Planktonic interactions and chaotic advection in Langmuir circulation

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Abstract

The role of unsteady laminar flows for planktonic communities is investigated. Langmuir circulation is used, as a typical medium-scale structure, to illustrate mechanisms for the generation of plankton patches. Two behaviours are evident: chaotic regions that help to spread plankton and locally coherent regions that do not mix with the chaotic regions and which persist for long periods of time. The interaction of populations of phytoplankton with zooplankton is discussed, taking into account the variations in plankton buoyancy.

1   Introduction

Recent studies of plankton dynamics (e.g. Solow & Steele, 1995; Pinelalloul, 1995; Gallager *et al.* 1996) identify plankton patchiness as a major cause of the discrepancies between predictions from bulk-averaged models and field measurements. In particular, local aggregations of planktonic species have been observed that are entrained in larger scale oceanic and limnetic circulations (Gallager *et al.* 1996; Wiafe & Frid, 1996; Owen, 1989; Haury & Wiebe, 1982). These "patches" of phytoplankton can persist for long periods of time irrespective of the apparently strong mixing processes characteristic of turbulent flows.

In this paper, a mechanism for the spread and aggregation of advected, buoyant plankton is presented that employs a deterministic near-integrable flow field. We do not include turbulence or any stochastic forcing in the description but its possible effects are discussed and will be included in later publications. We choose Langmuir circulation in a stably stratified fluid, a typical medium-scale structure, to demonstrate our approach in detail.

Langmuir circulations (Langmuir, 1938) occur as a result of a balance between a destabilizing, wind induced, Stokes drift gradient and a stabilizing, temperature driven, vertical density stratification (Craik & Leibovich, 1976). They typically manifest themselves as long roll structures of width between 2 m and 200 m commonly identified from the debris at regions of surface convergence, which are called windrows (Barstow, 1983). Rather than studying plankton transport in Langmuir circulation in the field, we choose to simulate a mathematical flow field, that can be directly controlled, and insert plankton into the flow in order to investigate their passive behaviour. We insist that the plankton can do no more than swim up or down (effectively modelled as buoyancy). In this way we are able to study the effect of the flow on the plankton without getting distracted by other physical or biological factors.

A successful physical model of Langmuir circulation was derived by Craik & Leibovich (1976). This was subsequently used by Moroz & Leibovich (1985) to generate a reduced-dimensional system that adequately describes key features of the phenomenon. The reduced system was applied to investigate the bifurcation structure of Langmuir circulation, employing methods from dynamical systems. Both steady and unsteady flow regimes were observed. We shall consider the same reduced model in our description only with an additional time-dependent perturbation. The particular perturbation that we will use, whilst being physically realizable, is somewhat arbitrary and similar results can be obtained with other perturbations. However, we wish to emphasize our qualitative arguments and interpretations with quantitative results.

Chaotic advection is a fashionable mechanism for the deterministic transport of scalars that is independent of molecular diffusion (Jones & Young, 1994; Hydon, 1994; Camassa & Wiggins, 1991). Unsteady or quasi-steady flows can exhibit non-integrable dynamics that can induce transport of advected scalars across what would normally be impenetrable barriers (or equivalently streamsurfaces) for steady inte-

grable flows (Arnold, 1989). Small time-dependent perturbations to steady flows can break up these barriers and produce an "effective diffusivity" for purely advected scalars. The resulting lobe dynamics (Wiggins, 1990) for heteroclinic connections may describe important mixing processes and diffusion in Langmuir circulation. This phenomenon is thought to play a significant role in causing planktonic mixing and/or patchiness (e.g. Stommel retention zones; Stommel, 1949, 1951). This mechanism is likely to work in addition to other patch-forming mechanisms, such as reaction-swimming-diffusion (Davis *et al.* 1991; Bees, 1996; Bees & Hill, 1997) and reaction-advection-diffusion (Spiegel & Zaleski, 1984; Malchow, 1996), but tends to work on shorter time scales; hours instead of tens of days (see Malchow, 1993).

This study aims to clarify the relationship between plankton interactions (such as growth, predation, swimming and diffusive processes) and the aggregation and transport of ecosystems due to physical forcing. In particular, the low-dimensional system of Moroz & Leibovich (1985) is used to investigate the role of chaotic advection in Langmuir circulation and how it couples with strategies and lifecycles of individual plankton. By simulating the trajectories of buoyant particles, we can investigate the dispersion of plankton in a typical unsteady flow field, paying particular attention to the qualitative effect on the overall cross-sectional structure of planktonic communities. This enables us to discuss, in a relevant language, the implications on the planktonic food-web, taking into account the diversity of foraging and evasion strategies. In particular, simulation aids in the discussion of the following questions:

1. How does chaotic advection help to disperse phytoplankton and do patches emerge and persist as noted in the field studies?

2. How do zooplankton minimize their foraging time (or effort) and, hence, maximize their growth in an unsteady flow field? Should predators "do as the prey do", or is there a better strategy to find food in unsteady flows?

3. Does plankton patchiness persist? What are the effects of variations in light, temperature and forcing frequency on Langmuir circulations and what consequences do these have for plankton patchiness and their dynamics?

Section 2 describes the key mathematical features of the model, the results of the simulations are presented in Section 3 and we interpret the results in Section 4.

2   Model foundations

Here, we make use of the reduced dimensional system of Moroz & Leibovich (1985) to form a simple velocity field which adequately describes basic Langmuir circulation. The fluid velocity, $\mathbf{u} = (u, v, w)^T$, is given by

$$
\begin{aligned}
u &= 1 + z - C(t)\cos{(\pi z)} - B(t)\cos{(l\pi y)}, \\
v &= A(t)\pi\cos{(\pi z)}\sin{(l\pi y)}
\end{aligned}
$$

and

$$
w = -A(t)l\pi\sin{(\pi z)}\cos{(l\pi y)}. \tag{1}
$$

This naturally satisfies the incompressibility condition, $\nabla \cdot \mathbf{u} = 0$. l is the aspect ratio of circulation depth (i.e. depth of the thermocline), D, to circulation width. Figure 1 shows the coordinate system

and portrays the flow described by the equations for which typical field measurements (Leibovich, 1983; Barstow, 1983) have been added. Both field observations (see Leibovich, 1983) and theory (Craik & Leibovich, 1976; Moroz & Leibovich, 1985) find that there is a critical windspeed, above which Langmuir circulation is evident. The critical windspeed is most often found to be approximately 3 m s^{-1} (e.g. Faller & Woodcock, 1964; Walther, 1967). For regions of parameter space for which steady states are stable, the steady states are given by

$$B = \frac{8A}{\pi^2 l(4 + A^2)}$$

and

$$C = \frac{ABl}{2}, \tag{2}$$

where A is a parameter that represents the speed of the circulation and is a function of the eddy viscosity, ν_T, thermal diffusivity and the Stokes drift gradient (as detailed in Moroz & Leibovich 1985) all of which are difficult to estimate or measure. For our purposes, A may be regarded as a constant determined directly from observations. In order for us to do this, we require the dimensional variables (indicated by hats), which are given by

$$(\hat{y}, \hat{z}) = (y, z)D \tag{3}$$

$$\hat{u} = u\frac{u_*^2 D}{\nu_T}, \qquad (\hat{v}, \hat{w}) = (v, w)\frac{\nu_T}{D} \tag{4}$$

and

$$\hat{t} = t\frac{D^2}{\nu_T}, \tag{5}$$

where ρu_*^2 is the stress acting in the x direction applied to the surface of a mass of fluid having density ρ. u_* is the water friction velocity determined by the applied wind stress. A typical value of ν_T is 20 cm^2 s^{-1} (see Leibovich, 1977). Simple calculus reveals that $u \geq 0$ for $-1 \leq z \leq 0$ unless l is unphysically very small.

