concentrations (Ellertsen *et al.*, 1977, 1980; Tilseth and Ellertsen, 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 (Wurstbaugh and Neverman, 1988); (vii) abiotic factors such as wind mixing altering the existing migration patterns (Tilseth and Ellertsen, 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
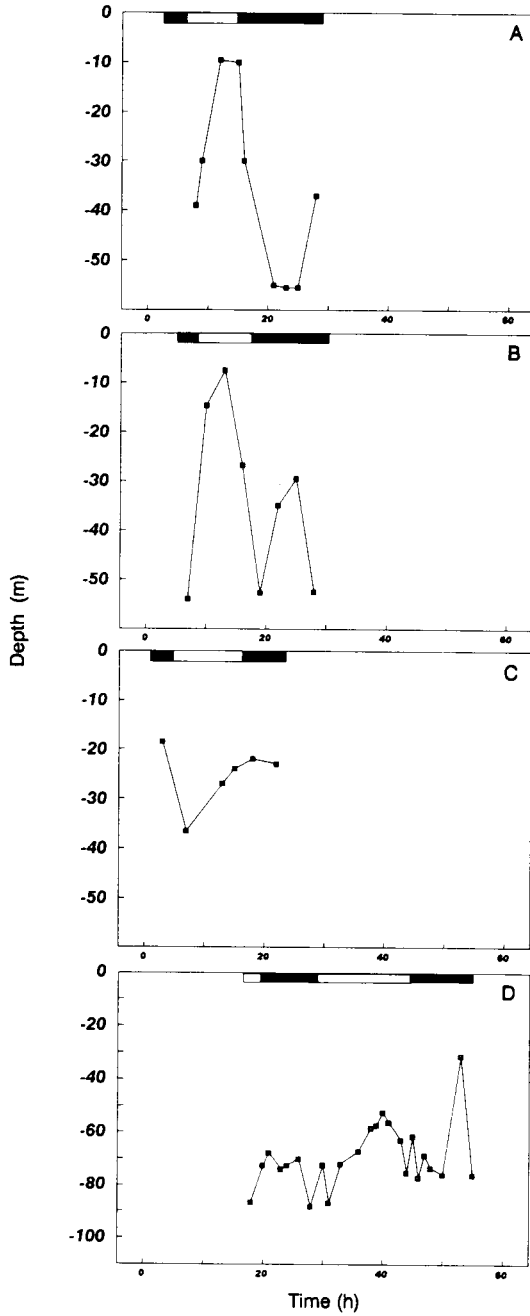
Fig. 1. Temporal changes in the depth distribution of larval herring: **A** and **B**, averaged maximum larval concentrations (Stephenson and Power, 1988, 1989); **C** and **D**, centres of mass (Nichols *et al.*, 1986; Fossum *et al.*, 1987). Black and white bars indicate night and day periods in each 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 (ρ_1) and sub-pycnocline (ρ_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:

$$F = \exp \left[- \frac{(z - h_1)^2}{2\sigma^2} \right] \qquad (1)$$

Note that the food concentration reaches its maximum of unity at the pycnocline
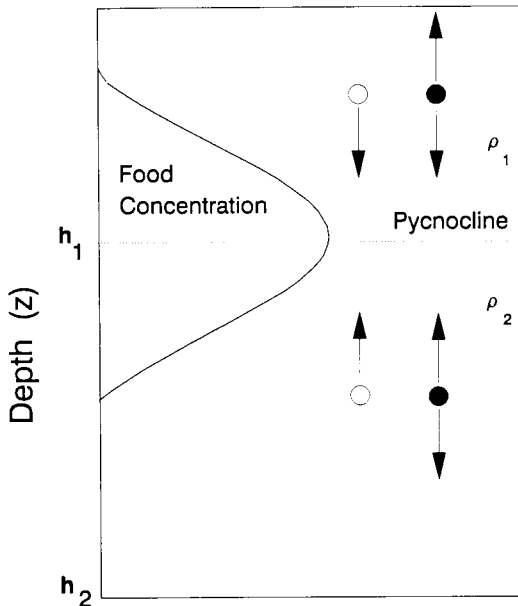
Fig. 2. The physical and biological components of the condition-driven buoyancy model consisting of a stratified water column with upper depth (h_1) and density (ρ_1), and lower depth (h_2) and density (ρ_2). The food maximum is distributed around the pycnocline. Open circles represent larval fish and their potential daytime movements, and solid circles represent their potential night-time movement.

