How does the ocean's circulation alter the dispersal life-history of benthic coastal organisms?

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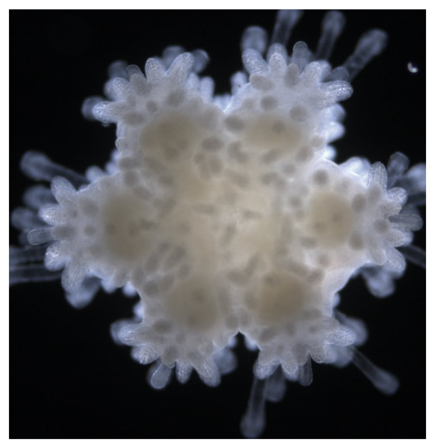
1: There are two dominant dispersal modes

Most benthic species have either well provisioned larvae that move only a short distance from their parents after a planktonic duration of a few days or less: E.g. this Leptasterias which broods in the mother for months:

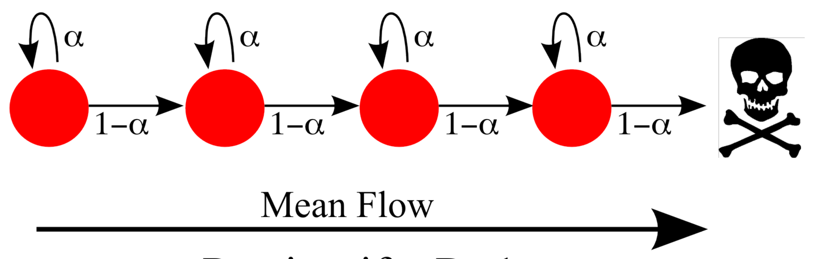


Or very many smaller larvae that can drift for tens of days, and will actively eat and grow in the plankton, as in this gastropod larvae:

Pictures from: http://invert-embryo.blogspot.com/2011_05_01_archive.html

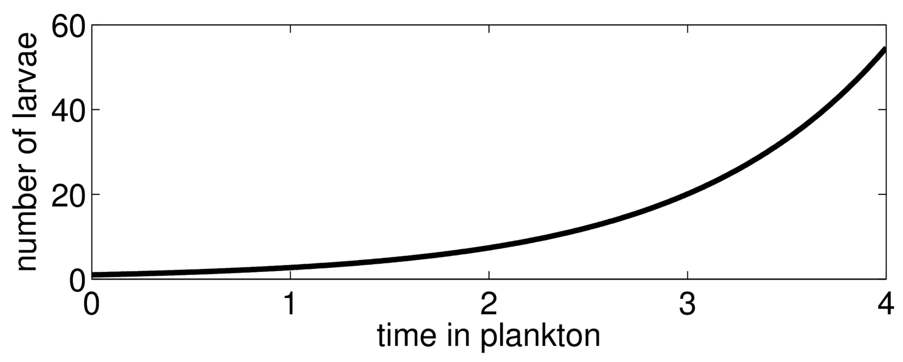
2: Long distance dispersal has tradeoffs

The upstream most edge of a species range is maintained by the few larvae that are returned there by stochastic processes (eddies that move larvae against the mean currents, etc). If this does not happen, the species will go locally extinct there, and eventually everywhere!



Persists if $\alpha R>1$

But if your larvae can eat and grow large enough to settle on their own, then the maternal investment per larvae goes down, and each parent can have more children for the same effort if mortality in the plankton is low!



3: A simple quantitative model of dispersal

(All of the science really resides here; the rest is just math)

Assume mean downstream dispersal L_{adv} scales linearly with time in plankton T_{PLD} and mean current, and stochastic dispersal L_{diff} scales as a diffusive process scaled by the standard deviation of the currents and the timescale of fluctuations.