The above description of a velocity field is from what is commonly called a Eulerian point-of-view, where the whole system is observed with respect to a fixed location. In some instances it is beneficial to follow a single "blob" of fluid, or a particle, through the flow and track its path. This is a Lagrangian perspective and is straightforward for velocity fields, for which we study the dynamical system

$$\frac{dx}{dt} = u(y, z), \quad \frac{dy}{dt} = v(y, z) \quad \text{and} \quad \frac{dz}{dt} = w(y, z) \tag{6}$$

and follow the trajectory of the particle.

The velocity field is independent of x and the cross-sectional velocities can be written in terms of a streamfunction, ϕ, as

$$v = \frac{\partial \phi}{\partial z} \quad \text{and} \quad w = -\frac{\partial \phi}{\partial y}, \tag{7}$$

where

$$\phi = A \sin(\pi z) \sin(l\pi y). \tag{8}$$

In this sense the flow is Hamiltonian (and integrable), with Hamiltonian ϕ, where all the streamlines are closed and can be found explicitly (see Fig. 2). Clearly, in the absence of diffusion, an advected particle will remain on the closed orbit that it started on. To follow an individual particle with (positive or negative) buoyancy, V_s, we amend the above equations by putting

$$\frac{dz}{dt} = w(y, z) + V_s(z). \tag{9}$$

We make sure that V_s goes rapidly to zero at the upper and lower boundaries by insisting

$$V_s = V \left(1 - e^{z/d}\right) \left(1 - e^{-(z+1)/d}\right), \tag{10}$$

where the relaxation length, d, is very small and V is a constant buoyancy. By defining $\phi_b = \phi - Vy$ we see again that the system is Hamiltonian and incompressible for the main body of the flow where the buoyancy cut-off terms are insignificant. Flows in the sea are unlikely to be as perfect as the above description suggests. To investigate the effects of a small time-dependent variation we consider small amplitude fluctuations of the flow perpendicular to the direction of the wind such that the flow is unchanged at $z = -1$. Figure 3 indicates the type of perturbation that is considered. This is obtained by the transformation

$$y \longrightarrow y + \epsilon g(t)(z+1), \tag{11}$$

where $g(t)$ is the time-periodic forcing function given by

$$g(t) = \sin \omega t. \tag{12}$$

It is hoped that more field data will become available in order to validate this type of periodic perturbation or suggest another one. Theoretical studies, at least, indicate the potential for complex behaviour in Langmuir circulation including the possibility of secondary Hopf bifurcations (see discussion). To first order in ϵ, the streamfunction becomes

$$\psi_\epsilon = A \sin \pi z \sin l\pi y + \epsilon A g(t) l\pi (z+1) \sin \pi z \cos l\pi y \tag{13}$$

which defines a very similar flow to the full streamfunction and, hence, we will use the above truncation throughout the remainder of the paper. The above system is similar to the "even" oscillatory instability for Rayleigh-Bénard convection as studied by Camassa & Wiggins (1991) and many of the techniques that they employ can be used here (e.g. Melnikov theory can be used to investigate the spread of plankton). However, important distinctions are made here in the application and interpretation of the results.

3   Results

For the case of steady state circulation, the cross-sectional streamlines for neutrally buoyant particles are portrayed in Fig. 2. All streamlines are closed and in the absence of any diffusive processes, particles stay on streamlines for all time.

The cross-sectional streamlines for positively buoyant particles are displayed in Fig. 4 where it is clear that there are two qualitatively different behaviours for particles; some particles are trapped in closed orbits at some distance below the surface whereas others accumulate at the point (or line when also considering the longitudinal flow) of convergence of streamlines at the fluid surface. There is a clear boundary between these two regions of varying behaviour. The set of closed orbits form what is called a Stommel retention zone (after Stommel 1949, 1951). In the absence of any other transport or diffusive processes, buoyant particles that begin at the surface cannot submerge due to the upward vertical component of the buoyant particle trajectories (Fig. 4) and, hence, will not enter the Stommel retention zone no matter how fast the fluid flow is in the Langmuir circulation (in contrast to the conclusions of Woodcock, 1993).

We now consider the streamfunction given by Eq. (13) for an unsteady flow field. To simplify the analysis, we calculate the Poincaré section; we record the position of an advected particle at times,

$t = 0, 2\pi/\omega, \ldots, 2n\pi/\omega$, where n is an integer (i.e. at times t when $g(t) = 0$). A good measure of how much the time-dependent perturbation affects the trajectory of a particle is to calculate the particles "escape time", or the value of n for which a particle first leaves the Langmuir cell that it started in. Figures 5 to 9 display the escape time as a function of the particles initial condition within a Langmuir cell. In contrast to the steady velocity field, particles are not constrained to a closed orbit and can wander through the whole space. There are no clear boundaries between regions of varying escape times. In fact, the boundaries are fractal in nature. The dark regions in Figs. 5 to 9 indicate that the particle "never" leaves the Langmuir cell and, in this paper, we call these regions "retention zones". By varying the frequency of the unsteady perturbation the structure of the escape space changes dramatically. Increasing the frequency from $\omega = 0.24$ (Fig. 5) to $\omega = 0.6$ (Fig. 6) reduces the size of the "central retention zone" but introduces extra "resonant retention zones". In particular, the 1:1 resonance retention zone is clearly visible orbiting the central retention zone. These resonant retention zones are advected with the flow but remain separate from the surrounding fluid. In Fig. 10 we plot the cross-sectional positions of a uniform grid of neutrally buoyant particles after 50 forcing oscillations ($n = 50$) allowing particles to escape from the Langmuir cell. No particles were allowed to enter the Langmuir cell from elsewhere, but a similar picture was obtained when particles were allowed to re-enter the Langmuir cell. There are clear regions which exhibit coherent behaviour and have been left behind after approximately half the initial number of particles have escaped. The coherent behaviour is even more evident when we also consider the longitudinal displacement as a function of the particles' initial conditions, as shown in Fig. 11. Particles in the retention zones, on average, all travel at the same longitudinal speed whereas particles in the mixed, or chaotic, regions are widely dispersed in the longitudinal direction. All the figures clearly show the stretching and folding that occurs in the coherent regions. Increasing the forcing frequency further to $\omega = 1.2$ (Fig. 7) we see that the central retention zone decreases in size again but higher order resonant retention zones are produced; well defined 2:1 and 3:1 retention zones orbit the central retention zone. The resonant retention zones persist for as long as the physical forcing remains constant. The escape times for positively buoyant particles (i.e. $V_s > 0$) are displayed in Figs. 8 and 9 in which we keep the same forcing frequency as in Fig. 6 (i.e. $\omega = 0.6$). The figures share characteristics from both Figs. 4 and 6, but it is evident that the total area of the retention zones in Figs. 8 and 9 are less than the area of the corresponding Stommel retention zones for the steady flow. Again, resonant retention zones are produced that circulate the central retention zone.

4 Interpretation and Discussion

As pointed out previously, we could apply the Melnikov theory to this problem and extract a measure of the size of the coherent regions (Wiggins, 1990). It is also possible to calculate an estimate of the heteroclinic lobes and, hence, quantify the transport and effective diffusivity of plankton due to the forcing (Camassa & Wiggins, 1991). Because of the rather arbitrary nature of the time-dependent perturbation, we refrain from performing such analysis in this paper and concentrate on the qualitative interpretation.