$(z = h_1)$ 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:

$$\frac{dC}{dt} = \frac{1}{T_c} (F - C) \tag{2}$$

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:

$$C(t + \Delta t) = e^{-(\Delta t/T_c)} C(t) + [1 - e^{-(\Delta t/T_c)}] F(t) \tag{3}$$

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):

$$w = 2gr^2 \left(\frac{\rho_w - \rho_L}{9\nu}\right) \tag{4}$$

where g is acceleration due to gravity, r is the radius of an equivalent larval spheroid, ρ_w is the density of the surrounding seawater, ρ_L is the density of a

larva and ν is the coefficient of viscosity of seawater (1.61×10^{-3} kg m^{-1} s^{-1} at 5°C and salinity 35‰; Dorsey, 1940). During the day, we assume the larva swims toward the food maximum at speed:

$$|w| = w_{max}C \tag{5}$$

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

$$z(t + \Delta t) = z(t) + w\Delta t + \epsilon \tag{6}$$

where $z(t + \Delta t)$ is the new larval depth, w is the vertical velocity and ϵ is a random perturbation added to simulate turbulence. We assume that ϵ is normally distributed with zero mean and standard deviation $(2K\Delta t)^{+\frac{1}{2}}$ (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 (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.* (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.* (1980) were averaged (Figure 3) and the original salinity-based units of density were converted to density (kg m^{-3}) using the UNESCO tables for 5°C water (Knauss, 1978). On the basis of these data, larval density at yolk-sac absorption (5 days after hatching) was set at 1027.5 kg m^{-3} and considered to be typical of a larva in its 'best' possible condition (Figure 3). Larval density just before moribund (15 days post-hatch; Ellertsen *et al.*, 1980) was set at 1024.0 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 (T_c) of ~3 days (Figure 3). Results from similar studies (Neilson *et al.*, 1986; Yin and Blaxter, 1987) for starved cod larvae are consistent with those of Ellertson *et al.* (1980) and show a general decrease in larval density after yolk-sac absorption.

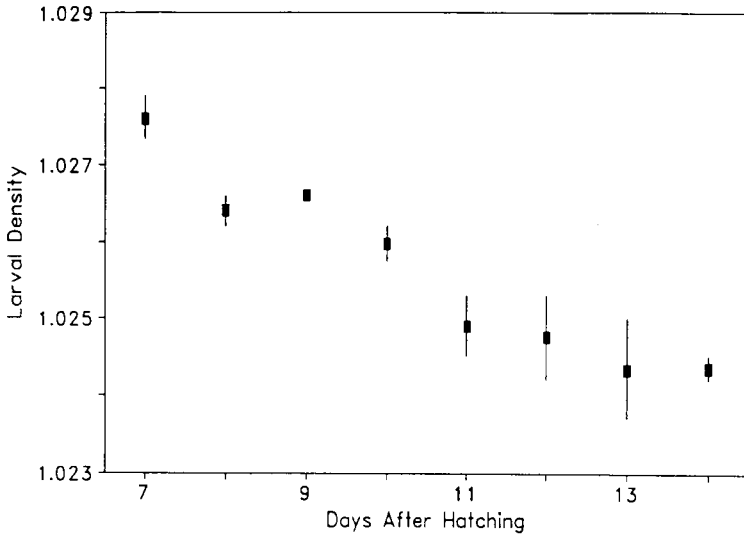The radius, (r), used in equation (4) for the terminal velocity was calculated using:

Fig. 3. The relationship between average larval density and days post-hatch for starved cod derived from two separate broods of larvae (after Ellertsen *et al.*, 1980). The vertical bars show the range of observations. Good-condition larvae are 1027.5 kg m^{-3} and poor-condition larvae are 1024.0 kg m^{-3}.

$$r = (\sqrt[3]{l_g^2\, l_h})\qquad\qquad(7)$$

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 (ρ_w) of 1026.5 kg m^{-3} and a 'best' condition larva with density (ρ_l) of 1027.5 kg m^{-3}, the terminal velocity (w) is -1.87×10^{-3} 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.