$$\text{Mean dispersal } L_{adv} = UT_{PLD}$$

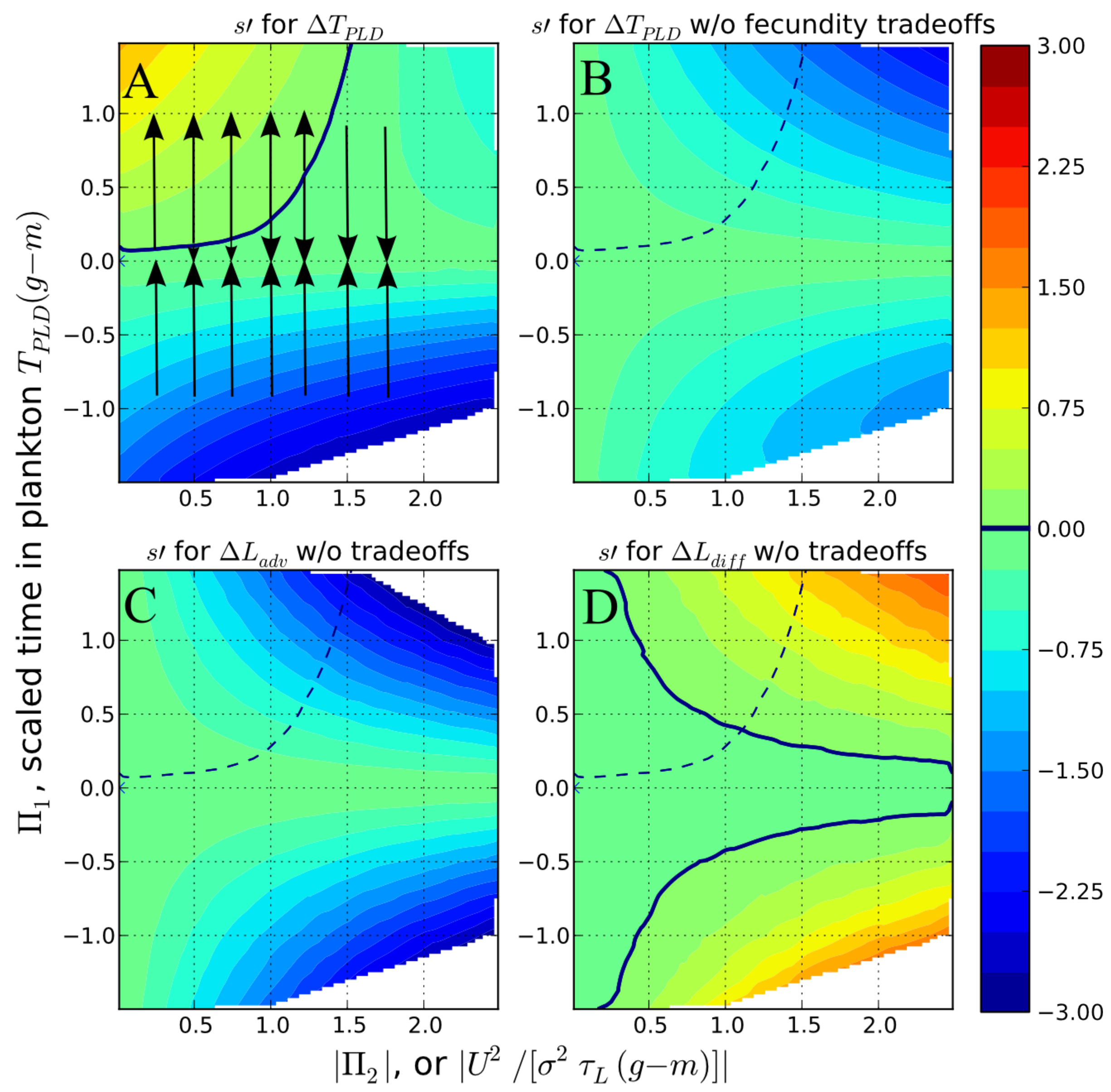
$$\text{Stochastic dispersal } L_{diff} = (\sigma^2 \tau_L T_{PLD})^{0.5}$$

Assuming steady growth and mortality of the larvae per time, that mom has fixed maternal investment for reproduction, and that larvae must grow to reach a certain size before recruitment, leads to a realized fecundity R that is exponential in time in plankton T_{PLD} and growth less mortality, $(g\text{-}m)$

$$\text{Realized fecundity } R \propto \exp[(g\text{-}m)T_{PLD}]$$

Implement this simple population model in a linear domain with density dependence implemented through competition for finite habitat at point of settlement. Dispersal via Gaussian dispersal kernel. Two kinds of critters are introduced with slightly different dispersal strategies (detailed latter), and there relative fecundity is adjusted until they are equally competitive. The difference in fecundity is used to calculate the change in fitness caused by the change in dispersal strategies; results are shown in the central figure. See manuscript for justification of dispersal and reproductive relationships shown above.