There are clear regions where phytoplankton tend to stay in the same patches, as can be seen in Figs. 5 to 10, and regions where much mixing is evident, both in the cross-sectional space and longitudinally (Fig. 11). The transport of particles in the chaotic regions is potentially much quicker than for molecular diffusion alone, as particles a small distance apart can move to adjacent Langmuir cells after only one period. Regions where particle trajectories can deviate quickly are clearly seen, particularly close to

the boundaries due to the structure of the heteroclinic connection. This is in contrast to particles that start in the coherent regions in which the structure is clear. The effect on a patch of plankton of a similar scale to the Langmuir cell is to quickly remove plankton in the chaotic region from the system and leave behind a skeleton of plankton in the coherent regions. The coherent regions are different for particles of varying buoyancy (see Figs. 8 and 9). In general, increasing the magnitude of the buoyancy of the particles decreases the size and changes the location of the coherent regions. Therefore, different species of phytoplankton with dissimilar buoyancy will form patches in a variety of locations and, hence, zooplankton must be able to adapt to locate and follow different prey efficiently. It is also likely that phytoplankton can adjust their buoyancy over a short time scale in response to the available light source (Moore & Villareal, 1996) and, hence, plankton could escape a coherent light-deficient patch by changing their buoyancy. This could result in the organism's local environment effectively changing into a chaotic region, thus allowing the plankton to harness the chaotic regions' transport and mixing dynamics.

The result of resonance between two types of physical forcing is to provide additional retention zones, which are advected with the flow and do not diminish in size. The retention zones consist of coherent motion and are isolated in regions of chaotic behaviour. Longitudinal transport of the retention zones is also coherent and the phytoplankton are given the opportunity to be surrounded by organisms of the same species. Given sufficient time, this may enable the phytoplankton to mate sexually and form high local concentrations. Clearly, the growth rate of phytoplankton will be limited depending on their time averaged depth dependent light source and, hence, some patches may be more populated than others. Field studies also report the presence of coherent patches, on a variety of scales, that are not destroyed by an otherwise turbulent velocity field (Benfield *et al.*, 1996; Wiafe & Frid, 1996; Lenz *et al.* 1995; Wishner *et al.* 1995; Visman *et al.* 1994; Owen, 1989, 1981; Haury & Wiebe, 1982; Denman & Herman, 1978).

The upshot of the difference in buoyancy between phytoplankton and purely advected particles is that their retention zones differ (i.e. the trajectories of the positively buoyant phytoplankton that get trapped in the retention zones of Fig. 9 will intersect the trajectories of neutrally buoyant particles in the chaotic regions of Fig. 6). This enables the phytoplankton to have a fresh mixed supply of essential nutrients.

Zooplankton are able to change their swimming characteristics in response to the availability of prey and their vulnerability to higher predators (e.g. Munk, 1995; Davis *et al.* 1991; Hunter & Thomas, 1974). Depending on the zooplankton's feeding characteristics, living in a chaotic region may either be beneficial or detrimental (Saiz & Kiorboe, 1995). For a filter feeder that doesn't swim and waits for prey to come close, the chaotic region has the effect of increasing the zooplankter's encounter rates with phytoplankton. However, for a zooplankter that actively pursues prey, the diverging flow trajectories could prove difficult to traverse, thus decreasing it's capacity for successful capture. Also, there may be less prey in chaotic regions as local patches may diffuse quicker. To leave the chaotic regions, the zooplankter must change it's effective buoyancy (i.e. swimming up or down) until the prey are encountered in the coherent region (similar to Davies *et al.* 1991, but transport of zooplankton can occur at much greater speeds making use of the flow than for swimming alone). It would obviously be beneficial for zooplankton to remain in this region until the foodsource has run out or if they get chased by larger predators and, therefore, they should match the buoyancy of the phytoplankton. Thus, zooplankton may make use of the chaotic regions to move swiftly and economically between phytoplankton coherent regions and to evade predators (Yen & Strickler, 1996). To do this they could make use of the light intensity and adjust their buoyancy accordingly. Analyses of field data suggest that zooplankton move into phytoplankton patches as soon as they form, then move on before getting eaten themselves.

In open oceans and lakes, it is likely that there will be significant variations in windspeed, illumination and forcing frequency. It is the timescales of these variations that are important for the construction and maintenance of the resonant retention zones. One can imagine a smooth transition between Figs. 5 to 7 for which certain retention zones would persist throughout the process but others would exist for relatively short periods of time.

Variations of light and wind lead to a path in the parameter space of Moroz & Leibovich (1985) and present the possibility of oscillatory solutions as well as steady solutions. Cox *et al.* (1992a; 1992b) demonstrate the existence of a whole range of solutions, which can co-exist, such as steady, oscillatory and multiple oscillatory states. They find, however, "that the only robustly observable motions that should be anticipated are travelling waves and steady states". Also, they report the existence of transversally drifting Langmuir circulations in field studies and indicate that stable stratification "causes the most unstable (linear) modes to to rotate from the wind direction", although this is only a minor affect. What we conclude from these studies is that a whole host of instabilities arise from the model irrespective of other arbitrary external forcing. It is expected that some of these oscillatory modes will exhibit similar behaviour to the system described in this paper.

If the Langmuir circulation slows down and stops it will leave behind patches that may diffuse relatively slowly due to turbulence but this could be balanced by the active aggregation of plankton (Davis *et al.* 1991). Therefore, the patches may persist in the absence of Langmuir circulation and may even be entrained in the flow if the circulation restarts. Some patches will be positioned within the coherent regions and others not and so some patches will remain and others will quickly disappear. This may indeed benefit one species with a particular buoyancy and not another, but this would depend explicitly on the physical conditions.

The effect of other diffusive processes on the unsteady flow (such as turbulence) may do no more than blur the edges of the retention zones enabling particles to diffuse in and out. However, it has been shown by Davis *et al.* (1991) that by including the effects of the plankton's swimming behaviour (see also Pedley & Kessler, 1992; Hill & Häder, 1997; Bees *et al.* 1997) as a biological diffusivity, the plankton trajectories are no longer incompressible and plankton can actively aggregate. This may help plankton to accumulate in areas beneficial to them (such as, perhaps, the coherent regions), and is an obvious extension to the above work.

