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Cross-frontal entrainment of plankton into a buoyant plume: The frog tongue mechanism

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ABSTRACT

A mechanism for the cross-frontal entrainment of plankton by a buoyant plume influenced by wind stress is described and tested using an idealized numerical model. Under the right circumstances, plankton may enter a buoyant plume during an upwelling wind stress, then be transported shoreward during a subsequent downwelling wind stress. In order for the plankton to enter the plume, they must swim upward at a velocity (w_p) bounded by

$$H_{plume}/T < w_p < \kappa/H_{mix}$$

where H_{plume} is the thickness of the buoyant plume, H_{mix} is the thickness of the upper oceanic mixed layer ($H_{mix} > H_{plume}$), κ is the magnitude of vertical mixing within the mixed layer, and T is the time between upwelling and downwelling events. In words, this equation states that the plankton must swim slow enough so that they are evenly distributed through the mixed layer, so that the buoyant plume may override the plankton patch during upwelling. Once the plume has overridden the patch, in order to enter the plume, the plankton must swim fast enough to be able to enter the plume in the time while it is over them. These two bounds on the swimming rate suggest that, given various physical parameters, there may be a range of swimming speed that will maximize entrainment into a plume. Numerical experiments corroborate the feasibility of the proposed mechanisms and associated scaling.

1. Introduction

By definition, plankton are at best weak swimmers. Typical swimming speeds of motile species range from meters to hundreds of meters per day. Because ocean currents are

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several orders of magnitude stronger, plankton are effectively passive tracers in a lateral context. However, ocean currents are much weaker in the vertical than in the horizontal plane. Thus, even the modest swimming ability of planktonic organisms can permit them to control their vertical position.

Plankton can use their swimming ability to migrate between different vertically stratified water masses with more favorable characteristics. For example, dinoflagellates can swim upward to increase their exposure to light, and swim downward either to avoid turbulence or exploit higher ambient nutrient concentrations in deeper waters (e.g., Eppley *et al.*, 1968; Cullen and MacIntyre, 1998). Zooplankton populations exhibit a wide variety of vertical migration behavior on timescales from diel (e.g., Bary, 1967) to ontogenetic (e.g., Fulton, 1973).

When there are sharp lateral gradients in density, the behavioral capability of plankton gives rise to a wide variety of physical-biological interactions that create spatial heterogeneity in planktonic populations. In particular, plankton are often found at the frontal regions separating two water masses (e.g., Tyler and Seliger, 1978; Olson and Backus, 1985; Franks, 1992; 1997). For example, upward-swimming plankton will tend to aggregate in areas of convergence at surface fronts as the organisms' motion through the water compensates for downwelling imposed by the surface convergence.

In this paper, we describe a mechanism for cross-frontal exchange of plankton that results from conditions that are similar to those that give rise to frontal aggregation. We consider the problem of a patch of upward-swimming plankton located offshore of a coastally-trapped buoyant plume (i.e. river plume) subject to cyclic upwelling/downwelling wind stress. During an upwelling event (with seaward Ekman transport within the surface waters) the plume will become thin, and move offshore. The plume is thinner than the ambient mixed layer, and will travel offshore faster than the ambient surface water so that the plume overrides the plankton. The plankton swim upward and become entrained into the plume. A subsequent downwelling event (with shoreward Ekman transport in the surface waters) may then carry the plankton shoreward along with the buoyant water.

This mechanism could act as a means of transporting offshore populations of plankton to the coast. Such a mechanism could be exploited by planktonic larvae with estuarine nursery areas (e.g., Epifanio and Garvine, 2001), or may cause a seed population of toxic phytoplankton to be transported to the coast, where a toxic phytoplankton bloom could affect shellfish fisheries and recreation. These various weakly swimming organisms will be referred to in general as 'plankton' for the remainder of this paper. This mechanism has been dubbed the 'frog tongue' because of the similarity between the plume stretching offshore and collecting plankton and a frog sticking out its tongue to catch a fly.

This study complements a related mechanism described by McGillicuddy *et al.* (2003), who consider upward-swimming plankton germinated from benthic cysts, which may then swim up into an upwelled buoyant plume directly overhead. They did not distinguish between plankton that swim directly up into the plume (i.e. the underside of the frog tongue) and those that become entrained at the nose of the front (i.e. the tip of the frog

tongue) by subduction and subsequent upward swimming. The present study is distinct in that it focuses on entrainment of pre-existing near-surface plankton patches and further identifies optimal behavior (swimming rate) to maximize migration into the plume under differing dynamical conditions.

The specific case modeled in this paper was motivated by the potential for entrainment of the toxic dinoflagellate *Alexandrium fundyense* into the Kennebec River plume. *Alexandrium fundyense* has the capability to swim on the order of ten meters per day (Anderson and Stolzenbach, 1985), and blooms of this organism are frequently associated with fresh waters of coastal river plumes in the Gulf of Maine (Franks and Anderson, 1992). However, potentially significant sources of *A. fundyense* lie outside the river plume. Large deposits of resting cysts are located in sediments well offshore of the plume's mean position. Wind-driven upwelling events can cause the thinned plume to extend well offshore, such that cells germinated from the offshore cyst beds can swim directly up into the plume (McGillicuddy *et al.*, 2002). Alternatively, Townsend *et al.* (2001) suggest that an upstream population of *A. fundyense* with a cyst bed near the mouth of the Bay of Fundy may travel along a branch of the Eastern Maine Coastal Current that flows seaward of the Kennebec River plume may also be a potential source population. In either case, offshore *A. fundyense* populations may have an opportunity to become entrained into the Kennebec River plume through the frog tongue mechanism.

