What is the windage of zooplankton? Turbulence avoidance and the wind-driven transport of plankton.

James M. Pringle[1]

[1]jpringle@cisunix.unh.edu

142 Morse Hall, UNH

39 College Str.

Durham, New Hampshire, 03824-3525

ABSTRACT

  Observations of turbulence avoidance in zooplankton are compared to estimates of the
wind-driven turbulence in the upper ocean. Turbulence avoidance is found to prevent the
transport of zooplankton in the surface Ekman layer at realistic wind speeds. Plankton that
avoid turbulence by moving deeper are no longer transported by the wind-driven Ekman
currents near the surface because they are no longer near the surface. Turbulence
avoidance is shown to lead to near-shore retention in wind-driven upwelling systems, and
to a reduction of the delivery of zooplankton to Georges Bank from the deeper waters of
the Gulf of Maine.

1.   Introduction

Some zooplankton species are observed leaving the surface ocean to avoid wind-forced
turbulence. *Incze et al.* [2001] examined a single wind event and found that copepodite
stages of *Temora* spp., *Oithona* spp. *Pseudocalanus* spp. and *Calanus finmarchicus* all
avoided wind driven turbulence. *Lagadeuc et al.* [1997] observed similar results in *Temora
longicornis* and *Pseudocalanus* spp.. and *Mackas et al.* [1993] found what appeared to be
turbulence avoidance in the feeding copepodite stages of *Eucalanus bungii* and
Neocalanus cristatus, but not in *N. plumchrus* or *N. flemingeri*. *Heath et al.* [1988]
observed turbulence avoidance in herring larvae, and similar behavior has been seen in
larval cod, haddock and hake [*Gallego and Heath*, 1999; *Lough and Mountain*, 1996;
Reiss et al., 2002].

   The origin of this behavior is not understood. The influence of turbulence on
zooplankton has been debated since *Rothschild and Osborn* [1988] argued that turbulence
would enhance encounter rates, and thus would benefit zooplankton feeding. It has since
been pointed out that at higher levels of turbulence, increased encounter rates could be
offset by decreased capture efficiency [*Kiørboe and Saiz*, 1995; *MacKenzie and Kiørboe*,
2000; *Sundby and Fossum*, 1990]. Others have pointed out that increased potential
encounter rates in turbulent waters could be offset by decreased prey density in the
turbulent water, leading to higher feeding rates in less turbulent water (*Franks* [2001] and
refs. therein). Observations in the field are contradictory, with some studies showing
enhanced feeding success in more turbulent waters, and others showing a negative
correlation (reviews in *MacKenzie* [2000] and *Visser and Stips* [2002]). Whether enhanced
encounter rates are beneficial to predators that are also potential prey has been little
discussed. Regardless of why turbulence avoidance is adaptive, it is credibly observed in

1

ecologically and economically significant species, so its implications for their transport should be explored.

Turbulence avoidance will greatly reduce the directly wind driven transport of plankton. The direct effect of wind-forcing is transmitted through the surface Ekman layer by turbulent momentum fluxes, and thus the Ekman layer is turbulent. Turbulence avoidance is nearly equivalent to Ekman layer avoidance. Plankton which remains in the Ekman layer will be moved to the right (in the northern hemisphere) of the wind, and can be moved five to tens of kilometers a day. Those that flee turbulence by moving downward out of the surface Ekman layer will not be transported in it.

Turbulence avoidance will be shown below to act as a retention mechanism in wind-driven coastal upwelling systems, keeping zooplankton from moving across the shelf. It will also be shown to alter the transport of copepods in the Gulf of Maine, helping to keep plankton that flee turbulence over the deeper interior basins, while those that remain in the surface Ekman layer are moved to the very different environments of to Georges Bank or the coast. Turbulence avoidance will be important anywhere the wind-driven transport of zooplankton is important.

In the following sections, the structure of the surface Ekman layer is described, and the strength of wind-forced turbulence in it is given. These results are used to quantify the wind strength needed to trigger turbulence avoidance, and then to describe the effects of turbulence avoidance on the transport of zooplankton. The importance of turbulence avoidance is then described for two regions, the wind driven coastal ocean and the Gulf of Maine, followed by a discussion of its larger importance.