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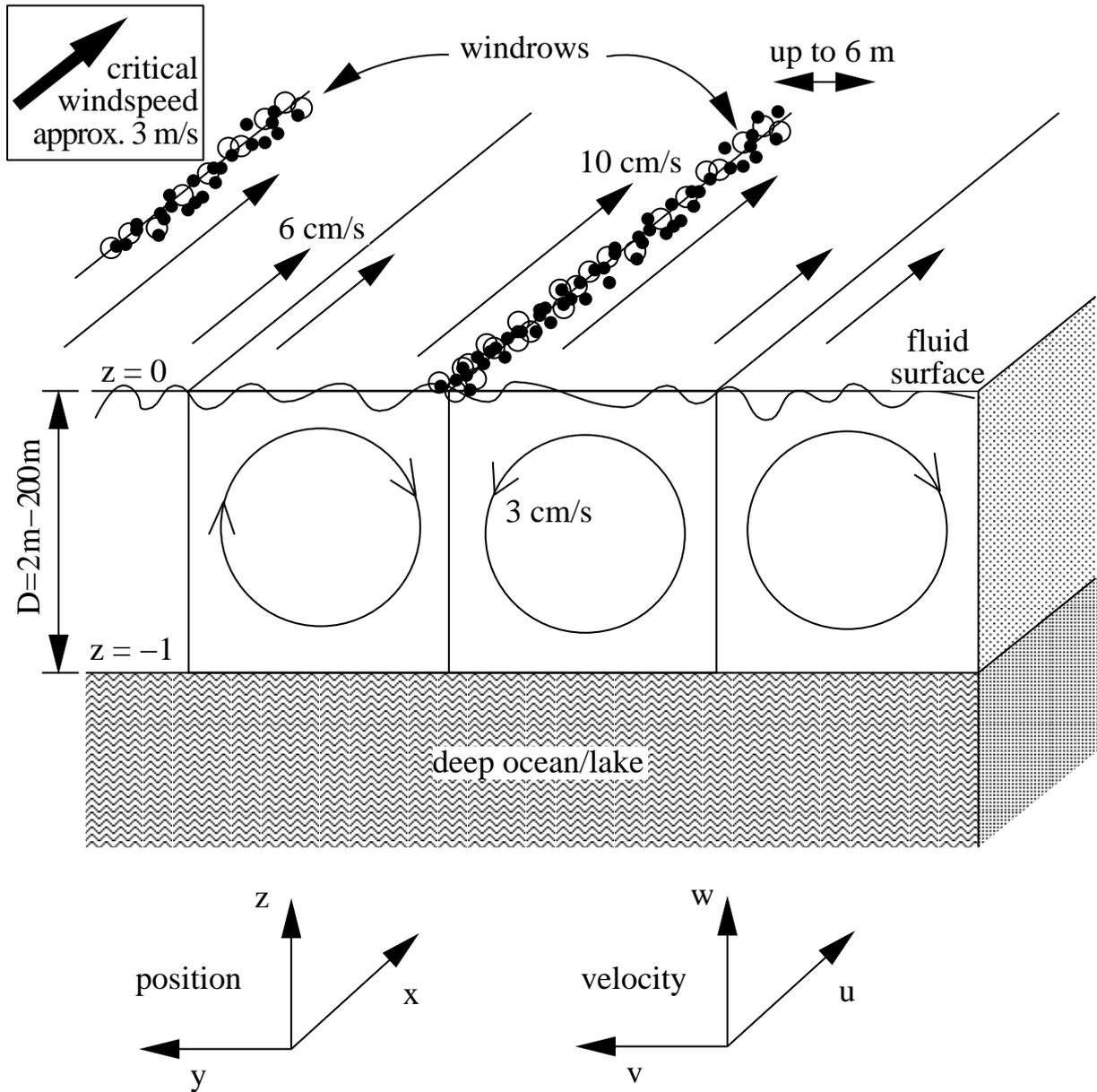
Figure 1: Coordinate system and representation of the steady flow. Typical field measurements, as collated by Leibovich (1983) and Barstow (1983), are indicated. The windrows consist of floating debris at regions of surface convergence.

regions of convergence or windrows

surface

deep ocean/lake
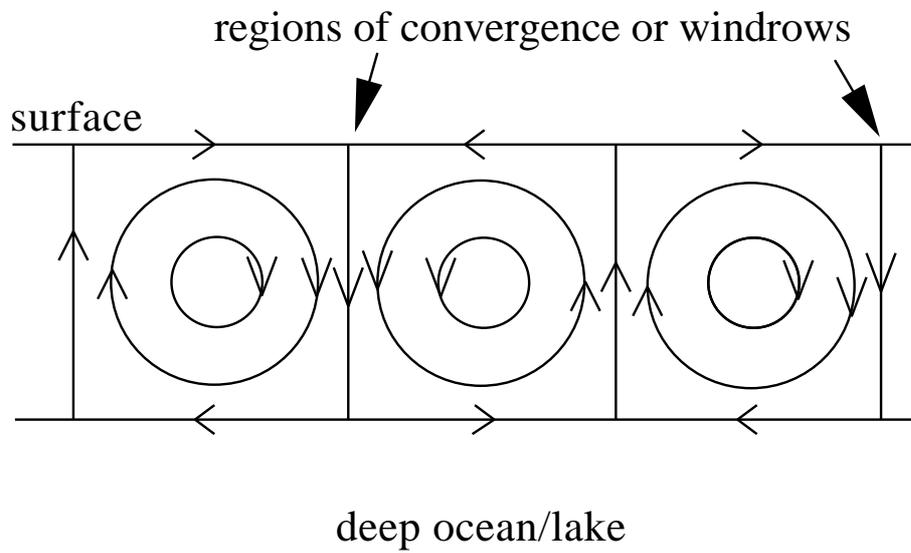
Figure 2: Steady cross-sectional streamlines for particles of neutral buoyancy.