Burst speeds for a 4–6 mm cod larva can reach 4.5–5.0×10^{-1} 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 larvae 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 (h_1). 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 (Sclafani, 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 (*Limnada 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 (ρ_1) was chosen to be 1026.0 kg m^{-3} and the lower layer density (ρ_2) 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 (h_2) 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 ($2.0 \times 10^{-3} \, \text{m}^2 \, \text{s}^{-1}$; Loder *et al.*, 1988). A complete list of parameters and the values used in the simulations is provided in Table I.

Model results

Three simulations, using the parameters in Table I, 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 I. Summary of variables, parameters and values used in the condition-driven buoyancy model simulations

Variable	Symbol	Value	Source
Larval density: 'best' condition	ρ_L	1027.5 kg m^{-3}	Ellertsen et al., 1980
Larval density: 'poorest' condition	ρ_l	1024.0 kg m^{-3}	Ellertsen et al., 1980
Surface layer water density	ρ_1	1026.0 kg m^{-3}	Ellertsen et al., 1980
Sub-pycnocline water density	ρ_2	1026.5 kg m^{-3}	Ellertsen et al., 1980
Bottom depth	h_2	100 m	Valentine and Lough, 1991
Pycnocline and food maximum mean depth	h_1	40 m	Buckley and Lough, 1987
Food maximum standard deviation	σ	10 m	Buckley and Lough, 1987
Maximum daytime swimming speed	w_{max}	10^{-2} m s^{-1}	Blaxter, 1986
Larval density e-folding scale	T_c	3 days	Ellertsen et al., 1980
Eddy diffusivity coefficient	K_v	2.0×10^{-3} m^2 s^{-1}	Loder et al., 1988
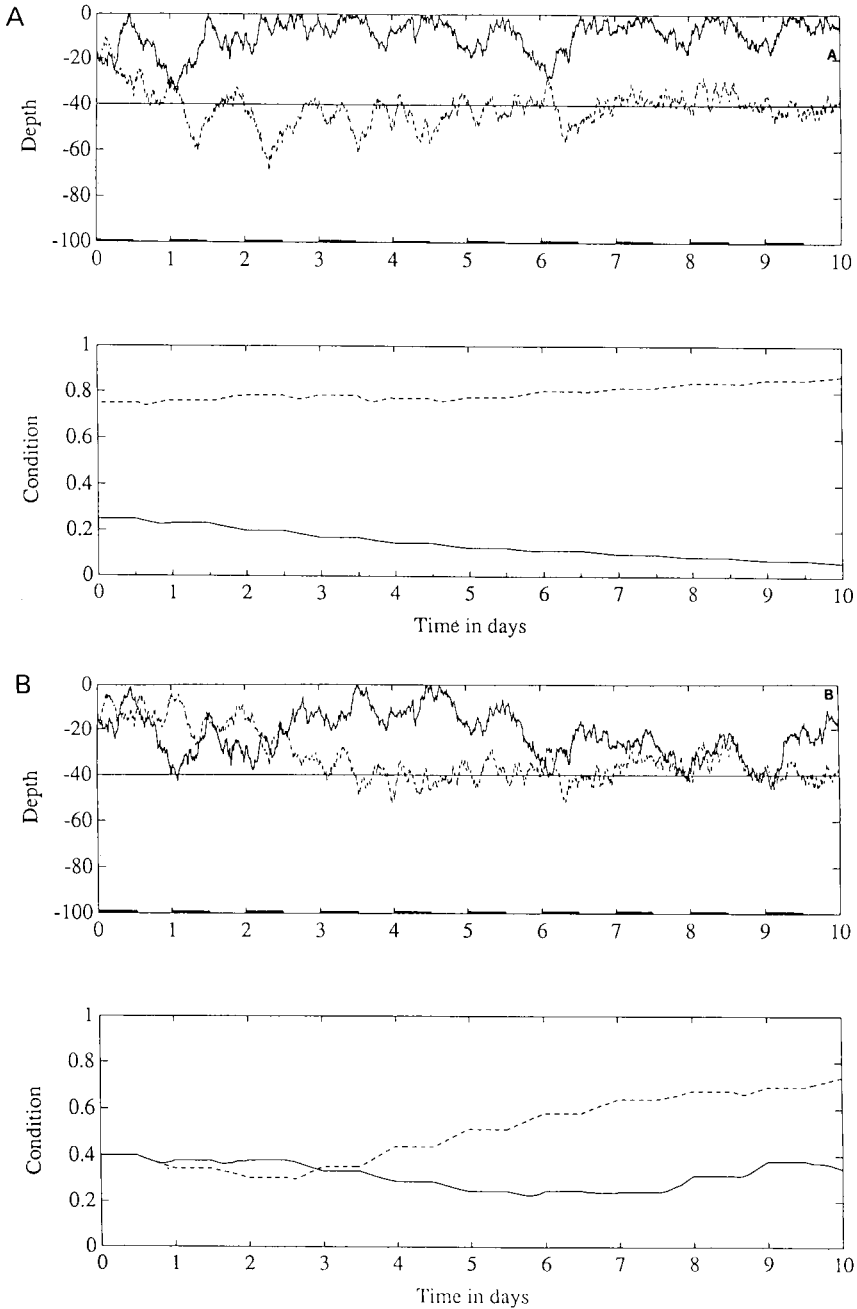
Fig. 4. The 10 day evolution of depth and condition of (**A**) a good-condition (dashed) and poor-condition (solid) cod larvae initialized at the same depth, and (**B**) two neutral-condition cod larvae initialized at the same depth. Black and white stippling indicate night and day periods in each study.