In Section 2, a criteria for entrainment into the plume based on vertical swimming speed and other environmental factors is developed. The primary result is given in Eq. 10. The theoretical results are confirmed using a numerical model, described in Section 3. Discussion and conclusions are in Sections 4 and 5, respectively.

2. Mixed layer theory and scaling

a. Theory

The oceanic surface mixed layer is defined by a relatively homogeneous mass of water bounded below by strong stratification that suppresses turbulent mixing. Over timescales long enough for the earth's rotation to become important, more than a few hours, there is a net transport to the right of the wind within the mixed layer referred to as Ekman transport (e.g., Cushman-Roisin, 1994). In this paper, we will ignore the details of the mixed layer flow (e.g., Price *et al.*, 1987), and approximate the mixed layer as a homogeneous slab, as is common in simple models of stratified flow (e.g., Csanady, 1977; Garvine, 1987; Fong and Geyer, 2001).

The magnitude of this depth-integrated transport is dependent only upon the magnitude of the wind stress, τ , and the Coriolis parameter, f , in particular,

$$U_{mix} = \frac{\tau}{\rho_0 f} \quad (1)$$

where ρ_0 is a constant representing the mean density of ocean water, and U_{mix} is the depth integrated transport in the mixed layer.

Although, at a given latitude, for a given wind stress the *transport* is constant, the average current *speed*, \bar{u}_{mix} , depends inversely on the depth of the mixed layer since $\bar{u}_{mix} = U_{mix}/H_{mix}$, where H_{mix} is the depth of the mixed layer. The actual speed of the current becomes important when the flow becomes fast enough to excite shear instabilities. Shear-induced mixing will occur when the Richardson number, a ratio of the potential to kinetic energy anomalies in the flow, dips below a critical value. The exact value of the critical Richardson number depends upon the formulation of the Richardson number used (e.g., Price *et al.*, 1987). Following Fong and Geyer (2001), we will use the ‘bulk’ Richardson number, appropriate for layer models such as the one considered here, which is defined as

$$Ri_b = \frac{g' H_{mix}^3}{4u_{mix}^2}. \quad (2)$$

where $g' = g\Delta\rho/\rho_0$ is the reduced gravity, with $\Delta\rho$ representing the density difference between the mixed layer and the ambient fluid below. The factor of four comes from assuming a linear decay in velocity from u_{mix} at the surface to zero at the base of the mixed layer. The mixed layer will undergo turbulent mixing if the bulk Richardson number falls below a critical value, Ri_c , typically 0.6 to 0.8. The active upper layer will entrain ambient fluid until the Richardson number becomes larger than Ri_c .

According to Fong and Geyer (2001), during an upwelling wind, a plume transported offshore by the Ekman transport will thin until it reaches a critical, minimum thickness, H_{plume} , determined by solving Eq. 2 for H_{mix} given Ri_c , so that

$$H_{plume} = \left(\frac{4Ri_c u_{mix}^2}{g'} \right)^{1/3} \quad (3)$$

The plume will become thinner until the vertical velocity shear created by the Ekman transport of the plume over still water generates shear instabilities, which cause the plume to mix and thicken.

b. Scaling

In the vicinity of a coastally trapped buoyant plume, there are two distinct regimes with respect to the penetration of wind energy, and speed of the Ekman flow. There is the region where the upwelled plume is present, with a mixed layer depth of a few meters, and the region where the plume is not present, with a mixed layer depth of tens of meters. The latter will be referred to as the ‘ocean’ mixed layer, to distinguish it from the shallower mixed layer created by the upwelled buoyant plume. The order of magnitude change in the layer thickness allows the buoyant plume to ride over the ambient mixed layer water, since the plume’s speed is greater than that of the mixed layer by a proportion equal to the ratio of layer thicknesses, or

$$\frac{u_{plume}}{u_{mix}} = \frac{H_{mix}}{H_{plume}} \sim O(10). \quad (4)$$

A patch of plankton initially seaward of the plume may be overridden by the faster moving buoyant plume. The plankton then have the opportunity to swim up into the plume. A cartoon depicting this sequence of events is shown in Figure 1.

The initial placement of the patch and the plume are important if the two are to interact; the patch must be within reach of the plume. Over a given time interval, Δt , representing the duration of upwelling winds, $\tau^y(t)$, the offshore displacement of the plume, ΔL , can be approximated by

$$\Delta L = \int_{t_0}^{t_0 + \Delta t} u_{plume} dt = \int_{t_0}^{t_0 + \Delta t} \frac{\tau^y(t)}{\rho_0 f H_{plume}} dt, \quad (5)$$

similar to the result of Fong *et al.* (1997). Thus, the plankton patch must be within ΔL of the plume front in order to interact with the plume. Of course, this value is only approximate since the plankton patch will also be pushed offshore by the upwelling winds, albeit much slower.

i. The ocean mixed layer region. As stated above, the ocean mixed layer is constantly being stirred by the wind. The turbulence in the ocean mixed layer will act to diffuse the plankton evenly throughout the layer. This diffusive effect will be offset by the upward swimming of the plankton, giving rise to an advective-diffusive balance for the vertical plankton distribution,

$$w_p \frac{\partial P}{\partial z} = \frac{\partial}{\partial z} \left(\kappa \frac{\partial P}{\partial z} \right) \quad (6)$$

where P is the plankton concentration, w_p is the vertical swimming rate of the plankton, and κ is the turbulent eddy diffusivity. Note that the advection in this advective-diffusive balance is provided by the motion of the cells through the water, not the motion of the water itself.