ε

$z = 0$

z

y

frequency
$= \omega$

$z = -1$
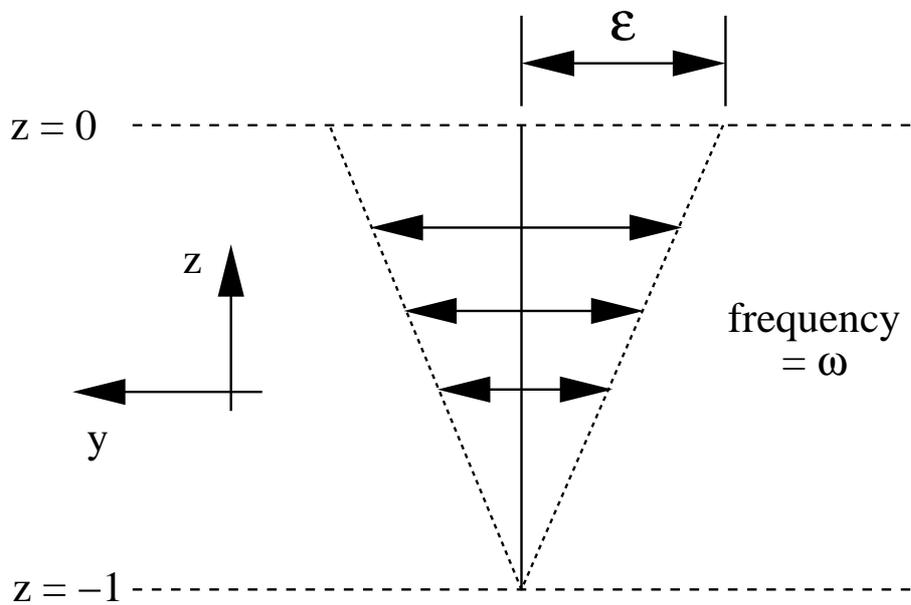
Figure 3: The time-dependent perturbation which is superimposed on the steady flow
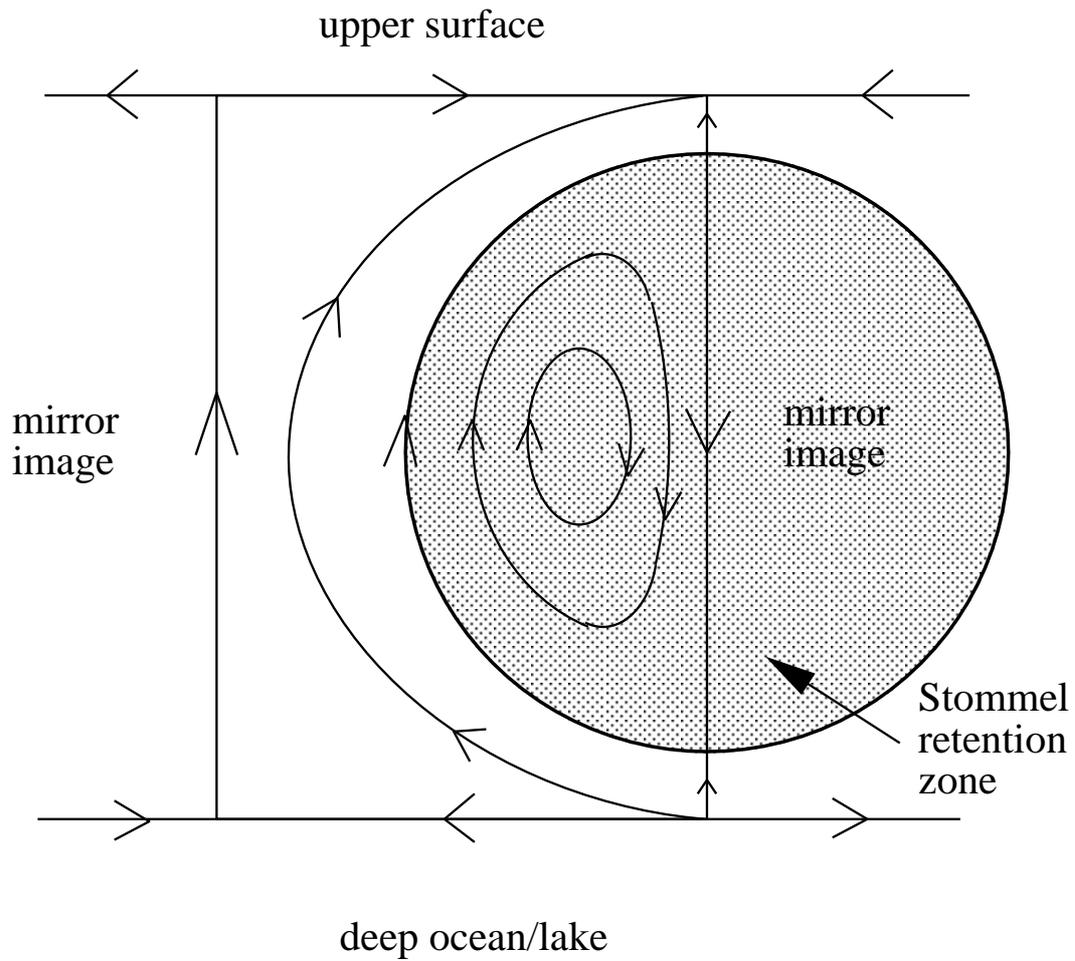
Figure 4: Steady cross-sectional streamlines for particles of positive buoyancy. Sufficiently near to the upper surface, all trajectories have a vertical component which points upwards. Therefore, no positively buoyant particles can move downwards from the upper surface no matter how strong the Langmuir circulation. The shaded region indicates a region of closed streamlines and is called a Stommel retention zone.
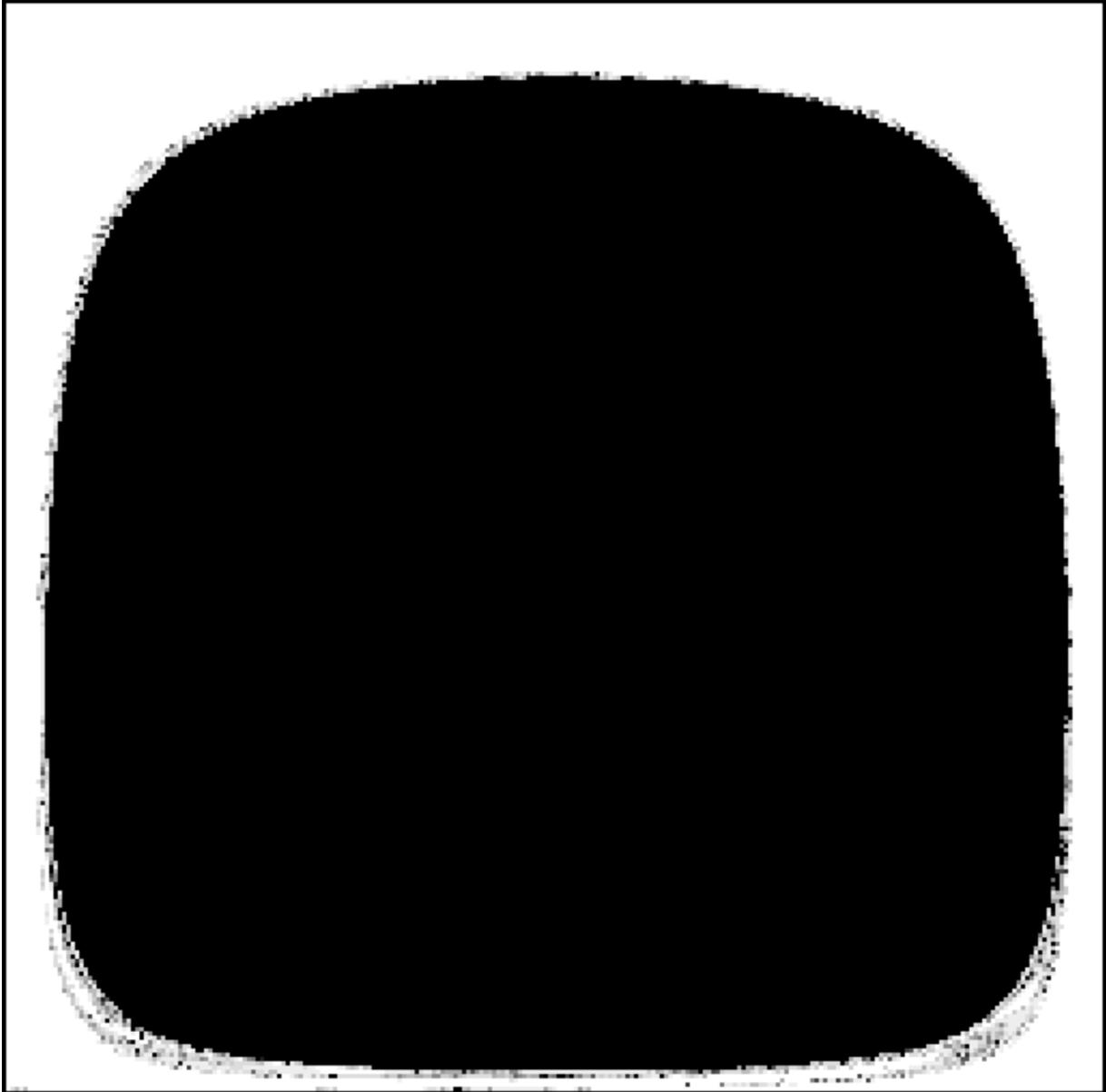