2.   Method

Stratification and the Depth of the Ekman Layer– The depth of wind driven currents is set by the strength of the earth's rotation and by the strength of the vertical turbulent mixing of momentum [*Ekman*, 1905]. The strength of the vertical mixing is, in turn, set by the strength of the wind and by stratification.

In the absence of stratification, wind driven transport is largely confined above a depth of $\kappa u^* f^{-1}$ where f is the Coriolis parameter, κ is von Karmen's constant 0.41, and u^* is the velocity scale of the turbulence, given by $u^* = \left(\tau \rho_0^{-1}\right)^{-\frac{1}{2}}$ where τ is the wind stress and ρ_0 is the mean water density [*Madsen*, 1977]. The velocity turbulence scale u^* is about one-thousandth of the wind speed. The *Madsen* [1977] solution is recreated in

figure 1 with the General Ocean Turbulence Model [*Burchard et al.*, 1999] using the Mellor-Yamada level 2.5 turbulence closure with the *Galperin et al.* [1988] lengthscale limitations and stability functions. This turbulence closure scheme is well tested, and is capable of calculating not only diffusivity and currents, but also the profile of turbulence intensity. At depths below $\kappa u^* f^{-1}$, both the Ekman currents and the dissipation of turbulent kinetic energy ϵ, an indicator of the strength of turbulence, become small very quickly.

If the water below the surface mixed layer is stratified even after wind has been blowing for an inertial period, the stratification will trap turbulence in the surface well mixed region [*Pollard et al.*, 1973; *Price et al.*, 1986]. This can be seen in left hand side of figure 1, in which strong stratification has been inserted below the mixed layer at a depth less than $\kappa u^* f^{-1}$. This stratification arrests the turbulence and currents at the base of the mixed layer, so that there is little of either in the stratified waters. In observations, there are indications that a significant fraction of the Ekman transport extends below the mixed layer [*Lentz*, 1992], but usually most transport lies within it. Thus it is the lesser of the two depths, the mixed layer depth or $\kappa u^* f^{-1}$, that marks the lower limit δ_{Ek} of most of the wind-driven Ekman currents.

The Magnitude of ϵ in the Surface Ekman Layer– Many zooplankton are able to sense Kolmogorov scale shear in their environment (e.g. *Fields and Yen* [1997]), and so most studies of the interaction of zooplankton and turbulence have focused on ϵ, the dissipation of turbulent kinetic energy by viscous processes, for it scales as the square of the Kolmogorov scale shear [*Oakey*, 1985]. An entirely general estimate of ϵ in the surface ocean can only be made with complex and somewhat empirical numerical turbulence closure schemes. However, a simple scaling for ϵ can be made in the unstratified surface mixed layer in areas where the only source of energy is the wind and by assuming that the flow in the mixed layer can be treated as an irrotational turbulent boundary layer (e.g. *Oakey* [1985]):

$$\epsilon = \frac{u^{*3}}{\kappa z} \tag{1}$$

where z is the distance from the surface. *MacKenzie and Leggett* [1993] compared this estimate to direct measurements of ϵ, and found that it predicted the magnitude of the turbulence well, and explained 58% of the variace in ϵ in locations where wind forcing dominated the turbulence production (as opposed to, e.g. surface cooling). They did not

find wave breaking enhanced turbulence levels outside of the top few meters of the ocean (c.f. *Craig and Banner* [1994]). *Anis and Moum* [1995] discuss cases where wave breaking and surface heat fluxes become significant.

The boundary layer scalings do not include the effects of rotation and the entrainment of buoyancy from beneath the mixed layer, both of which would reduce the turbulence. To estimate this reduction, ϵ was calculated with the General Ocean Turbulence Model (GOTM) [*Burchard et al.*, 1999] and the turbulence closure described above. The GOTM model was run with a windstress which varied from 0.005 to 0.2 Pa, a Coriolis parameters representative of either $30°$ or $60°$N, and stratifications of $N^2 = 0$, 10^{-4} and 4×10^{-4}, for a total of 240 model runs. The model was started from rest, and the wind applied in two steps- half strength for the first half inertial period, and full strength thereafter. This two step forcing greatly reduces the inertial oscillations after an inertial period [*Mellor and Strub*, 1980]. The dissipation ϵ was measured after four inertial periods. In all cases, the boundary layer estimate of ϵ was within a factor of four of the more complex numerical turbulence closure scheme. This discrepancy is consistent with the results of *MacKenzie and Leggett* [1993].