It should be noted that the turbulence in the mixed layer, κ , is known to be large, but specific values are not well known. A very coarse upper bound for the diffusivity may be estimated by

$$\kappa \sim H_{mix} \sqrt{\frac{\tau}{\rho_0}} \equiv u^* H_{mix}, \quad (7)$$

where u^* is the velocity of the turbulent fluctuations in the mixed layer. The interested reader is referred to Large *et al.* (1994), who present a detailed survey of oceanic mixed layer studies. For observational work, it may be simpler to ascertain if the plankton are distributed evenly through the mixed layer or not, rather than try to estimate κ directly.

Numerical model results indicate that unless the plankton are relatively evenly distributed across the mixed layer, they will simply be pushed ahead of the nose of the buoyant plume, and will never be subducted underneath the plume. Thus, the first requirement for

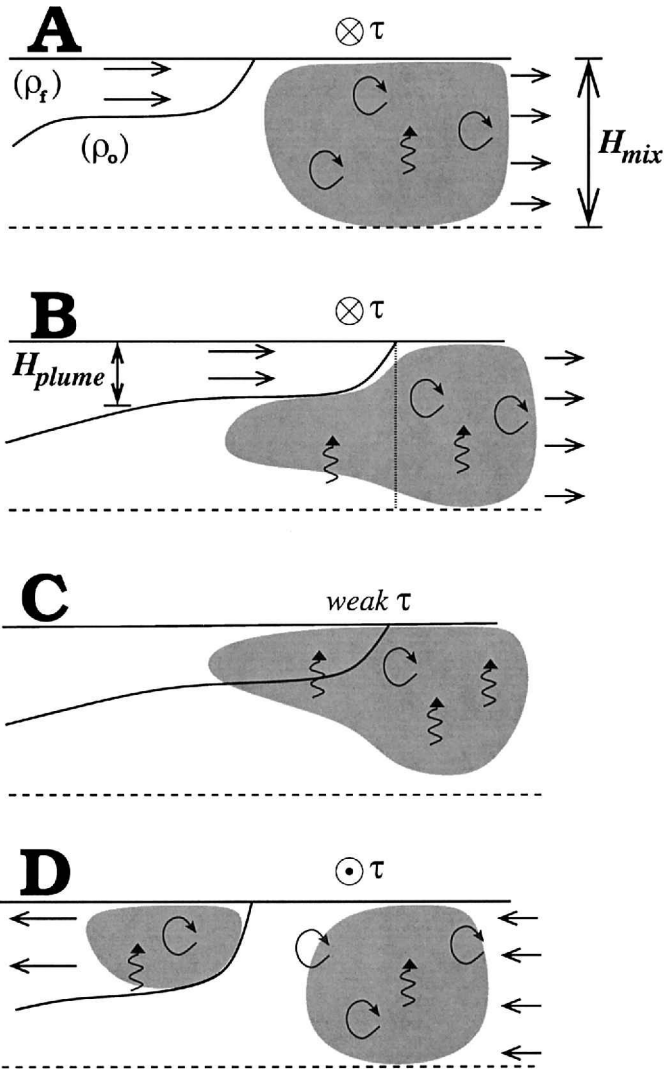


Figure 1. This cartoon shows the sequence of entrainment of a portion of a plankton patch into a buoyant plume. The case shown represents the ‘sweet spot’ scenario of maximum plankton entrainment into the plume. The dark gray represents the core of the plankton patch. The straight, horizontal arrows represent the Ekman transport velocity, with higher values in the shallower plume. The circular arrows represent turbulent mixing, and the squiggly arrows represent upward swimming. More of either type of arrow signifies that process is dominant, although both mixing and swimming are always present to some degree. (A) A plume approaching a plankton patch, mixed throughout the ocean mixed layer of depth H_{mix} . (B) The thin plume (with a thickness of H_{plume}) overrides the plankton patch. Turbulence is suppressed below the plume (to the left of the dotted line), and the plankton begin to swim upward uninhibited by turbulence. (C) The wind is calm, and the plankton swim upward everywhere. The subducted plankton swim up into the plume while it is overhead. (D) The plume is downwelled back toward the coast, carrying with it a portion of the plankton patch.

the plankton to enter the plume is that their swimming rate must be slow enough to be affected by turbulence enough to be evenly distributed through the mixed layer, or

$$w_p < \frac{\kappa}{H_{mix}} = u^*. \quad (8)$$

This well-mixed limit is equivalent to stating that the velocity fluctuations of the turbulent motions, u^* , are greater than the swimming speed of the plankton, w_p .