Scaled Selection for 4 traits



A) the scaled selection for time in plankton, with fecundity tradeoffs; B) time in plankton without fecundity tradeoffs; C) mean dispersal distance and D) stochastic dispersal distance; where positive an increase is selected for.

4: Non-Dimensionalization & Results

The parameters of the model can be combined into two non-dimensional parameters that determine which life-histories are favored. In both, the time-scale is given by the difference of the growth and mortality rates, $(g\text{-}m)^{-1}$.

The first is a non-dimensional time in plankton:

$$\Pi_1 = T_{PLD}(g\text{-}m)$$

The second is the ratio of advection to diffusion; essentially, a Péclet number

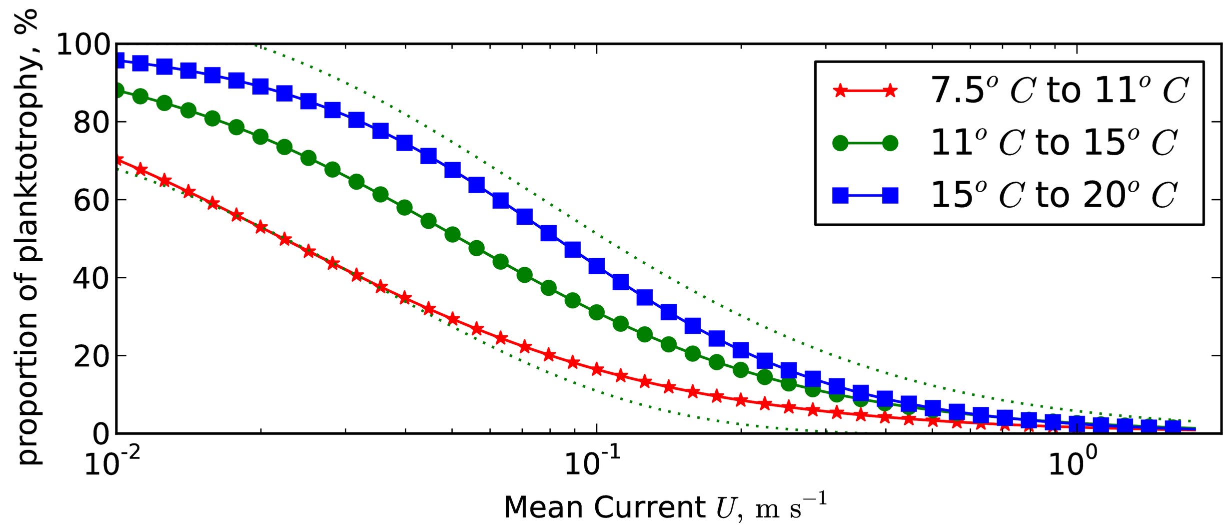
$$\Pi_2 = U^2/((g\text{-}m)\ \sigma^2 \tau_1)$$

Results: In the central panel, we can see the results of the model as function of the two important parameters: Where the plots are positive, there is selection for an increase in the parameter, where it is negative, there is selection for decrease. Panel A) gives the scaled selection for time in plankton, with fecundity tradeoffs; B) time in plankton without fecundity tradeoffs; C) mean dispersal distance and D) stochastic dispersal distance

5: Weak currents encourage drifting larvae

In panel A of the central figure, we can see that a longer time in plankton is only an evolutionarily stable strategy if growth exceeds mortality ($g\text{-}m>0$) and the mean currents are relatively weak compared to the fluctuations in the currents ($\Pi_2<1.9$). Zero time in plankton is always evolutionarily stable. Thus we would expect as mean currents decrease, planktonic larvae would become more common.