Both the numerical modeling and the boundary layer approximations for ϵ will miss turbulence generated by infrequent, large amplitude mixing events such as inertial oscillations induced by abrupt wind shifts and mixing caused by large amplitude internal solitons. These infrequent events can dominate the net mixing. But, as the work of *MacKenzie and Leggett* [1993] shows, most of the time turbulence levels in the surface mixed layer are controlled by wind strength. It is, presumably, these more common turbulence levels that zooplankton respond to, not the extremely infrequent but very intense events.

What strength wind can cause plankton to flee the surface? There are relatively few direct simultaneous measures of turbulent dissipation and zooplankton abundance in the surface mixed layer and immediately below, and thus little guidance to the amount of turbulence needed to cause zooplankton to move below the surface mixed layer. *Incze et al.* [2001] measured the vertical profile of ϵ and the abundance of copepodite and naupliar stages of *Temora* spp., *Oithona* spp. *Pseudocalanus* spp. and *Calanus* finmarchicus on the southern flank of Georges Bank for several days through a wind event. They found that all but *Temora* spp. nauplii moved into stratified waters from the surface mixed layer at the onset of the wind event in order to stay in waters of $\epsilon = 10^{-8}$ W kg^{-1} or less. The ϵ in the waters above increased to greater than $\epsilon = 10^{-6}$ W kg^{-1}. *Lagadeuc et al.* [1997] found

that *Temora longicornis* and *Pseudocalanus* sp. (but not *Oithona similis*) left the surface mixed layer for deeper stratified waters when the wind-driven turbulence in the surface mixed layer was estimated to exceed $1.88 \times 10^{-7} \mathrm{W\,kg}^{-1}$. *Visser et al.* [2001], in a similar study, found a significant response of *Oithona similis* to measured turbulence in the North Sea, with stronger turbulence leading to deeper average depths of both the copepods and their copepodites in a region where mixed layer ϵ was nearly always above 10^{-7}, and the maximum abundance of *O. similis* was already in the stratified pycnocline below the mixed layer. *Incze et al.* [1996] found that most unsorted copepod nauplii on Georges Bank were more likely to be found in stratified low turbulence water of the mid-water column. *Reiss et al.* [2002] found that hake larvae less than 5 mm and copepodites on the Scotian Shelf avoided the turbulent surface waters and were associated with turbulence levels estimated to be below $10^{-7} \mathrm{W\,kg}^{-1}$, large Richardson numbers, and weak turbulence. *Lough and Mountain* [1996] found that larval cod were preferentially found in waters where ϵ was less than $10^{-7} \mathrm{W\,kg}^{-1}$, and haddock in even more quiescent waters. From this limited set of observations, $\epsilon_{\mathrm{crit}} = 10^{-7}\,\mathrm{W\,kg}^{-1}$ is somewhat arbitrarily chosen as the threshold level of TKE dissipation which triggers turbulence avoidance.

The turbulence levels cited above are those that, when exceeded in the mixed layer, cause plankton to leave the mixed layer. Thus when ϵ exceeds ϵ_{crit} in the Ekman layer, the zooplankton are not moved by the Ekman currents. The critical value of u^*, u^*_{crit}, above which ϵ exceeds ϵ_{crit} everywhere in the Ekman layer is (from (1))

$$u^*_{\mathrm{crit}} = \left(\kappa z \epsilon_{\mathrm{crit}}\right)^{\frac{1}{3}} \tag{2}$$