ii. The plume region. In the region where the plume is present, only the buoyant water within the plume is well mixed. Beneath the plume, turbulent mixing is weak, and the plankton subducted below the plume during upwelling may swim upward uninhibited. In order for the plankton to reach the core of the plume, they must swim up fast enough to enter the plume before a downwelling event brings it back to the coast. Thus, the condition for plankton beneath the plume to enter the plume is

$$w_p > \frac{H_{plume}}{T} \quad (9)$$

where T is the amount of time the plume is in an upwelled state, approximately the time between upwelling and downwelling events. We have assumed that the thickness of the plume is proportional to the pycnocline thickness, a harder scale to quantify, and that the two scales have similar magnitudes. The idealized model results support this assumption.

iii. Bounds on vertical swimming rate. Combining requirements 8 and 9 gives the following constraint on the vertical swimming rate in relation to other environmental variables:

$$\frac{H_{plume}}{T} < w_p < \frac{\kappa}{H_{mix}}. \quad (10)$$

This constraint requires that the plankton must be weak enough swimmers to be evenly distributed throughout the mixed layer, to allow the plankton patch to be subducted underneath the upwelled plume. At the same time, they must be strong enough swimmers to be able to swim up into the plume while the plume is present. The two constraints may be combined to determine if *any* swimming speed exists that would allow entrainment. An entrainment is possible for some swimming speed if

$$\frac{H_{mix}H_{plume}}{\kappa T} \ll 1. \quad (11)$$

3. Numerical model

a. Model description and configuration

The Regional Ocean Modeling System (ROMS) (Haidvogel *et al.*, 2000), a 3-dimensional primitive equation ocean circulation model, was configured to simulate an infinite

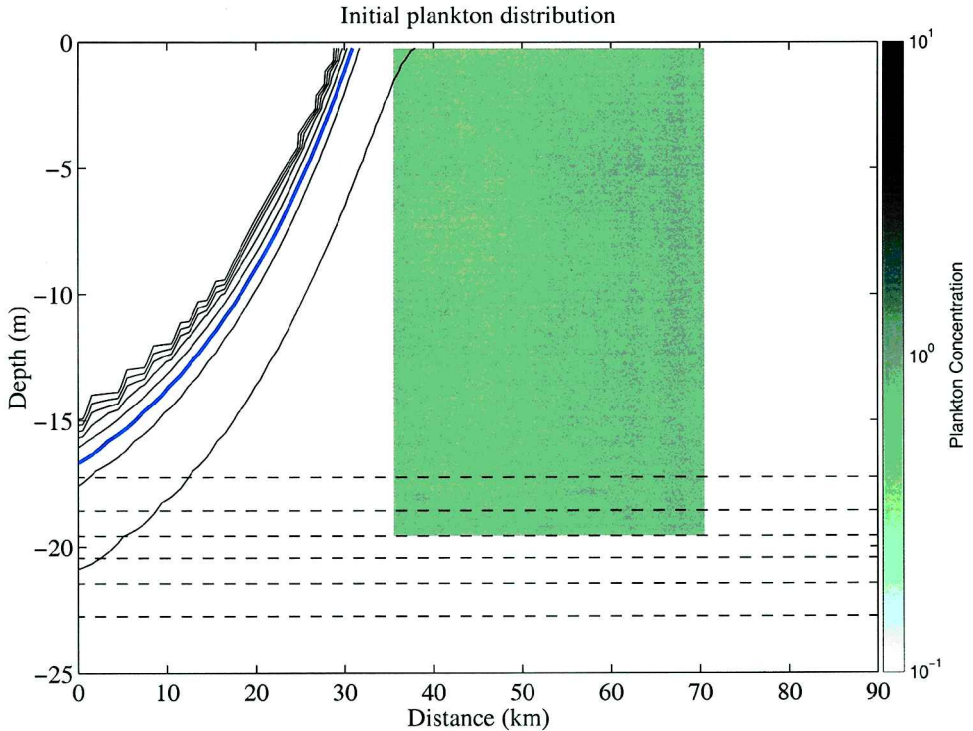


Figure 2. A plot of the initial condition, showing a buoyant plume (24.0 psu) attached to the coastal wall. Background salinity is 32.0 psu and the contour interval is 1.0 psu; the thick blue line shows the 30.0 psu contour. Temperature is 11.0°C in the ocean mixed layer, and 4.0°C below. The thermocline is contoured with dashed lines every 1.0°C. The initial position of the plankton patch (concentration defined as one) is shown by the green rectangle.

channel (i.e., periodic along-channel), with a buoyant plume initialized on one side with a patch of plankton just offshore, as shown in Figure 2. A seasonal thermocline, represented by an increase in stratification at 20 m depth was also included to simulate an ocean mixed layer (i.e., $H_{mix} = 20$ m).

The model was forced with a time dependent along-channel wind stress, to generate upwelling, and then downwelling, as well as a small cross-channel wind stress designed to maintain the vertical mixing throughout the simulation, shown in Figure 3. The cross-shore wind was increased during strong upwelling and downwelling winds to mimic increased variance in the winds (and corresponding vertical mixing) during strong wind events. The cross-shore wind-stress has little dynamical significance—an opposing pressure gradient due to set-up at the coast is formed along with a small along-shore current. The motions of the plume on and off shore are due almost exclusively to the along-shore wind stress and associated Ekman transport. The maximum of upwelling and downwelling were separated by four days, so there was approximately three days during which the plankton had opportunity to swim up into the plume.

