COMMENT

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Plankton layer profiles as determined by shearing, sinking, and swimming

Thin layers of plankton in the ocean often exhibit striking ''sharp'' profiles (Fig. 1a; Cowles and Desiderio 1993; Rines et al. 2002). Such profiles are often the only biological data available to diagnose the dynamics underlying the thin layer formation. As we show below, only a limited set of dynamics can create a sharp profile (i.e., continuous but non-differentiable at the peak) instead of a smooth profile, such as a Gaussian distribution (Fig. 1a). Stacey et al. (2007) argue that sharp plankton profiles can be produced by a balance between constant turbulent diffusion and three different thinning mechanisms: steady vertical shear, buoyancy, and directed swimming to a target depth. Competition between these thinning mechanisms and diffusion can produce thin layers, and the scalings for layer thickness presented by Stacey et al. (2007) are correct. However, shear and buoyancy cannot produce the sharply peaked profiles often observed in the field: solving the advection–diffusion equations corresponding to the models proposed by Stacey et al. (2007) shows that the predicted thin-layer profiles are smooth, not sharp. The only mechanism to produce sharp peaks is directed swimming towards a target depth with a swimming speed that is discontinuous at the target depth. These results may help to constrain the dynamics underlying observations of thin layers in the field.

First, consider steady vertical shear α acting on an initial distribution of plankton with concentration $p_0(x,y,z)$. Neglecting diffusion, the equation describing the time evolution of the plankton distribution $p(x,y,z,t)$ is

$$\frac{\partial p}{\partial t} + \alpha z \frac{\partial p}{\partial x} = 0 \tag{1}$$

The solution is $p(x,y,z,t) = p_0(x - \alpha tz,y,z)$, and therefore the derivative of p in the vertical (z direction) is given by

$$\left.\frac{\partial p}{\partial z}\right|_{(x,y,z,t)} = -at\left.\frac{\partial p_0}{\partial x}\right|_{(x-\alpha tz,y,z)} + \left.\frac{\partial p_0}{\partial z}\right|_{(x-\alpha tz,y,z)} \tag{2}$$

If the initial distribution $p_0(x,y,z)$ is smooth, then all of the terms on the right-hand side are well-defined and p will remain smooth for all finite times; including diffusion will result in further smoothing of an already smooth profile. In particular, if p_0 is a Gaussian patch, then the profile remains Gaussian at all times (Fig. 1b). Thus we conclude that steady vertical shear cannot create a sharp profile. Birch et al. (2008) contains a complete description of the shear-thinning mechanism applied to thin layer formation (*see* Young et al. 1982; Rhines and Young 1983 for a collection of Gaussian solutions to the vertically sheared advection–diffusion equation).

Turning to the buoyancy mechanism, consider the distribution of plankton in a linearly stratified water column with buoyancy frequency N and the plankton neutrally buoyant at $z = z_0$ (the neutral depth). Let the diffusivity be κ and assume that the plankton distribution is uniform in the x and y directions. Then the equation describing the time evolution of $p(z,t)$ is

$$\frac{\partial p}{\partial t} + \frac{\partial[w_{\mathrm{sink}}p]}{\partial z} = \kappa\frac{\partial^2 p}{\partial z^2} \tag{3}$$

The vertical velocity w_{sink} is modeled by Stokes' law for a sinking sphere of diameter D in a fluid with kinematic viscosity ν:

$$w_{\mathrm{sink}}(z) = -\gamma(z - z_0) \tag{4}$$

where $\gamma \equiv D^2N^2/18\nu$. Stokes's law may be inappropriate for particles settling in a stratified fluid (Srdic-Mitrovic et al. 1999), but following Stacey et al. (2007) we will use it for simplicity. Let P be the total amount of plankton in the water column. Then if we assume that the plankton concentration and its derivative in the z direction vanish at $z = \pm\infty$, the equilibrium solution p_{sink} of Eq. 3 is again a Gaussian:

$$p_{\mathrm{sink}}(z) = P\sqrt{\frac{\gamma}{2\pi\kappa}}\exp\left(-\frac{\gamma(z - z_0)^2}{2\kappa}\right) \tag{5}$$

Thus we see that buoyancy balanced by diffusion produces a smooth plankton profile. Here we have assumed that the entire water column is linearly stratified. If we instead assume that the neutral depth is in a region of linear stratification lying between two unstratified layers, then the sinking and floating speeds will be bounded far from the neutral depth and the layer will resemble one formed by the directed swimming mechanism.