The critical value of u^* that induces zooplankton to leave the surface Ekman layer is then

$$u^*_{\mathrm{crit}} = \left(\kappa \epsilon_{\mathrm{crit}}(\text{mixed layer depth})\right)^{\frac{1}{3}} \tag{3}$$

if the mixed layer depth is less than $\kappa u^* f^{-1}$ and

$$u^*_{\mathrm{crit}} = \left(\kappa^2 \epsilon_{\mathrm{crit}} f^{-1}\right)^{\frac{1}{2}} \tag{4}$$

if the neutral Ekman depth $\kappa u^* f^{-1}$ is less than the mixed layer depth. In the latter case, for typical mid-latitude values of the Coriolis parameter, $f = 10^{-4}\,\mathrm{s}^{-1}$, $u^*_{\mathrm{crit}} = 0.01\,\mathrm{m\,s}^{-1}$, roughly corresponding to a $10\,\mathrm{m\,s}^{-1}$ wind. In the former case, u^*_{crit} is about $0.01\,\mathrm{m\,s}^{-1}$ for a 40 m mixed layer and $0.006\,\mathrm{m\,s}^{-1}$ for a 5 m mixed layer (corresponding roughly to 10 to $6\,\mathrm{m\,s}^{-1}$ winds). Thus 5 to 10 $\mathrm{m\,s}^{-1}$ winds are sufficient to drive the turbulent sensitive species discussed above out of the Ekman circulation. The extent to which this can be

generalized to other populations in other places depends on the variation of ϵ_{crit} between species, life stages and individuals, an important matter for future study.

Once ϵ has exceeded ϵ_{crit} and zooplankton begin to sink or swim downward, turbulence does not hinder their ability to leave the surface Ekman layer. *Franks* [2001] showed that turbulence can only speed the flight of downward swimming or sinking organisms from the upper ocean. Even neglecting the role of turbulence in clearing the surface waters, for typical copepod and fish larvae swimming speeds of 0.001 to $0.02\,\text{m}\,\text{s}^{-1}$, and Ekman depths of order of tens of meters, the plankton can leave the Ekman layer in well less than an inertial period, and thus before the wind driven Ekman transport is established. The zooplankton thus leave before being transported to right (in the northern hemisphere) of the wind.

Thus for moderate and stronger winds, those exceeding 5 to $10\,\text{m}\,\text{s}^{-1}$, the turbulence avoiding species discussed above are not likely to be strongly moved by the surface Ekman transport. These results can be extended to other species by quantifying ϵ_{crit} for those species.

3. Results

Any plankton population dynamics involving the advection of plankton in the upper ocean would be strongly modified by turbulence avoidance. The average velocity in the surface Ekman layer is roughly $\tau \, (\rho_0 f \delta_{\text{Ek}})^{-1}$, which, for reasonable mid-latitude parameters ($10\,\text{m}\,\text{s}^{-1}$ winds, $f = 10^{-4}\,\text{s}^{-1}$, and $\delta_{\text{Ek}} =$10m) is a current of about $0.1\,\text{m}\,\text{s}^{-1}$ or about 10 kilometers a day. Plankton that avoid turbulence avoid this transport. The significance of this avoided transport is illustrated in two scenarios below: a coastal upwelling system, and the Gulf of Maine during the winter.

Turbulence Avoidance and Retention in an Upwelling System– Phytoplanktivorous zooplankton in an upwelling system face a dilemma: near-surface upwelled waters is often quickly filled with a phytoplankton bloom – but if the zooplankton grazers are already in the surface waters, they are swept offshore by the surface Ekman transport and never enter the newly upwelled water. Turbulence avoidance would help them avoid this fate.

Within an inertial period of the onset of an upwelling favorable wind, an offshore transport is generated in the surface Ekman layer. In a moderately stratified ocean with no great alongshore variation, this offshore transport is balanced first by an onshore transport

6

spread throughout the water column, and then, after a frictional spindown time (1-5 days on most shelves), an onshore transport in the bottom Ekman layer forced by a barotropic alongshore downwind flow [*Austin and Lentz*, 2002; *Dever*, 1997]. Turbulence avoidance would make the zooplankton leave the surface region of offshore transport (figure 2). The zooplankton would then move a small distance onshore in the initial period where the return flow is spread throughout the water column, and then would move mostly alongshore in the direction of the alongshore component of the wind as onshore flow was limited to the turbulent bottom boundary layer. When the winds subside, the turbulence will subside, and the zooplankton could rise into the newly upwelled waters.

Barange and Pillar [1992] may have observed retention in an upwelling zone caused by turbulence avoidance. They found that on the Namibian shelf, the larvae of the euphausid *Nyctiphanes capensis* remains within 25 km of the shore despite persistent active upwelling. They attribute this to the vertical distribution of the larvae, for the larvae remain immediately below the Ekman layer, consistent with turbulence avoidance. Unfortunately, there is no data showing that this vertical distribution arises from turbulence avoidance, and not some other environmental cue.