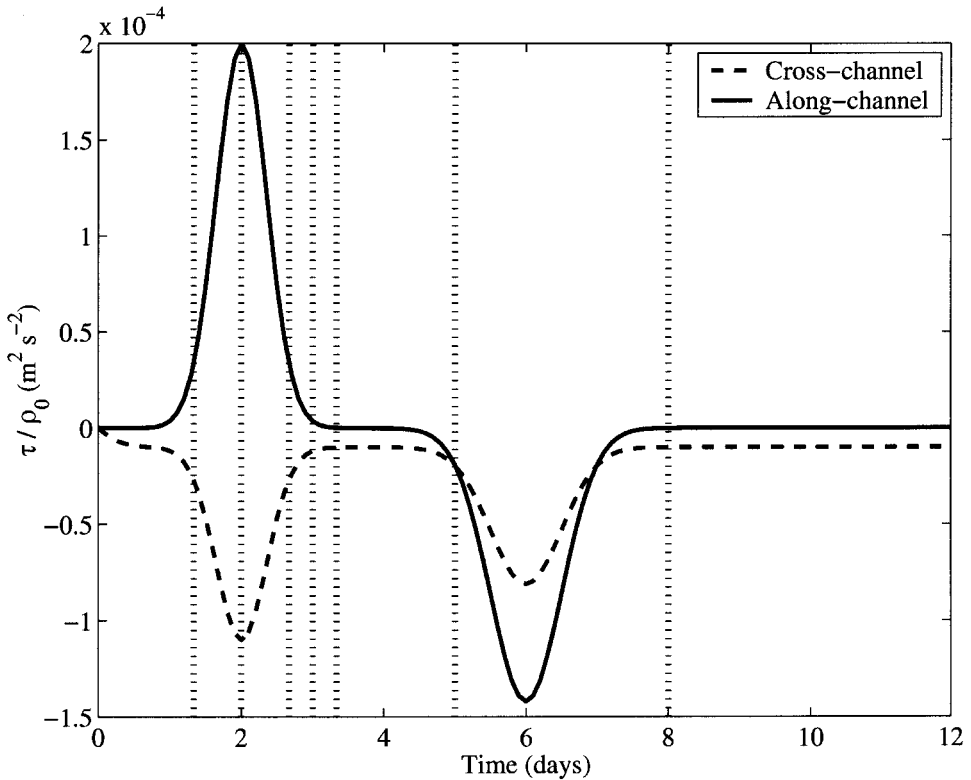


Figure 3. Wind stress used in the model is plotted against time. The vertical dashed lines show the times of the cross-sectional snapshots, shown in Figure 4.

Although the patch of plankton was initialized in the model with a uniform distribution throughout the ocean mixed layer, the vertical distribution of plankton relevant for comparisons with the initial condition of the scaling analysis is determined by the vertical structure of the plankton patch just before the upwelling wind stress occurs (one day into the simulation). The advective/diffusive balance of upward plankton swimming versus vertical mixing will be achieved on the diffusive timescale or faster. This is because if the advective timescale is much longer than the diffusive timescale, the vertically homogeneous initial condition will be very close to the final, steady solution. If the advective timescale is smaller than the diffusive timescale, the system will still come to a steady state within the slower diffusive timescale.

The turbulence closure used [KPP, described by Large *et al.* (1994)] has a specified upper bound on the turbulent diffusivity. Since in the modeled mixed layer this bound is often reached, it will serve as an estimate for κ for scaling. For the model runs presented, the diffusive timescale was approximately 0.5 days (estimated from H_{mix}^2/κ). The upwelling wind begins to strengthen after day 1.0, so the plankton have time to adjust to the advective/diffusive balance assumed in the scaling arguments above. It should be noted

that the magnitude of vertical mixing changes within the ocean mixed layer as the speed of the wind changes. However, the timescale of the wind is approximately 2 days, so that advective/diffusive balance still controls the vertical distribution of plankton, but it will be modified slowly (relative to the advective/diffusive adjustment timescale) as the wind stress changes.

Formation and maintenance of the ocean mixed layer and the buoyant plume are not directly simulated since there are no sources or sinks of buoyancy within the model. Over the period of the runs, the ocean mixed layer diffuses, since there is no maintaining heat flux applied, but maintains enough coherence to keep the turbulence due to the wind confined to above approximately 20 m. Also, the fresh, buoyant plume loses much of its original structure during the two wind events since there is no source of fresh water at the coast. These sources of buoyancy would need to be included to obtain a quasi-steady solution. Due to the lack of buoyant sources in this simple model, the stratification of the ocean mixed layer and buoyant plume will eventually be destroyed by subsequent upwelling/downwelling cycles of the wind stress. This is why we focus on only one cycle of upwelling/downwelling.

b. Model results

The simulated plankton patch follows, qualitatively, the same sequence of events laid out in Figure 1. The time-dependent plankton distribution for different swimming rates is shown in Figure 4. For weak swimming (top panel), very few plankton arrive in the plume, although the plume does override the plankton patch. For moderate swimming (middle panel), the patch is overridden, and the plankton swim fast enough to enter the overlying buoyant water. For strong swimming (bottom panel), the plankton are concentrated at the surface, and are unable to be entrained underneath the plume. Thus, only plankton swimming at a moderate rate are able to enter the buoyant plume.