In the directed swimming mechanism the plankton swim towards a target depth z_0. Assume that the plankton have a maximum swimming speed $w_{\max}$ and that they slow down within a distance δ of their target depth (Franks 1992):

$$w_{\mathrm{swim}}(z) = -w_{\max}\tanh[(z - z_0)/\delta] \tag{6}$$

The specific functional form of w_{swim} in Eq. 6 is chosen for analytical tractability. Equation 6 may also be more realistic than Eq. 4 as a model of sinking, because the

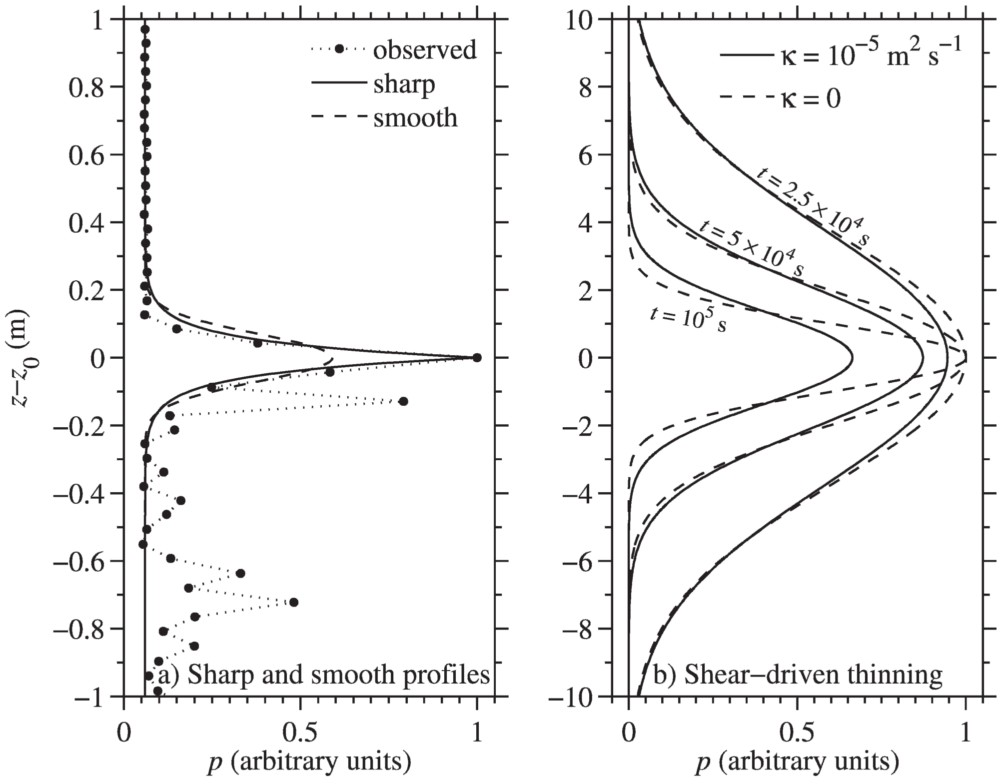

Fig. 1. (a) An observed sharp thin layer and prototypical examples of sharp and smooth layer profiles. The observed layer was recorded in Dabob Bay, Washington, on 04 May 2007 as an intense feature in fluorescence (volts); the profile has been normalized by the maximum observed voltage. Data courtesy of E. M. Karaköylü (unpubl.). The sharp example is the double-sided exponential distribution $p(z) = p_b + \left(P/\sigma\sqrt{2}\right)\exp\left(-\sqrt{2}|z - z_0|/\sigma\right)$ and the smooth example is the Gaussian distribution $p(z) = p_b + \left(P/\sigma\sqrt{2\pi}\right)\exp\left[-(z - z_0)^2\Big/2\sigma^2\right]$. In both examples $P = 0.093$ (arbitrary units) is the total amount of plankton in the layer, $\sigma = 0.07$ m is the characteristic profile width, and $p_b = 0.06$ (arbitrary units) is the background concentration. (b) Profiles of thin layers formed by the shear-thinning mechanism from an initially Gaussian plankton distribution. The solid lines are profiles computed with $\kappa = 10^{-5}$ m^2 s^{-1} and the dashed lines are computed with $\kappa = 0$. The shear is the same for both sets of profiles: $\alpha = 0.01$ s^{-1}. The profiles are plotted at $t = 2.5 \times 10^4$ s, 5×10^4 s, and 10^5 s and both sets of profiles remain smooth.