Turbulence avoidance is not the only way zooplankton could avoid significant cross-shelf transport during upwelling events. Others have pointed out that diel migration could slow cross-shelf transport by reducing the fraction of time the plankton spends in the surface, e.g. *Giraldo et al.* [2002]. It is worth noting, though, that diel migration has been observed to interact with turbulence avoidance. *Lagadeuc et al.* [1997] found that *Temora longicornis* only moved into the surface waters when turbulence was weak. Whether this interaction between turbulence avoidance and diel vertical migration leads to a net onshore motion depends on the depth of the migration and the vertical distribution of the return flow.

Winter in the Gulf of Maine & Turbulence Avoidance– The population dynamics of copepods in the Gulf of Maine and Georges Bank is strongly influenced by their advection to and from the deeper waters of the Gulf to Georges Bank during the winter. This, in turn, depends on the vertical distribution of the copepods. *Hannah et al.* [1998] found that the delivery of water from the basins of the Gulf of Maine to Georges Bank was dominated by transport in the surface Ekman layers, and that the strongest influence on the delivery of zooplankton to Georges Bank was their position relative to the surface Ekman layer. Zooplankton below the Ekman layer were much less likely to attain the bank, especially

its crest (c.f. *Lynch et al.* [1998], *Miller et al.* [2000]). Studies of the circulation of the Gulf of Maine find that this occurs because the depth-averaged wind forced flows are primarily along-isobath, and, as can be seen in the model results of *Greenberg et al.* [1997] (figure 3), the most vigorous cross-isobath flows are confined to the surface Ekman layer. This is typical of weakly stratified coastal systems, where potential vorticity constraints limit cross-isobath motions outside of the surface and bottom boundary layers (e.g. *Pringle* [2002]).

A rough estimate of the importance of the directly wind-driven transport of copepods in the surface Ekman layer can be gleaned from the bi-monthly mean winds and mean hydrography. The January/February mean winds show considerable interannual variability (figure 4 taken from *Lewis et al.* [2001]), and are often strong enough to move copepods in the surface Ekman layer a good distance. The mean winter mixed layer in the Gulf of Maine is from 20 m [*Hannah et al.*, 1998] to 50 m [*Brown and Irish*, 1992] in depth, so that a mean wind of 0.08 Pa moves the surface mixed layer 80 to 200 km to the right of the wind – a respectable fraction of the width of the Gulf of Maine. Northeast winds (1976 and 1990) deliver organisms from over the deep basins of the Gulf to Georges Bank, Southeast winds (many years, including 1982 and 1979) from over the deep basins to Massachusetts and Nantucket Shoals and from the Scotian Shelf to Georges Bank, and southwest winds (1983 and 1993) from over the deep basins to the New Hampshire/Maine coast – but only if the copepods do not avoid turbulence and exit the surface Ekman layer. (While the mean winds may be less than the threshold needed to trigger turbulence avoidance, they are the average of many strong events in different directions, each which could trigger turbulence avoidance.)

However, in the *Incze et al.* [2001] Gulf of Maine study, only the *Temora* spp. nauplii would have been directly transported by the surface Ekman transport from over the deep basins to either the coast or the bank, for only they did not avoid the turbulence by moving deeper. But that data is from a single wind event in a different season (summer) at a different time in the copepods life cycle. It is only by understanding the specific turbulence avoidance behavior of the zooplankton present in the winter that we can accurately understand how they would be transported by the wind to the coast or Georges Bank.

4.   Conclusion

Turbulence avoidance, if triggered at moderate levels of ϵ, can dramatically and predictably alter the wind-driven transport of plankton. This would be ecologically important, as illustrated above. The biggest barrier to understanding how turbulence avoidance alters wind-forced transport is the lack of quantitative knowledge of the details of turbulence avoidance behavior.

Even without the expensive and difficult direct measurement of ϵ, much can be gleaned about the turbulence avoidance of zooplankton by stratifying vertical net tows with respect to the mixed layer depth, rather than at fixed depths. This would partition the tows into quiescent and potentially turbulent samples. Zooplankton samples so partitioned, or in existing samples taken solely in the mixed layer, could be examined with respect to the history of wind and buoyancy flux at the sampling site, providing statistical evidence for or against turbulence avoidance. It will only be after turbulence avoidance behavior has been quantified that its potentially large importance to the horizontal advection of different species and their life stages can begin to be understood.

