Copepod aggregations: influences of physics and collective behavior

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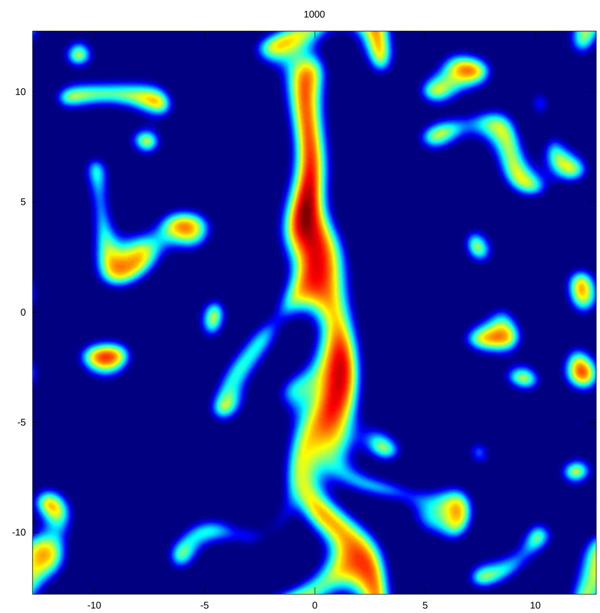


Motivation: copepods and whales

Right whales congregate in Cape Cod Bay during the spring and feed on the zooplankton (primarily *Calanus* copepods) blooming at that time. Most years, the copepods form very intense patches along tidal fronts off Provincetown or in the Great South Channel, and the whales cruise along these fronts.

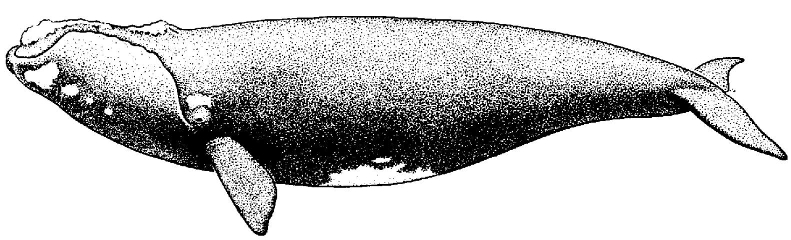
`Graphics:  map  Cape Cod Bay  Gulf of Maine [Manning, et al, 2009]`

Copepods: Calanus Finmarchicus

- LIFE HISTORY: (Tarrant et al., 2008; Durbin et al., 1997)
  - Pre-adults overwinter in "diapause"
  - Molt into adults and mate, hatch and molt through 13 stages
  - One or two generations per year
  - Eggs and nauplii stages are an important source of food for cod and haddock (Kane, 1984)
  - Later copepodite stages are the primary prey of right whales (Wishner et al., 1995) `Graphics: Prey species calanus [CCS] calanus [JHU, Lab Exp Fluid Dyn]`
- SWIMMING ABILITY: (Buchanan et al., 1982; Epstein and Beardsley, 2001; Genin et al., 2005; Lenz et al., 2004)
  - Typical: 0.1-10cm/s
  - Escape: Up to 80cm/s
- PATCHINESS: (Wishner et al., 1995; Beardsley et al., 1996; Baumgartner and Mate, 2003, Epstein, 1995)
  - SCOPEX study in the Great South Channel suggested densest patches coincide with salinity front.
  - Densest patches order 100-1000m across, 1-10m vertical, hours to days(?)
  - Peak densities 10^3 to 10^4 copepods/m^3. 10-1000 times background

Whales:

Copepod aggregations are a food source for many species, including the endangered right whales (*Eubalena glacialis*), which return to the southwestern GOM every spring to forage.



`Graphics: Predator species right whale underwater scale`

Outline:

- Vertical swimming and physics
- Horizontal convergence
- Social behavior
- Turbulent stirring
- Combined effects

Vertical swimming and physics

- Eulerian: $b(\mathbf{x}, z, t)$

$$\frac{\partial}{\partial t} b + \nabla_i (U_i b - K_{ij} \nabla_j b) = 0$$

  $\mathbf{U}$ and K_{ij} include both fluid motions, directed swimming, and drifts associated with variations in random motion.