Figure 5 shows the amount of plankton that enter the plume, defined as the amount of plankton within the 30 psu isohaline, as a function of w_p . The peak of entrainment of plankton into the plume, as estimated by the model, occurs within the bounds estimated by the above scaling analysis. Using Eq. 9, and realistic values of the associated parameters (see Table 1), the bounds on swimming rate, w_p , fall between $\sim 2 \text{ m day}^{-1}$ and $\sim 40 \text{ m day}^{-1}$, the shaded area in Figure 5.

We can estimate the bounds on swimming rate required for plankton to enter other river plumes. Table 2 shows estimated bounds for them Kennebec, Columbia, and Mississippi. Both the Columbia and Mississippi river plumes have a much narrower bounds on the swimming rate, also apparent in higher values of $(H_{mix}H_{plume}/\kappa T)$, indicating that the frog tongue mechanism may be more selective in the types of organisms entrained, or less important generally. However, the values in Table 2 represent climatological values of wind stress, mixed layer depth and plume characteristics. Particular events may have characteristics such that very different classes of plankton may become entrained in the plume.

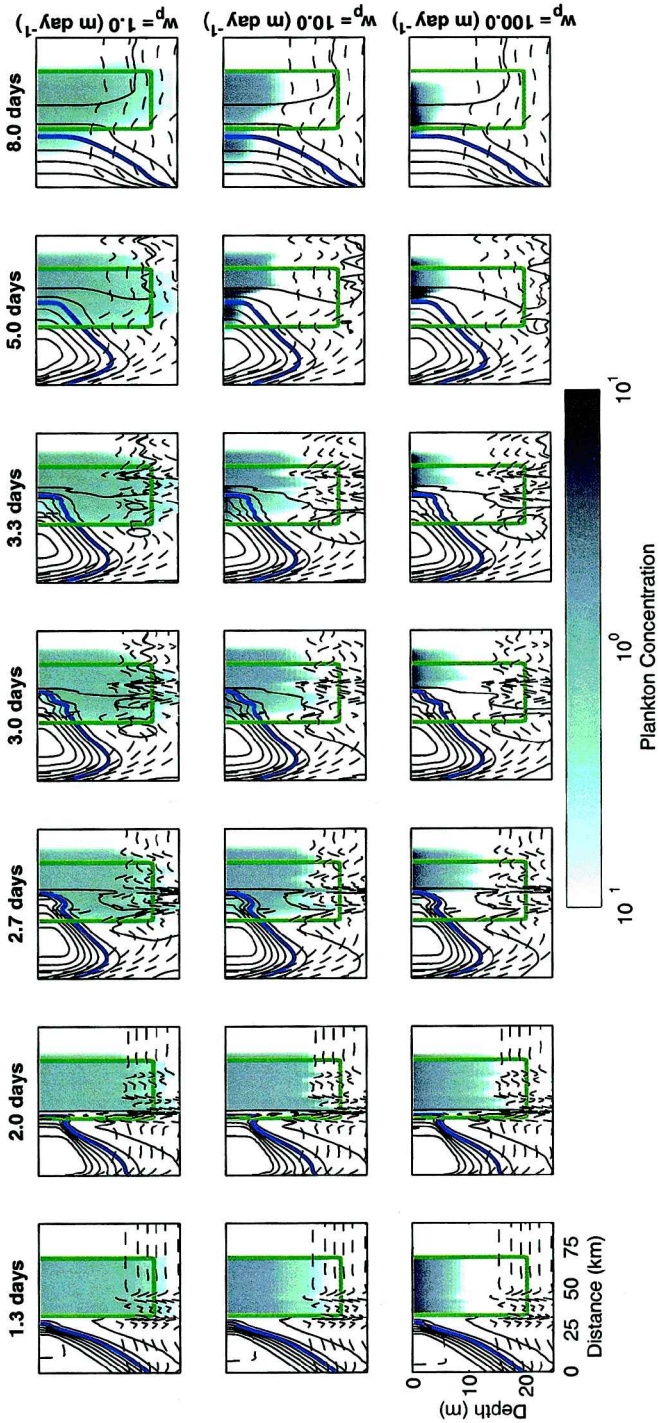


Figure 4. A figure showing the structure of the plankton patch in a sequence of snapshots in time for three representative swimming strengths. The timeline is *not* linear; snapshot times were chosen to best highlight the movement of the plankton patch.

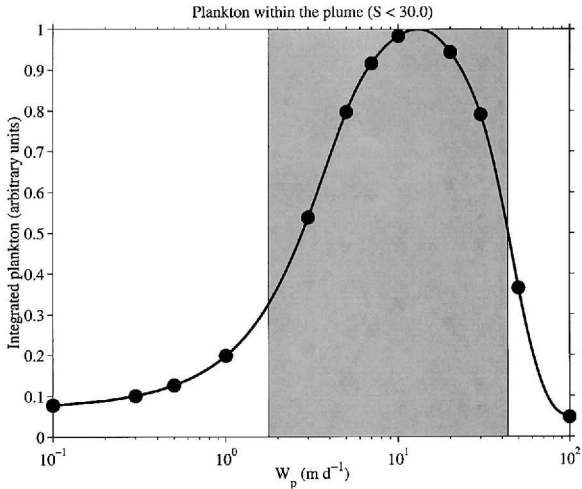


Figure 5. Integrated plankton within the plume (defined functionally as water with salinity less than 30.0 psu) after downwelling. The shaded box represents the estimated limits on w_p defined in equation 10.