5.   Acknowledgments

6.   References

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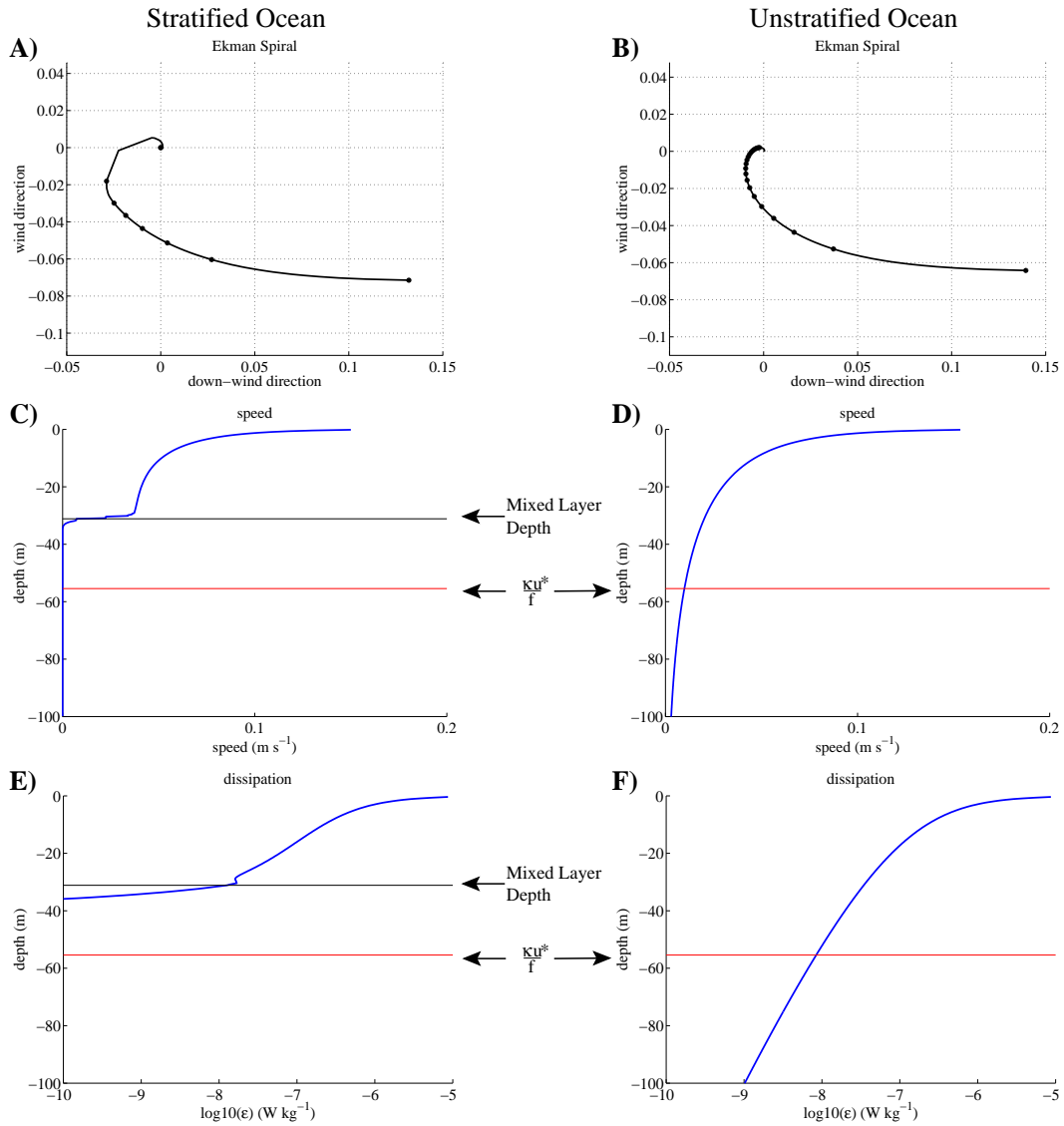
Figure 1: The wind driven currents and turbulence for two oceans – one stratified below 31 meters (left), the other unstratified (right). In both cases, $\tau = 0.1$ Pa. A&B) The Ekman spiral with and without stratification, respectively. Stars (*) every five meters. C&D) Vertical profiles of current speed. The mixed layer depth and the neutral Ekman depth $\kappa u^* f^{-1}$ indicated. E&F) Vertical profiles of turbulent kinetic energy dissipation.