- Concentration can only increase if biological velocities in $\mathbf{U}$ are convergent.
- Dominant directed motion is vertical swimming $w_s(z, t)$

$$\frac{\partial}{\partial t} b + \nabla \cdot (\mathbf{u} b - K \nabla b) + \frac{\partial}{\partial z}([w + w_s] b - K_v \frac{\partial}{\partial z} b) = 0$$

  (with $\mathbf{u}$ and ∇ being horizontal).

- strong swimming and randomness with preferred depth

$$\frac{\partial}{\partial z}(w_s b - K_v \frac{\partial}{\partial z} b) \simeq 0$$

$$\Rightarrow b = b'(\mathbf{x}, t) F(z) \quad \text{with} \quad \frac{\partial}{\partial z} \ln F = w_s / K_v$$

- Depth integrated equation ($\int dz\, F \equiv 1$)

$$\frac{\partial}{\partial t} b' + \nabla \cdot (\tilde{\mathbf{u}} b' - \tilde{K} \nabla b') = 0 \quad , \quad \tilde{\mathbf{u}} = \int dz\, F \mathbf{u} \quad , \quad \tilde{K} = \int dz\, F K$$

  Velocities $\tilde{\mathbf{u}}$ are divergent and have an associated stretching s

$$s = -\nabla \cdot \tilde{\mathbf{u}} = \int F \frac{\partial w}{\partial z}$$

If F is very sharply peaked, the velocities and stretching are just the horizontal flows and $\frac{\partial w}{\partial z}$ at the preferred depth; in any case, we'll drop the tilde and prime and use

$$\frac{\partial}{\partial t}b + \nabla \cdot (\mathbf{u}b - K\nabla b) = 0$$

or

$$\frac{\partial}{\partial t}b + \mathbf{u} \cdot \nabla b - \nabla \cdot K\nabla b = sb$$

Later the social movement will be included in $\mathbf{u}$. `Graphics: Lagrangian D/Dt ln b = s along-track integrals`

Steady state patches

$$\mathbf{F} = \mathbf{u}b - K\nabla b = \hat{\mathbf{z}} \times \nabla \chi$$

Gain insight from $K = const.$ and $\mathbf{u} = -\nabla \phi$

$$\nabla \ln b = -\frac{1}{K}\nabla \phi$$

$$b = b_0 \exp(-\phi/K)$$

Linear geometry

1) Pure strain $u = -U(x/L)$, $\phi = \frac{1}{2}UL(x/L)^2$
2) Localized front $u = U_0 - U\tanh(x/L)$, $\phi = -U_0 x + UL\ln[\cosh(x/L)]$

2a) $U_0 > U$ then $\mathbf{u}b - K\nabla b = (U_0 - U)b_{-\infty}$ $(\chi \neq 0)$

3) Localized velocities $u = -U(x/L)\exp(-x^2/2L^2)$, $\phi = -UL\exp(-x^2/2L^2)$ `Graphics: one d purestrain localfront u0=0.2 u0=0.5 u0=1.2 localvel`

Steady solutions exist with $b \to 0$ for cases 1, 2 but are proportional to the upstream value for 2a, 3. $U_0 = U$ does not have steady solutions (diffusively growing region). The amplitude depends on the Pèclet number of the convergent flow ϕ/K.

`Graphics: t 1/2 development max`

2D steady

Decompose the velocities

$$\mathbf{u} = \mathbf{u}_\psi - \nabla\phi$$

There is a solution $b = b(\phi)$

$$\nabla \ln b = -\frac{1}{K(\phi)}\nabla\phi$$

if K, ϕ, and ψ contours are parallel.

Ekman transport from bottom friction or eddy-wind effect (stress related to $\mathbf{W} - \mathbf{u}$) indeed has the divergent flow perpendicular to the rotational flow. For a bottom boundary layer, linear Ekman theory gives $\phi \simeq \frac{1}{2}\psi$.