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0 and 1 at depths between 35 and 45 m (Figure 5). 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 1.5×10^{-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
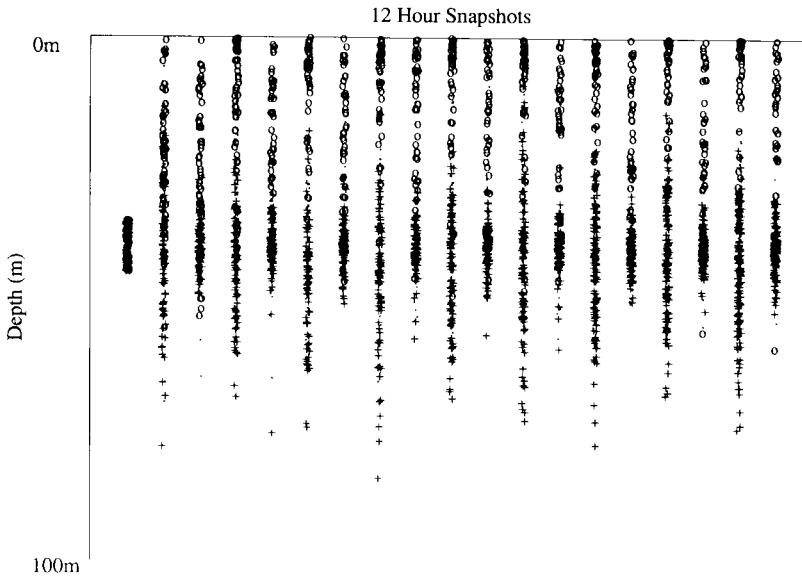
Fig. 5. Sequential vertical profiles of a larval cod population showing the depth and condition distribution over a 10 day period at 12 h intervals representing midday and midnight (crosses represent individual larvae in good condition, dots are average condition and circles are poor condition).
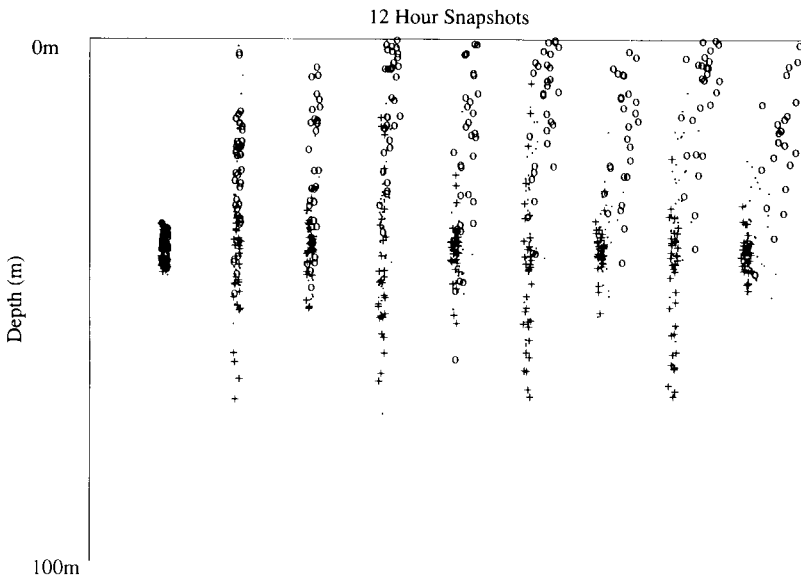