Figure 5: Escape times for neutrally buoyant advected particles whose initial cross-sectional positions are plotted. The greyscale indicates the number of oscillations required before the particle leaves the Langmuir cell, where white represents one oscillation and black represents more than 100 oscillations. The circulation speed, A, and the perturbation amplitude, ϵ, both equal 0.1, and the forcing frequency, ω, equals 0.24.
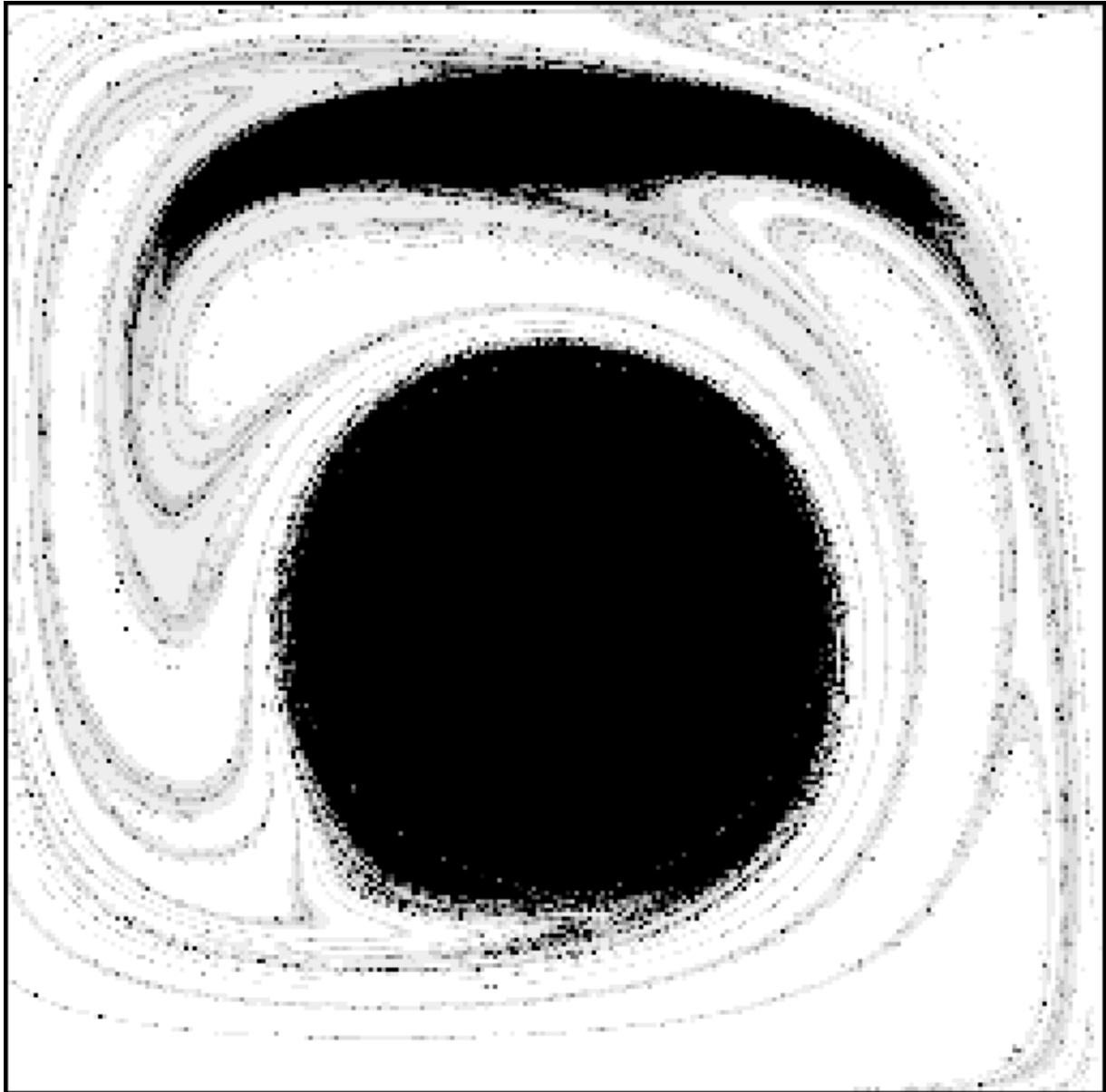
Figure 6: Escape times for neutrally buoyant advected particles whose initial cross-sectional positions are plotted. The greyscale indicates the number of forcing cycles required before the particle leaves the Langmuir cell, where white represents one oscillation and black represents more than 100 oscillations. The circulation speed, A, and the perturbation amplitude, ϵ, both equal 0.1, and the forcing frequency, ω, equals 0.6.