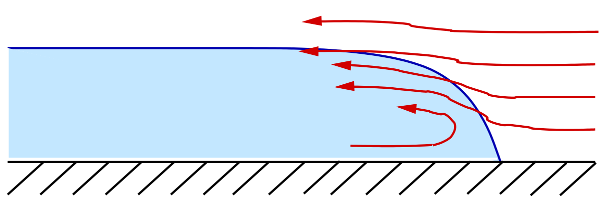
Time dependence and spatial inhomogeneity

Time scales:

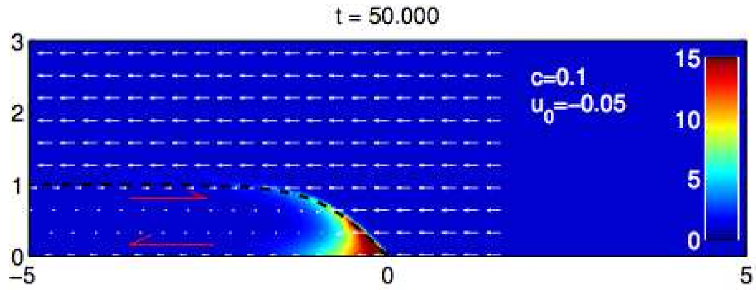
- Homogenization along ψ lines
- Initial growth (exponential)
- linear growth as b fluxes in
- equilibration when outward diffusive flux compensates `Graphics: example swirling flow maximum`

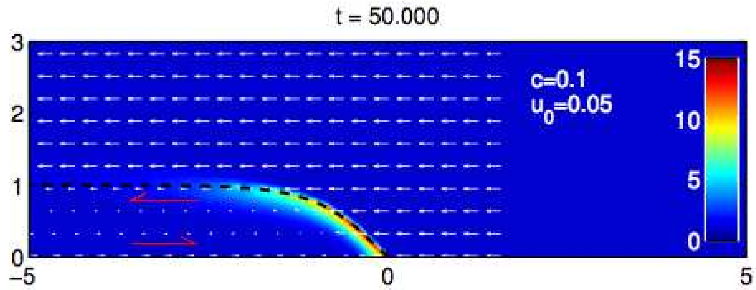
Buoyant plume

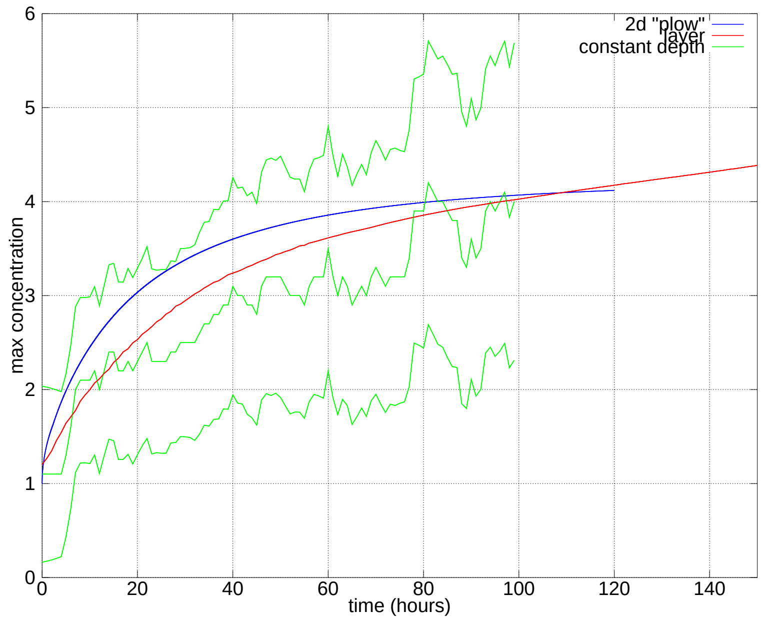
Buoyant fresh plumes from snowmelt run down the coast, enhancing the normal coastal jet. Can they "snowplow" up enough copepods?



Interior plume-relative circulation may be either sign.