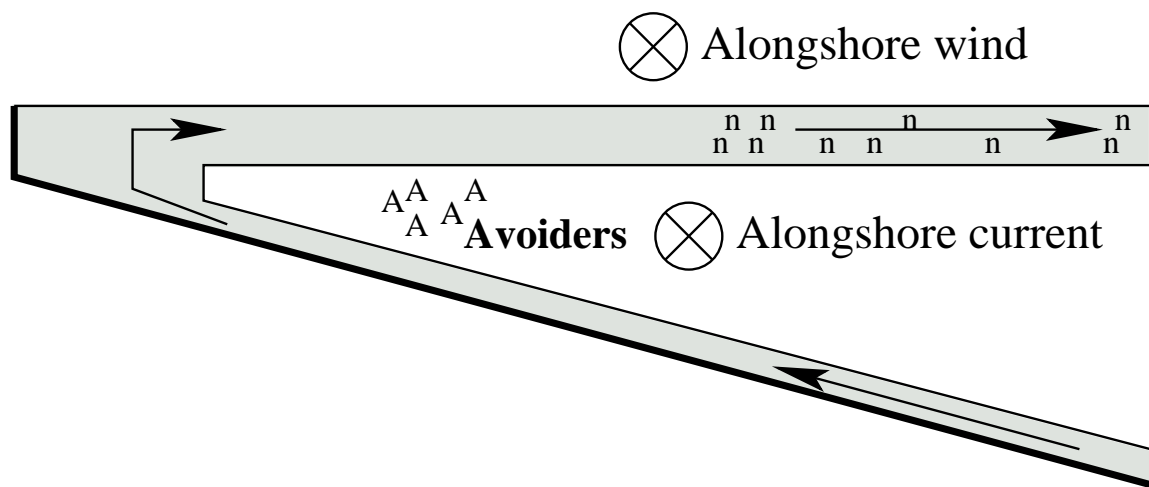
Figure 2: The cross-shore retention and alongshore transport of turbulence avoiding zoo-plankton ("A") in an upwelling zone, and the offshore transport of non-turbulence avoiders ("n"), in an idealized, two-dimensional, moderately stratified wind-driven upwelling system. The shaded regions are those of high turbulence, and include the surface and bottom Ekman layers.
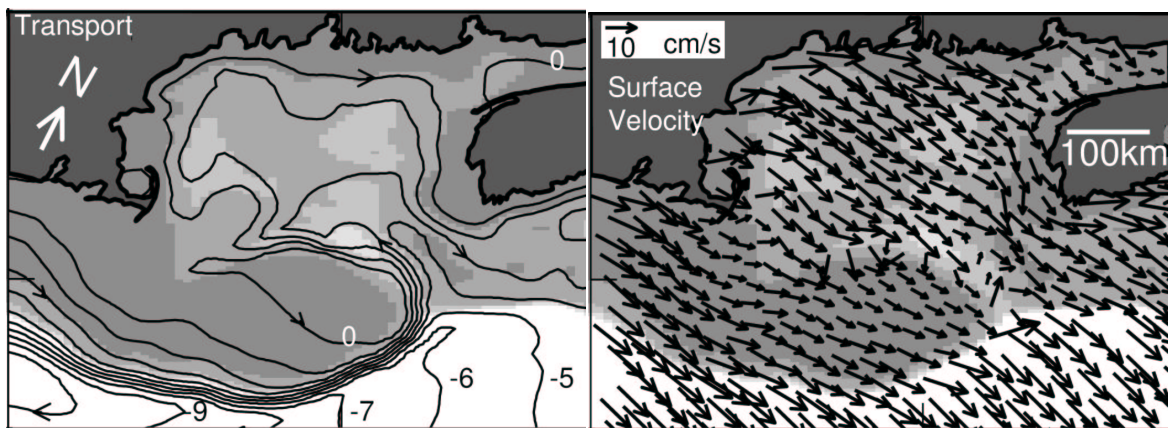