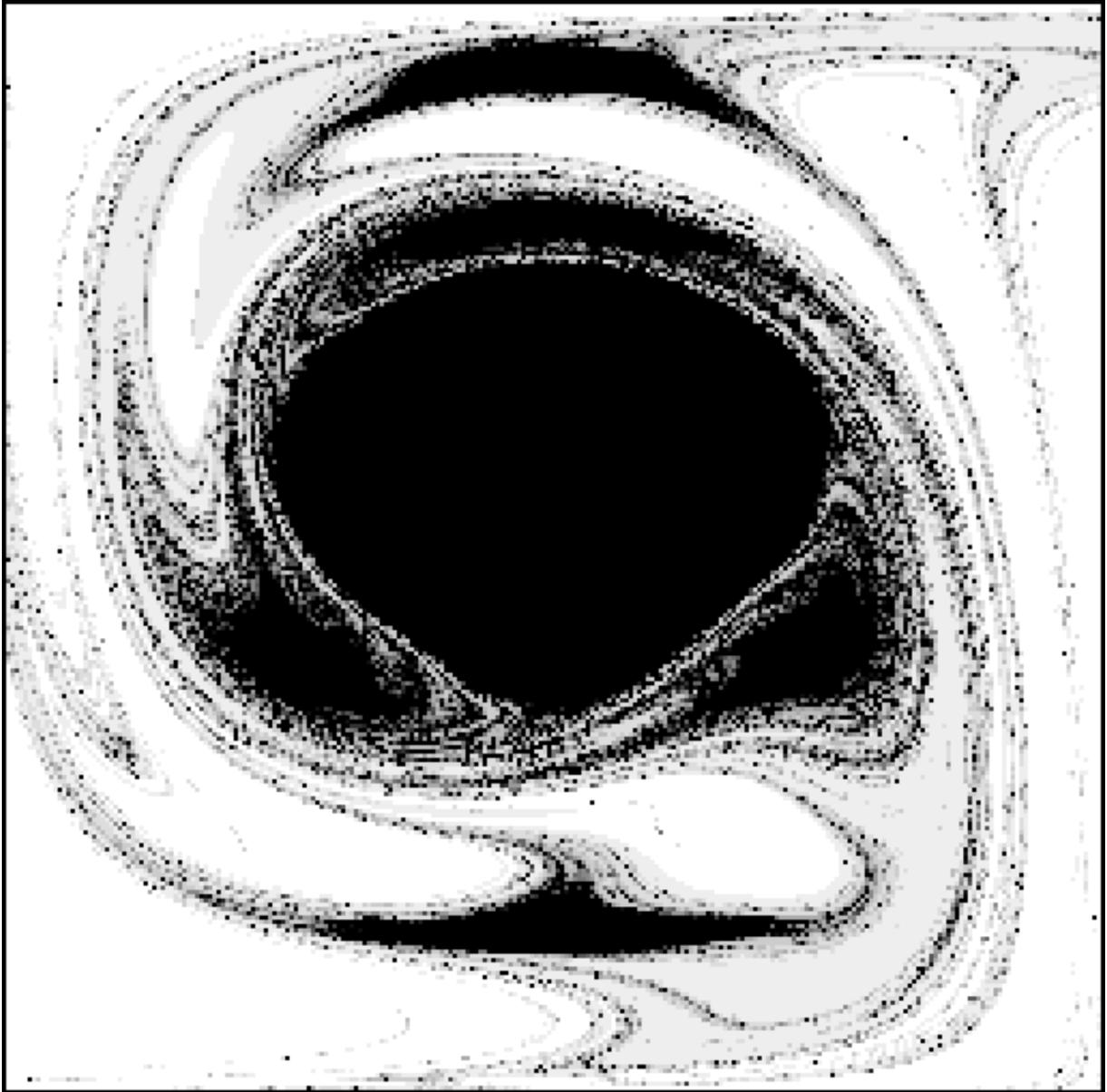
Figure 7: Escape times for neutrally buoyant advected particles whose initial cross-sectional positions are plotted. The circulation speed, A, and the perturbation amplitude, ϵ, both equal 0.1, and the forcing frequency, ω, equals 1.2.
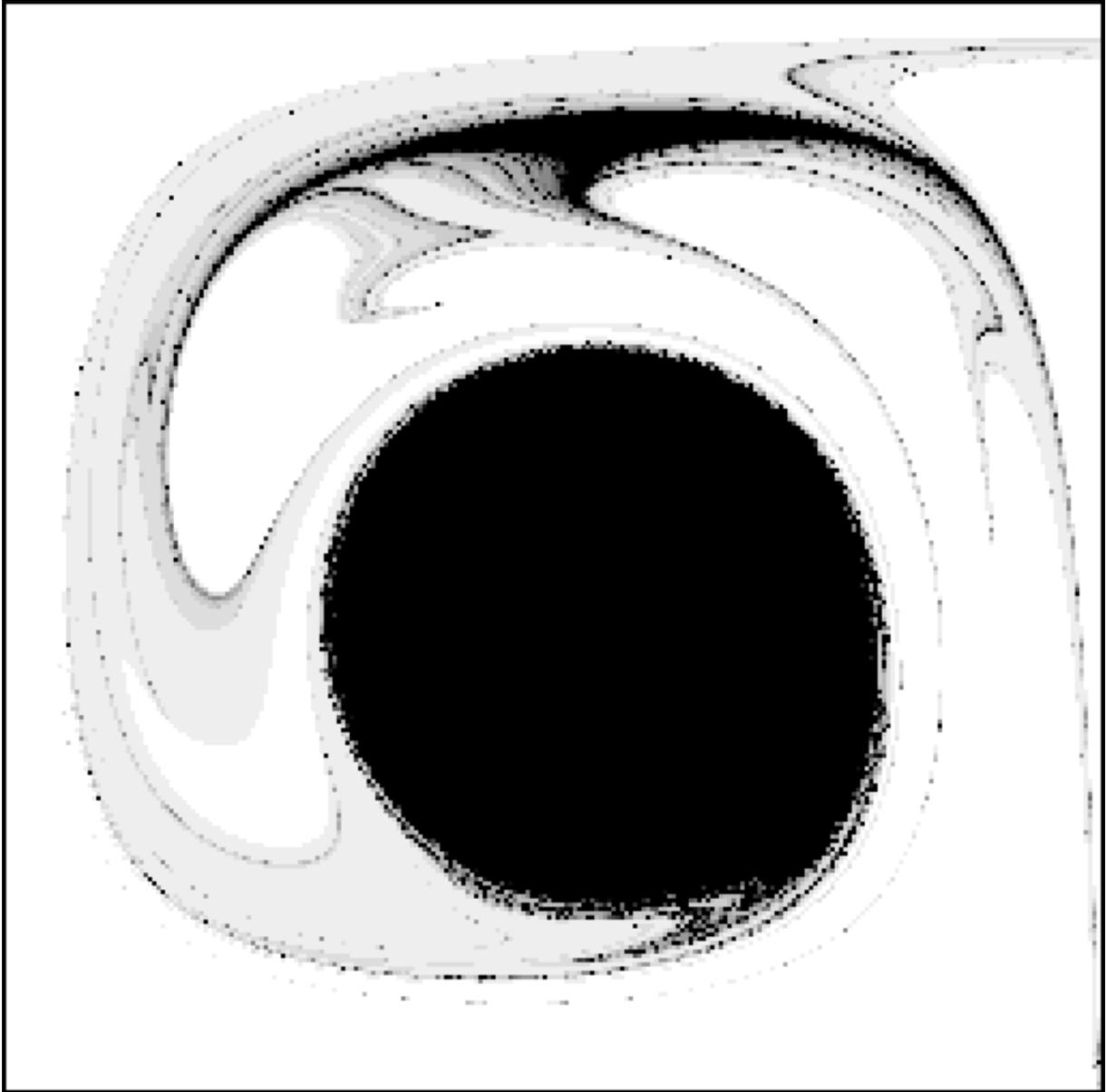
Figure 8: Escape times for positively buoyant ($V_s = 0.032$) advected particles whose initial cross-sectional positions are plotted. The remaining parameters are the same as Fig. 6.
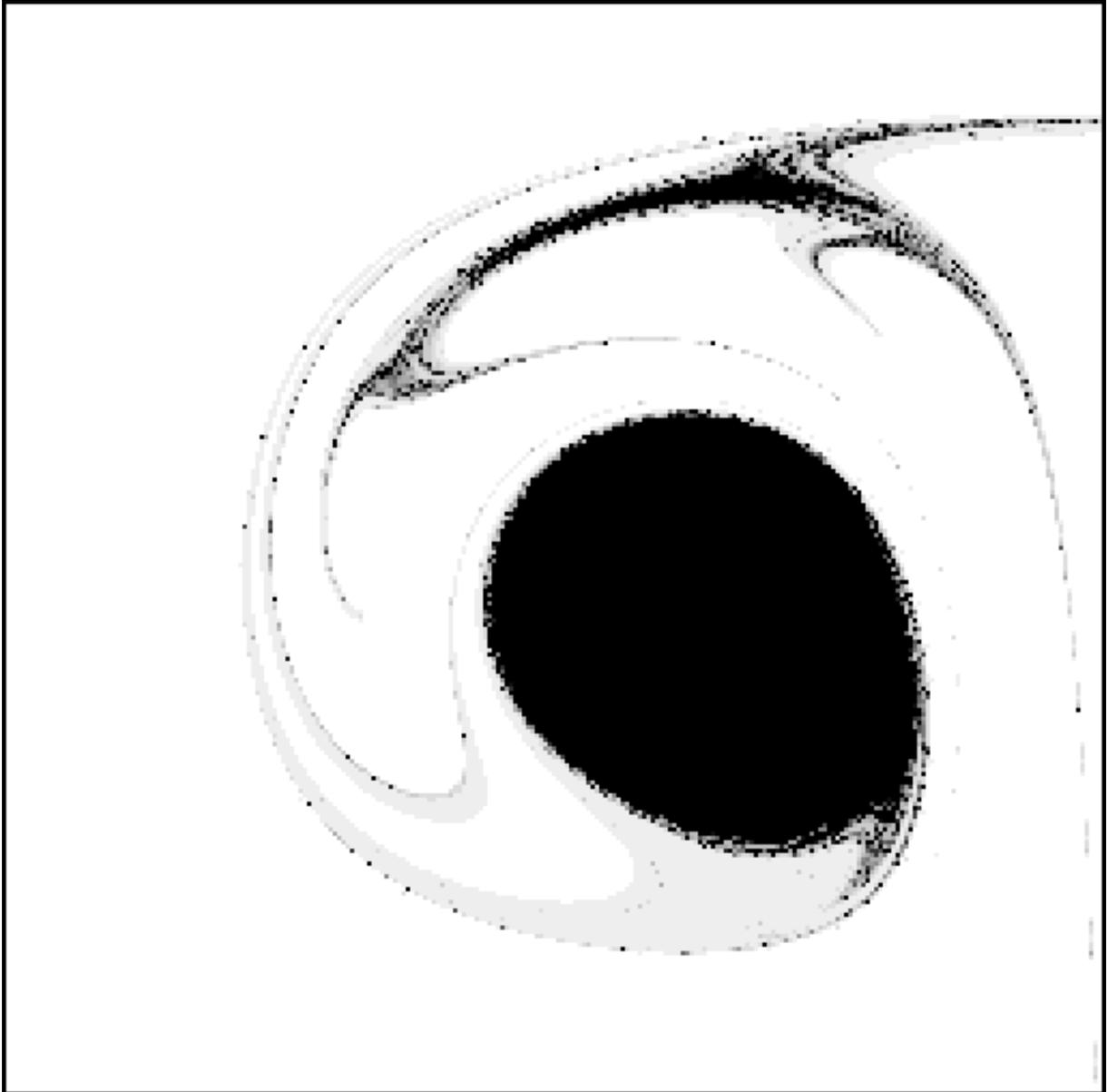
Figure 9: Escape times for positively buoyant ($V_s = 0.1$) advected particles whose initial cross-sectional positions are plotted. The remaining parameters are the same as Fig. 6.
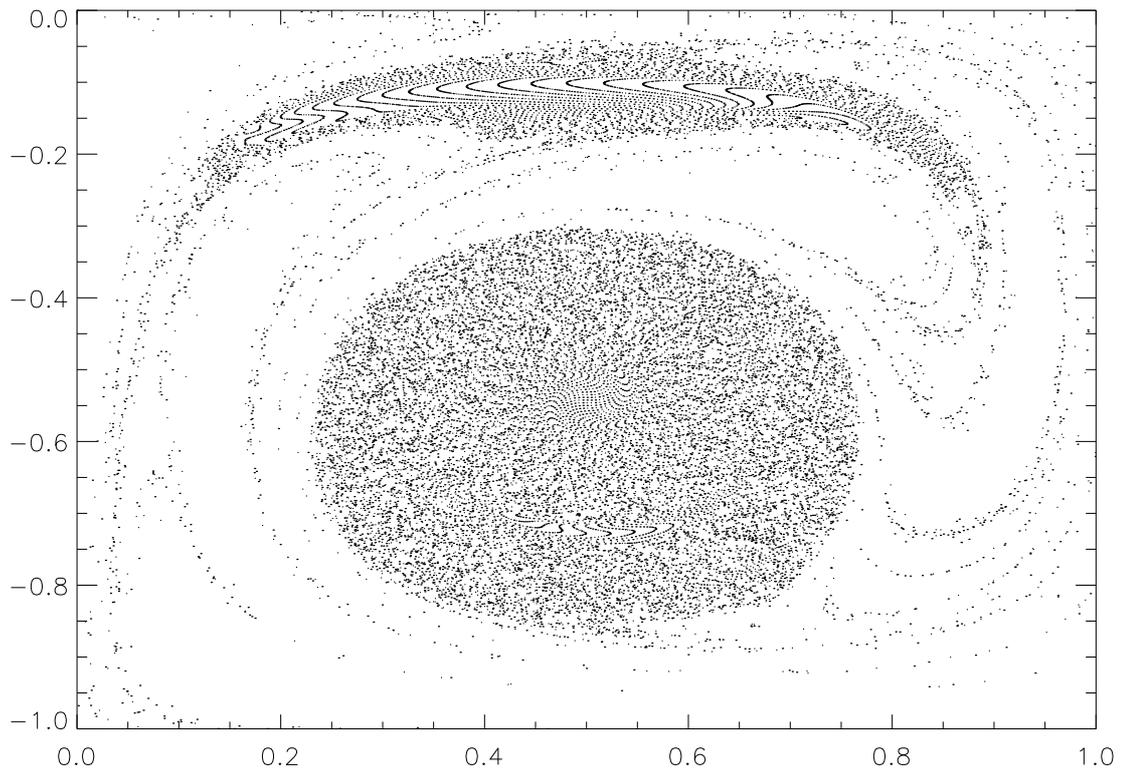