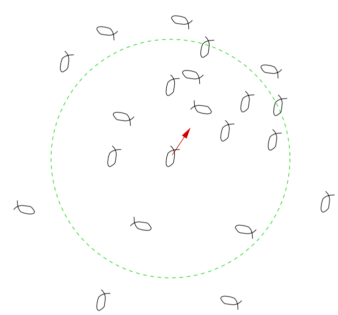


Physics would need to act on long times, gather copepods from large areas, and have small turbulent losses

Social behavior

Desirable features of the social grouping model we shall consider include:

1) Spontaneous break-out of patchiness. Not surprisingly, this tends to occur at the sensing scale.
2) Shear resistant. Patches should be maintained under reasonable shear or strain in the fluid flow.
3) Sticky. If two patches are brought near enough by the eddies or other motions, they should coalesce to form a larger patch which can hold together.
4) Potential for large-scale patches. If patches begin to coagulate, but then break apart again, dense aggregations on a scale much bigger than the sensing scale are unlikely.



For the n^{th} organism,

$$
\begin{aligned}
d\mathbf{X}^{(n)} &= \mathbf{V}^{(n)} dt \\
d\mathbf{V}^{(n)} &= -r(\mathbf{V}^{(n)} - \mathbf{u} - \mathbf{u}_b)dt + d\mathbf{W}
\end{aligned}
$$

$\mathbf{u}_b[b]$: preferred swimming velocity
$d\mathbf{W}$: a random increment $\langle d\mathbf{W} \rangle = 0$, $\langle dW_i dW_j \rangle = 2K_b r^2 \, dt \, \delta_{ij}$
$K_b[b]$: biological diffusivity associated with random swimming

Translates to

$$
\frac{\partial}{\partial t} b + \nabla \cdot \left[\mathbf{u}b + \mathbf{u}_b b - \frac{1}{r}\nabla(rK_b)b - (\kappa + K_b)\nabla b \right] = 0
$$

- $K_b = const.$
- $\mathbf{u}_b = -\nabla\phi_b$
  - Local density: $\beta(\mathbf{x}) = \iint d\mathbf{x}' \, w(\mathbf{x} - \mathbf{x}')b(\mathbf{x}')$
  - Weighting function $w(r) = \frac{3}{\pi a^2}(1 - r^2/a^2)^2$ $(r \leq a)$
  - Potential: $\phi_b = -Ua\beta/(1 + \beta)$

Stability of uniform states

For $b = \overline{b} + A(t)\exp(\imath\mathbf{k}\cdot\mathbf{x})$, we have

$$\frac{\partial}{\partial t}A = |\mathbf{k}|^2(\overline{b}\Phi(|\mathbf{k}|) - K_b)A$$

with

$$\Phi(|\mathbf{k}|) = \frac{Ua}{(1+\overline{b})^2}\iint d\mathbf{x}' w(|\mathbf{x}'|)\exp(\imath\mathbf{k}\cdot\mathbf{x})$$

implying instability for

$$Pe\,\frac{\overline{b}}{(1+\overline{b})^2} > 1$$

with $Pe = Ua/K_b$ the Pèclet number for the organism's taxis velocity. `Graphics: critical curves linear log example`

Note: both low and high densities are stable; thus a large, dense patch will not break up by the behavioral processes.

Patch sizes

$$b = b_0\exp(-\phi_b/K_b) = b_0\exp\left(Pe\frac{\beta}{1+\beta}\right)$$

Iteration: $b \to \beta \to \exp(Pe\,\beta/[1+\beta]) \to b_0[\text{normalization}] \to b$ `Graphics: patch size max b area`

Shear:

$u = U_s\cos(k_0 y)$ `Graphics: shear merger example`

More complex flows

Unlike the purely physical problems where ϕ can become large and positive, and $\exp(-\phi/K)$ can decay towards zero, the social model has ϕ_b always negative so that in steady state $b \geq b_0 > 0$. b_0 is related to the far-field value:

$$b_\infty = b_0 \exp\left(Pe \frac{b_\infty}{1 + b_\infty} \right)$$

$$b_0 \simeq b_\infty / (1 + Pe\, b_\infty)$$

$$b \sim b_\infty + C e^{-kx}$$

- Each patch has an exponentially small field which attracts other patches.
- But it will also tunnel out along axes of divergence