4. Discussion

As alluded to in the introduction, the notion of a ‘sweet spot’ in vertical swimming speed (Fig. 5) is related to the more general problem of planktonic aggregation at fronts. For example, Franks (1997) demonstrates how upward-swimming organisms can accumulate behind the leading edge of a propagating baroclinic front (also see Franks, 1992; Epstein and Beardsley, 2001). Franks used a two-layer (reduced gravity) model to simulate a homogeneous, uniformly propagating buoyant layer with a frontal outcrop. Plankton enter the buoyant layer immediately upon crossing the infinitesimally thin pycnocline, and maintain their position relative to the front thereafter. The plankton are pushed beneath the

Table 1. Parameters used in estimating the limits of W_p (Eq. 9) are listed. The bottom four parameters are those used to estimate H_{plume} from Eq. 3.

Parameter	Value
κ	$0.01 \text{ m}^2 \text{ s}^{-1}$
T	3 days
H_{mix}	20 m
H_{plume}	5.3 m
f	$1.0 \times 10^{-4} \text{ s}^{-1}$
Ri_c	0.3
$\max(\tau)$	$2 \times 10^{-4} \text{ m}^2 \text{ s}^{-2}$
$\Delta\rho/\rho_0$	0.0032

Table 2. Parameters used in estimating the bounds of W_p (Eq. 9) for various plumes are shown. Constant values of κ were chosen because the large mixed layer depths caused the estimate of κ from Eq. 7 to be unreasonably large. Physical parameters represent typical spring forcing [see Fong *et al.* (1997), Hickey *et al.* (1998), and Murray *et al.* (1997)], although there may be significant variations in these parameters for specific timeframes.

	H_{mix} (m)	H_{plume} (m)	T (days)	κ ($m^2 s^{-1}$)	w_{min} ($m d^{-1}$)	w_{max} ($m d^{-1}$)	$\frac{H_{mix}H_{plume}}{\kappa T}$
Kennebec	20	5	2–7	0.01	2	40	0.017–0.059
Columbia	80	10	2–10	0.01	1	10	0.10–0.20
Mississippi	50	10	4–5	0.01	2	20	0.11–0.14

plume by the strong downward vertical velocities near the nose of the propagating front. Swimming speed primarily affects the location of a concentrated plankton patch that forms relative to the front: Slower swimming plankton will create a patch further behind the front. Organisms with no directed motion through the water are simply subducted underneath the front, and do not enter the overlying buoyant water. Thus, as in the model presented herein, the degree of cross-frontal movement in the Franks model (interpreted here as how far into the buoyant layer the organisms accumulate) depends strongly on the swimming speed. However, the qualitative characteristics of this dependence are quite different in the two cases: Franks' model predicts an inverse relationship for non-zero upward swimming, whereas the present model suggests a more parabolic relationship between swimming rate and cross-frontal exchange. The reduction in cross-frontal exchange at low swimming speeds in the present model arises primarily from the time-dependence of the frontal motion—an effect not included in the Franks model.

Another difference between the classic models of frontal aggregation and the present model is in the way the vertical plankton distribution outside the plume is maintained. For example, Franks (1997) assumes depth dependent vertical swimming speed that decreases near the surface. This prevents plankton from aggregating very near the surface on short time scales, but will never reach a steady state. Our model assumes that stirring the mixed layer will counteract swimming, and help maintain a more uniform vertical plankton distribution within the mixed layer in the weak swimming case. If diffusion in the mixed layer is included, it is possible to reach a steady state in the vertical plankton distribution within the mixed layer; no steady state is possible with only vertical swimming (Epstein and Beardsley, 2001).

5. Conclusions

This paper presents a mechanism by which plankton may be transported shoreward through a combination of physics and simple behavior. In fact, the plankton do not need to change their behavior to take advantage of this mechanism—perpetual upward swimming suffices. The other requirement is that the buoyant plume override the plankton patch, and remain long enough for plankton to enter into it. This is not so much governed by the

physics of the plume, but the timing and magnitude of the wind forcing. In a given season, there are many upwelling and downwelling events; typical timescales for the weather band are 3 days to one week. If a plankton patch is offshore of a coastally trapped buoyant plume, there will be a number of opportunities for the patch to become entrained into the plume.

It is possible that the basic mechanism described here may be applicable to other situations in which plankton are intermittently subducted beneath lighter water, for example, a meandering jet or propagating eddy. The criteria may be modified for other physical situations, providing the fundamental constraints on the swimming speed are satisfied:

- Upper limit: The plankton swim slowly enough so that they are subducted beneath the propagating buoyant water.
- Lower limit: The plankton must swim quickly enough to enter the overlying buoyant water before the currents shift and the plankton are obducted to their original position.

There are many simplifying assumptions made in this work. Real buoyant plumes and plankton patches are fully three-dimensional features, and along-shore variations may play a crucial role in determining the interaction between real buoyant plumes and patches of plankton. Also, this model contains no biological behavior other than swimming. Actual plankton will grow and die depending on environmental conditions and trophic interactions. For all of these reasons it is very difficult to test an idealized model such as this one via direct comparison with observations. However, despite the many simplifications, this model captures the essence of a mechanism that allows plankton to become entrained into a buoyant plume.