We compare the distribution of planktotrophic larvae observed by Marshall et al. 2012 to mean currents via a logistic regression. The analysis is done in different temperature ranges in order to control for the effect of temperature on the growth g and mortality m. Currents from the Surface Drifter Project. The results are consistent with our theory.

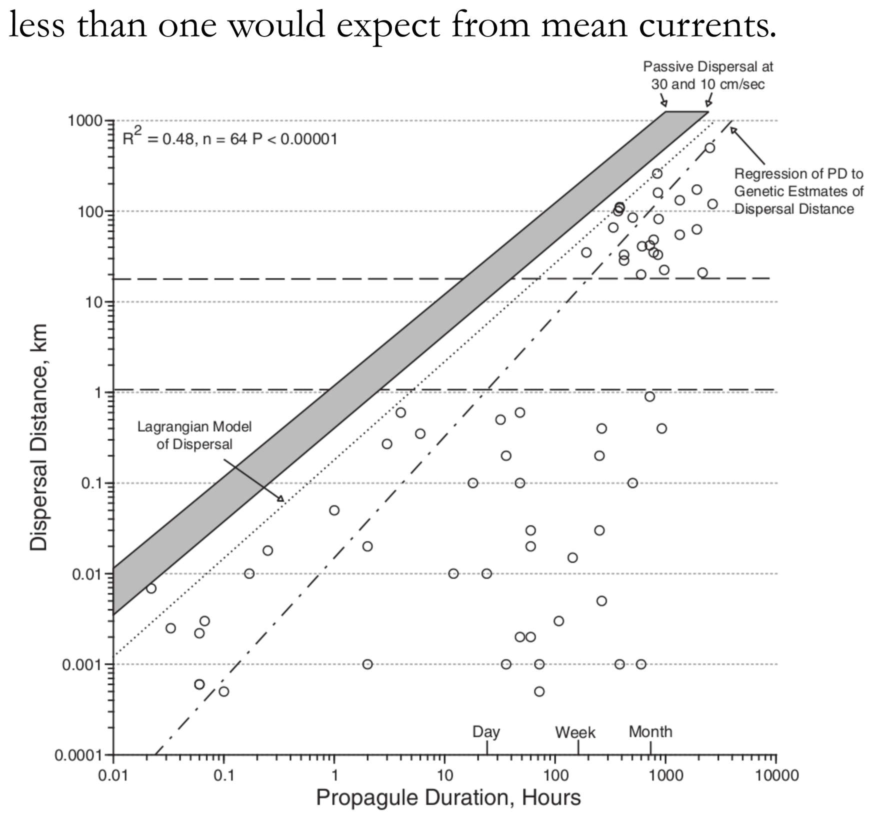


The proportion of larval planktotrophy as a function of the mean ocean currents for three temperature ranges. The dashed green lines are the one-standard error limits for the central temperature range.

6: Selection reduces mean dispersal

Panel C of the central figure shows that any change that increases the mean dispersal is selected against, so behavior that reduces downstream transport of larvae is evolutionarily favored. Panel B shows that any adaptation that increases time in plankton without increasing fecundity is also selected against.

Thus long distance dispersal by planktotrophic larvae is a side-effect of selection for higher fecundity, and any behavior that reduces mean dispersal is favored (at least in this model). This is consistent with widespread observations of behavior that reduces dispersal – for example the Shanks (2009) data below showing most larvae disperse, on average, substantially less than one would expect from mean currents.



7: Conclusions

For Biologists:

- Long-distance dispersal of larvae is a side effect of selection for greater fecundity
- Strong mean currents lead to reduced frequency of planktotrophic larvae
- Behavior to reduce downstream selection should be strongly favored
- Brooding, Direct-Development and other strategies with limited dispersal should always be an evolutionary steady state

For Physicists:

- Larvae will try to avoid being passive Lagrangian particles
- Mean and variable parts of circulation are both important to understanding distribution of species and life-histories

This is what we have done; ask what we are doing now!