Fig. 6. Sequential vertical profiles of a larval cod population simulation showing the depth and condition distribution over a 4.5 day period at 12 h intervals representing midday and midnight with a vertically sheared surface current of 1.5×10^{-1} m s^{-1} (crosses represent individual larvae in good 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.
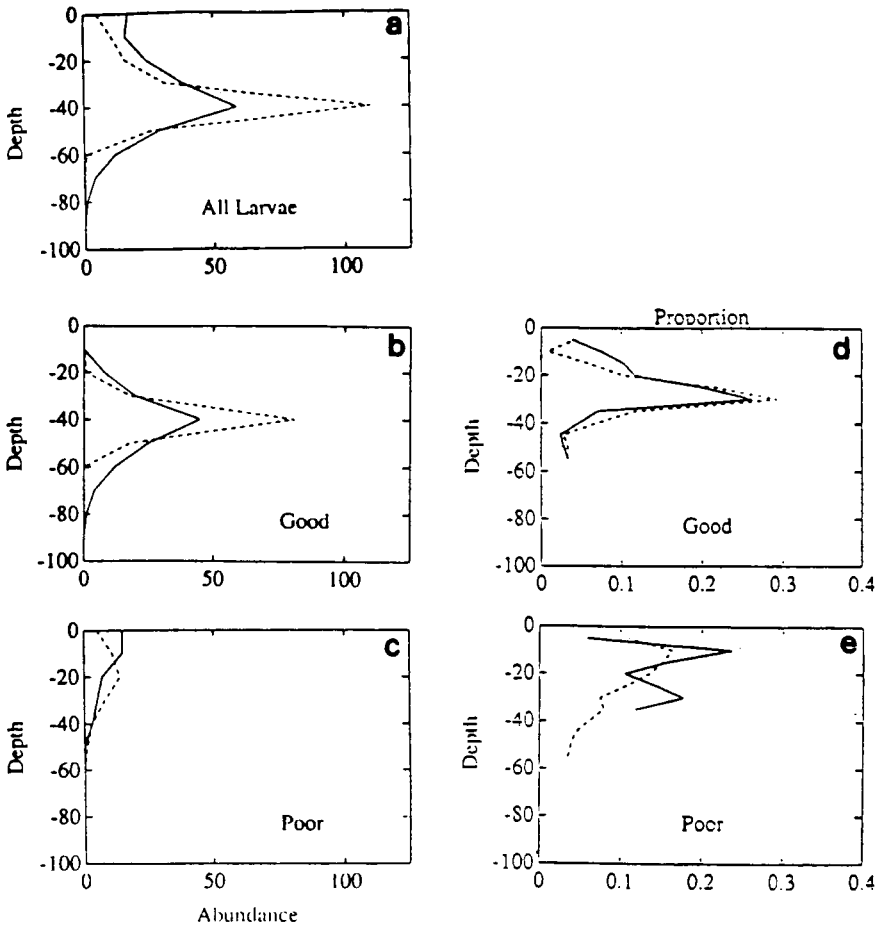
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Fig. 7. The vertical distribution of condition-based larval cod concentrations collected at 10 m intervals during the day (dotted line) and night (solid line). The left panels (**a,b,c**) represent model results without vertical shear. The right panels (**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 7e). 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.

The condition-driven buoyancy model also raises important questions about the diel vertical migration hypotheses often used to explain these movements. Are the observed vertical migrations and distributions of larval fish and zooplankton a result of active or passive movements, or both? Can we more easily explain vertical distribution and migration through condition and buoyancy than by behavioural rhythms (e.g. Hoss *et al.*, 1989)? If so, can we further explain how abiotic factors will affect the predicted distributions? It is unrealistic to expect this simple model to account for all vertical migration patterns for all species, but comparisons of our model results with ichthyo-plankton field data (e.g. Frank and McRuer, 1989) suggest it is a reasonable first approximation.

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

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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 (ρ_1 and ρ_2). 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 (ρ_1) and sub-pycnocline water density (ρ_2) as in the previous model simulations, and changing the surface layer water density (ρ_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 (*Euchaeta 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 their 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/descension 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 (Sclafani, 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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