Figure 10: Distribution of neutrally buoyant particles after 50 oscillations from a regular grid with a forcing frequency of $\omega = 0.6$. Here, plankton are allowed to escape from the region defined by $y \in [0, 1]$. Coherent regions of space can be observed as are regions where particles are quickly removed. $A = \epsilon = 0.1$ with 256^2 pixels.
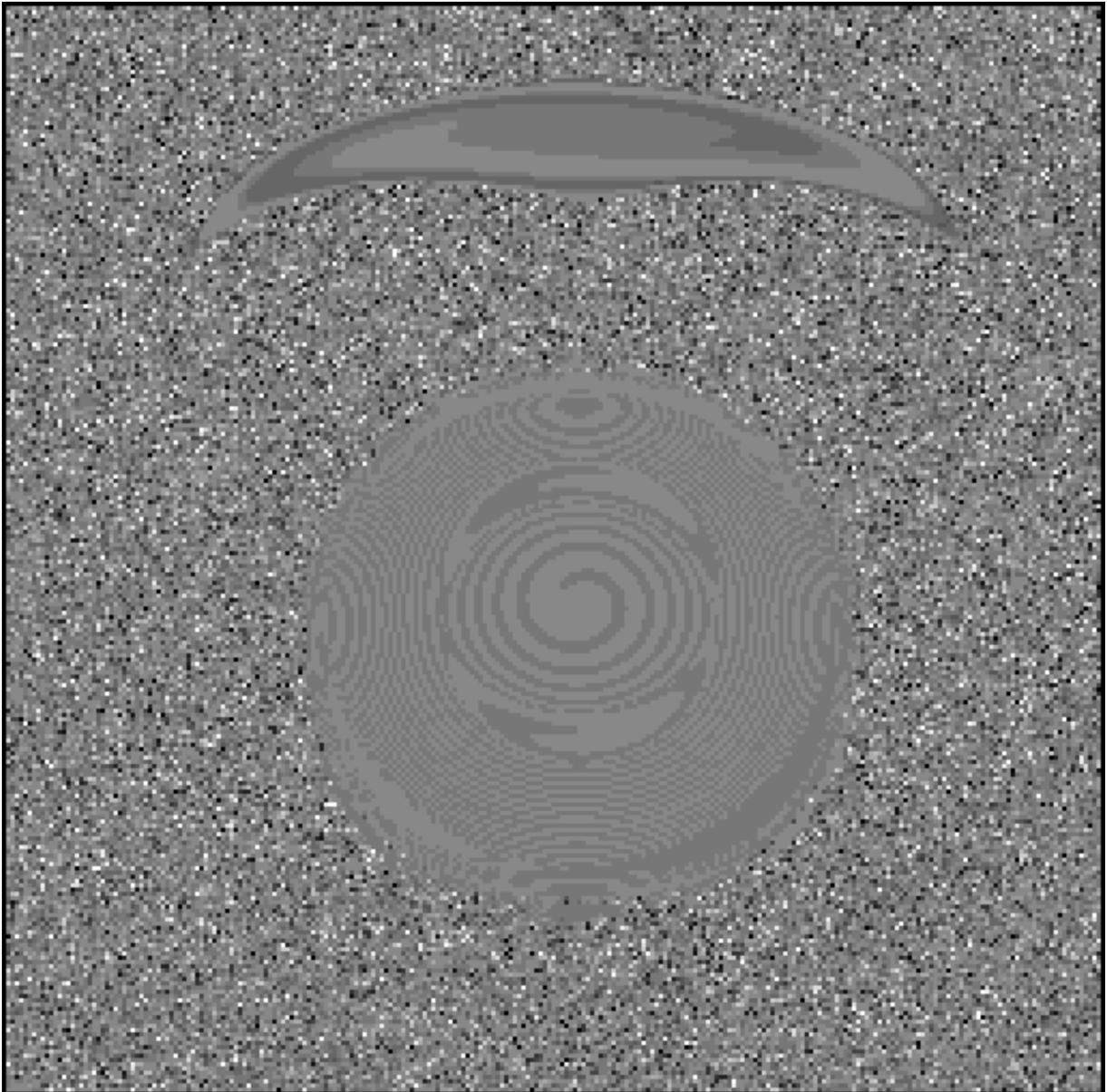
Figure 11: Longitudinal displacement of particles that start from $x = 0$ at the above cross-sectional location. Particles whose initial position is contained in the light coloured regions travel a greater longitudinal distance. $A = \epsilon = 0.1$ and $\omega = 0.6$ with 256^2 pixels. The direction of the longitudinal flow is generally with the wind, unless the aspect ratio, l, is unrealistically small (see text).