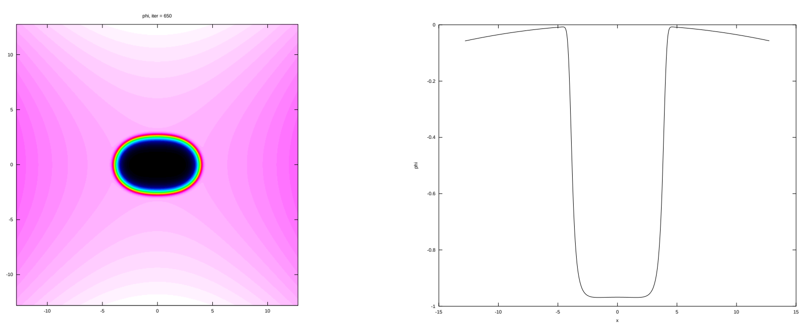
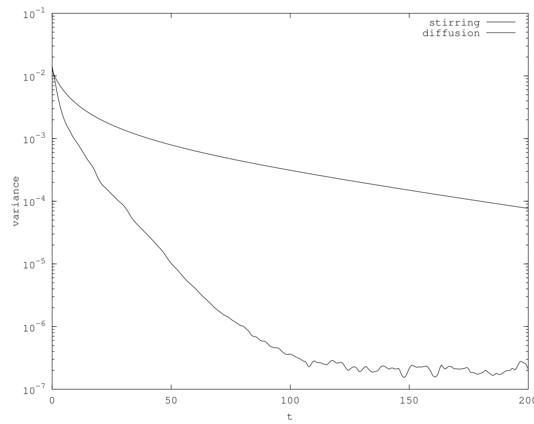


Fig. 20: The potential $\phi_{phys} + \phi_b$; the highest values are at the north and south, and it gets more negative to the east and west as shown on the east-west cross-section.

Stirring

$$\psi = \frac{U_s}{k\sqrt{7}} \Big[\cos(kx + \frac{\theta_{x1}}{3}) \cos(ky + \frac{\theta_{y1}}{3}) + \cos(2kx + \theta_{x2}) \cos(3ky + \theta_{y2}) + \cos(3kx + \theta_{x3}) \cos(2ky + \theta_{y3}) \Big]$$

$k = 2\pi/W$, θ_{xj} and θ_{yj}: independent random walks with $\delta\theta = 0.02$ for a time step of 2^{-9}.



`Graphics:  stirring  stirring plus social`

All together now...

Central point

1) Weak convergence and swirl

$$\phi = -0.1\psi \quad , \quad \psi = U_v L_v \exp(-\frac{1}{2}[x/L_v]^2 - \frac{1}{2}[y/L_v]^2)$$

2) Social grouping

$$\phi \leftarrow \phi + \phi_b \quad , \quad \phi_b = -Ua\frac{\beta}{1+\beta} \quad , \quad \beta = \iint d\mathbf{x}' w(\mathbf{x} - \mathbf{x}')b(\mathbf{x}')$$

3) Stirring

$$\psi \leftarrow -U_f y + \psi_{stir} \quad , \quad \phi \leftarrow \phi - 0.1\psi_{stir}$$

`Graphics:  center  physical  social  max b`

Front

1) Frontal flow and convergence

$$v = V_0 \operatorname{sech}^2(x/L_v) \quad , \quad \phi = -0.1V_0 L_v \operatorname{sech}^2(x/L_v)$$

3) Stirring only in ψ, not ϕ.
`Graphics:  front  social  fraction in front`

Summary

- Physical convergence is probably not strong enough, extensive enough, steady enough to enhance the concentration that dramatically
- Social behavior can produce large densities but on small scales; however some forms of behavior allow patches to merge into larger, stable aggregations.
- Stirring feeds small patches into the region of convergence where they can merge with the larger aggregations and, to some degree, resist detrainment
- The resulting dense aggregations are large compared with the se4nsing scale but small compared to the convergent regions (part of making b much larger than physics alone).
- In the ocean, this is probably involves a whole chain of merging processes, from individuals to social patches, then groups combining to larger groups, ... while the convergence acts overall.

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