speed in Eq. 6 is bounded far from $z = z_0$. The discontinuous swimming model used by Stacey et al. (2007) is recovered from Eq. 6 by taking the limit $\delta \to 0$. This amounts to assuming that plankton immediately detect whether they are above or below the target depth z_0 and take corrective action. Nonzero δ models the fact that motility toward the target depth may be imperfect. Replacing w_{sink} in Eq. 3 with w_{swim} and solving for the equilibrium solution yields

$$p_{\text{swim}}(z) = \frac{P}{\delta}\frac{\cosh[(z - z_0)/\delta]^{-w_{\max}\delta/\kappa}}{\mathrm{B}(1/2, w_{\max}\delta/2\kappa)} \qquad (7)$$

where B is the beta function (Lebedev 1972) and P is again the total amount of plankton in the water column. The shape of the profile is determined by the nondimensional combination $w_{\max}\delta/\kappa$ (Fig. 2b). If $w_{\max}\delta/\kappa \gg 1$, then the profile is smooth and resembles a Gaussian. If $w_{\max}\delta/\kappa \ll 1$, then the profile is almost sharp and resembles the double-sided exponential of Stacey et al. (2007). More precisely, when $w_{\max}\delta/\kappa \ll 1$, the profile width is much greater than δ, and so when viewed on the scale of the profile width, the peak appears sharp. Stacey et al. (2007) ensure this condition by taking $\delta = 0$.

Thus having examined shear-driven thinning, sinking in a linearly stratified water column, and directed swimming, all balanced by constant diffusion, we see that only directed swimming (and possibly sinking through a water column that is not linearly stratified) can result in non-Gaussian sharp layer profiles. These sharp profiles form only if the nondimensional control parameter $w_{\max}\delta/\kappa$ is small—meaning that weak swimming or strong diffusion can create sharp layers! This confusing result is made clear by noting that a layer's being sharp is unrelated to a layer's being thin. The first property is determined by the layer's shape, whereas the second is a classification based on the layer's width in dimensional variables.

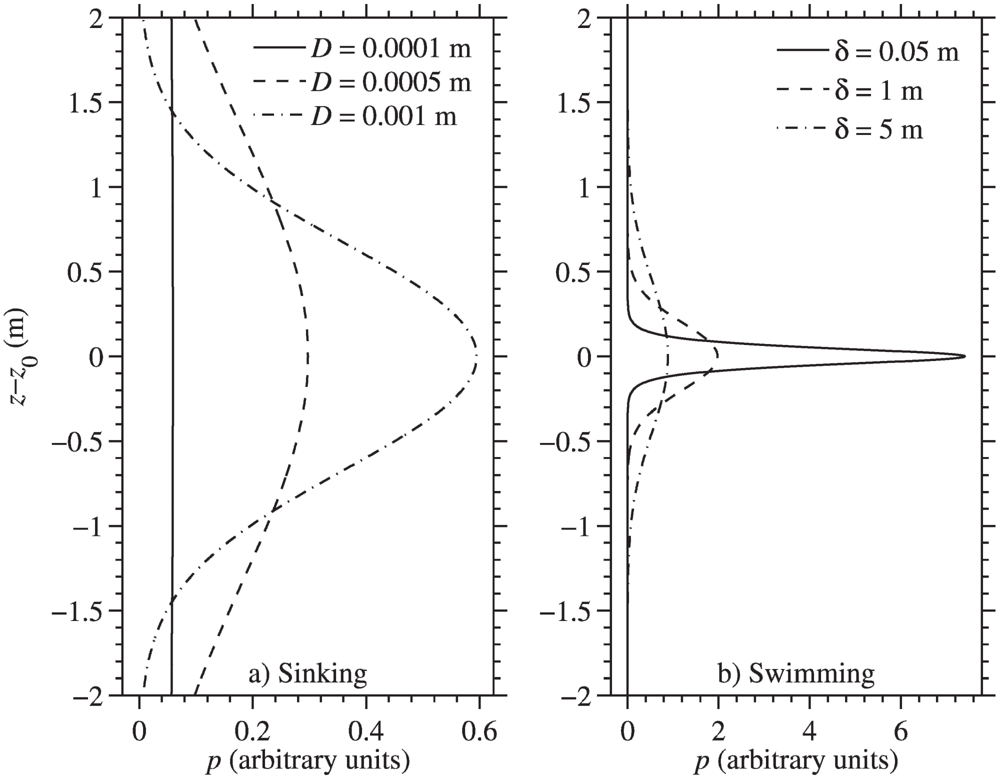

Fig. 2. (a) Equilibrium solutions of the buoyancy model in Eq. 3 for three different values of the particle diameter D. The remaining parameters are $P = 1$ (arbitrary units), $\kappa = 10^{-5}$ m^2 s^{-1}, $N = 2 \times 10^{-2}$ s^{-1}, and $\nu = 10^{-6}$ m^2 s^{-1}. Larger diameter particles sink faster and form thinner and more intense layers. (b) Equilibrium solutions of the directed swimming model using w_{swim} in Eq. 6 for three different values of δ. The remaining parameters are $P = 1$ (arbitrary units), $\kappa = 10^{-5}$ m^2 s^{-1}, and $w_{\max} = 2.5 \times 10^4$ m s^{-1}. Decreasing δ while holding the remaining parameters fixed decreases the nondimensional combination $w_{\max}\delta/\kappa$ and results in a thinner and sharper layer.

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