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REFERENCES

- Anderson, D. M. and K. D. Stolzenbach. 1985. Selective retention of two dinoflagellates in a well-mixed estuarine embayment: the importance of diel vertical migration and surface avoidance. *Mar. Ecol. Prog. Ser.*, 25, 39–50.
- Bary, B. M. 1967. Diel vertical migrations of underwater scattering, mostly in Saanich Inlet, British Columbia. *Deep-Sea Res.*, 14, 35–50.
- Csanady, G. T. 1977. Intermittent ‘full’ upwelling in Lake Ontario. *J. Geophys. Res.*, 82(3), 397–419.
- Cullen, J. J. and J. G. MacIntyre. 1998. Behavior, physiology and the niche of depth-regulating phytoplankton, in *The Physiological Ecology of Harmful Algal Blooms*, D. M. Anderson and A. D. Cembella, eds., Springer-Verlag, 559–579.
- Cushman-Roisin, B. 1994. Introduction to Geophysical Fluid Dynamics. Prentice Hall, 320 pp.
- Epifanio, C. E. and R. W. Garvine. 2001. Larval transport on the Atlantic continental shelf of North America: A review. *Estuar., Coastal Shelf Sci.*, 52, 51–77.
- Eppley, R. W., O. Holm-Hansen and J. D. H. Strickland. 1968. Some observations on the vertical migration of dinoflagellates. *J. Phycol.*, 4, 333–340.

- Epstein, A. W. and R. C. Beardsley. 2001. Flow-induced aggregation of plankton at a front: a 2-D Eulerian model study. *Deep-Sea Res. II*, 48, 395–418.
- Fong, D. A. and W. R. Geyer. 2001. Response of a river plume during an upwelling favorable wind event. *J. Geophys. Res.*, 106(C1), 1067–1084.
- Fong, D. A., W. R. Geyer and R. P. Signell. 1997. The wind-forced response of a buoyant coastal current: Observations of the western Gulf of Marine. *J. Mar. Syst.*, 12, 69–81.
- Franks, P. J. S. 1992. Sink or swim: accumulation of biomass at fronts. *Mar. Ecol. Prog. Ser.*, 82, 1–12.
- . 1997. Spatial patterns in dense algal blooms. *Limnol. Oceanogr.*, 42, 1297–1305.
- Franks, P. J. S. and D. M. Anderson. 1992. Alongshore transport of a toxic phytoplankton bloom in a buoyancy current: *Alexandrium tamarense* in the gulf of marine. *Mar. Biol.*, 112, 153–164.
- Fulton, J. 1973. Some aspects of the life history of *Calanus plumchrus* in the Strait of Georgia. *J. Fish. Res. Bd. Canada*, 30, 811–815.
- Garvine, R. W. 1987. Estuary plumes and fronts in shelf waters: A layer model. *J. Phys. Oceanogr.*, 17, 1877–1896.
- Haidvogel, D. B., H. Arango, K. Hedstrom, A. Beckmann, P. Malanotte-Rizzoli and A. Shchepetkin. 2000. Model evaluation experiments in the North Atlantic basin: Simulations in nonlinear terrain-following coordinates. *Dyn. Atmos. Oceans*, 32, 239–281.
- Hickey, B. M., L. J. Pietrafesa, D. A. Jay and W. C. Boicourt. 1998. The Columbia River Plume Study: Subtidal variability in the velocity and salinity fields. *J. Geophys. Res.*, 103(C5), 10,339–10,368.
- Large, W. G., J. C. McWilliams and S. C. Doney. 1994. Oceanic vertical mixing: A review and a model with a nonlocal boundary layer parameterization. *Rev. Geophysics*, 32, 363–403.
- McGillicuddy, D. J., R. P. Signell, C. A. Stock, B. A. Keafer, M. D. Keller, R. D. Hetland and D. M. Anderson. 2003. A mechanism for offshore initiation of harmful algal blooms in the coastal Gulf of Maine. *J. Plankton Res.*, (submitted).
- Murray, S. P. 1997. An observational study of the Mississippi-Atchafakya coastal plume: Final report. U.S. Dept. of the Interior, Minerals Mgmt. Service, Gulf of Mexico OCS Region, New Orleans, LA.: OCS Study MMS 98-0040, 513 pp.
- Olson, D. B. and R. H. Backus. 1985. The concentrating of organisms at fronts: A cold-water fish and a warm-core Gulf Stream ring. *J. Mar. Res.*, 43, 113–137.
- Price, J. F., R. A. Weller and R. Pinkel. 1987. Diurnal cycling: Observations and models of the upper ocean response to diurnal heating, cooling and wind mixing. *J. Geophys. Res.*, 92, 14,480–14,490.
- Townsend, D. W., N. R. Pettigrew and A. C. Thomas. 2001. Offshore blooms of the red tide dinoflagellate, *Alexandrium* sp., in the Gulf of Maine. *Cont. Shelf Res.*, 21, 347–369.
- Tyler, M. A. and H. H. Seliger. 1978. Annual subsurface transport of a red tide dinoflagellate to its bloom area: Water circulation patterns and organism distributions in the Chesapeake Bay. *Limnol. Oceanogr.*, 23, 227–246.

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