Figure 3: (Left) the depth averaged flow in units of 0.1 Sv forced by an alongshore wind (56°T, or from the left to the right of the figure). Note how flow on the shelf roughly follows the isobaths. (Right) near surface velocity in the surface Ekman layer. Note how it cross the isobaths. The bathymetry is indicated by shaded 100m bands for depths under 400m. From *Greenberg et al.* [1997].
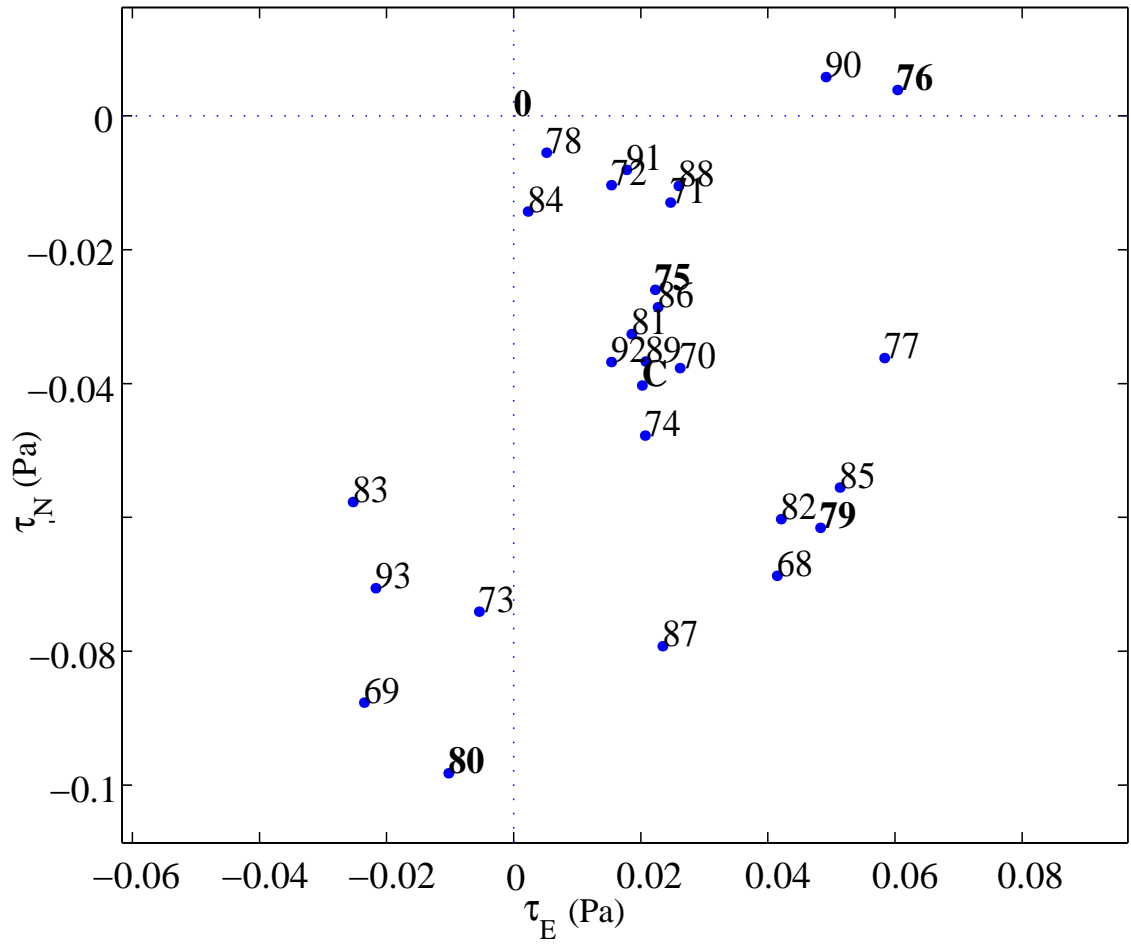
Figure 4: January/February mean windstress for the Gulf of Maine from 1963 to 1993. "C" indicates the climatological mean. From *Lewis et al.* [2001]