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THE ROLE OF TURBULENT DIFFUSION FOR COPEPODS WTH FEEDING CURRENTS

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ABSTRACT

The encounter rate between predator and prey is frequently modeled in terms of the 'swept volume' associated with the relative velocity of the two organisms and an appropriate cross-sectional area. For the copepods which use feeding currents, an alternative conceptual model of the process is that the food particles are diffusing towards the predators. Their feeding currents trap the prey (even though they are well beyond the range of either visual or chemical detection) and entrain them towards their waiting arms. The predators thus benefit from the turbulent motion and diffusion, even though much of it is due to motions with scales significantly larger than their body's size. The feeding currents serve to dramatically increase the flux of food.

INTRODUCTION

Rothschild and Osborn's (1988) major point is the existence of relative motion between predator and prey due to the turbulent motions in the water, and the concomitant increase in the interaction rate at any given local concentration of predator and prey. A corollary to this result is the potential for laboratory measurements to incorrectly measure feeding rates, due to the significant differences between turbulence in laboratory systems and turbulence in the ocean. That discussion of the role of turbulence in increasing planktonic contact rates was based on the conceptual model that predators feed by sweeping through the water and capturing the prey that is within their reach (Skellam, 1958; Gerritsen and Strickler, 1977). In this paper, we will look at an alternative model for the process to elucidate the role of turbulence in the case of copepods which use feeding currents.

For copepods, a large amount of information has come from the high-speed photographic observations of the detailed feeding activities (Strickler, 1958: Costello et. al., 1990; Marassé et. al. 1990; and Paffenhöffer and Lewis, 1990)). The feeding process consists of swimming slowly (on the order of 2 mm/s) and entraining particles from as far as 1 cm in front of the copepod. The food particles are entrained at a significant distance from the predator by "feeding currents", created by the copepod itself, which pull passive particles into the mouth parts where they are identified, sorted, and the choice morsels, eaten. The relatively slow swimming speed suggests that the predators may not be swimming through the water and sweeping up the food but rather capturing local particles which are replenished by diffusion. Our picture is that particles are captured by the act of entrainment into the feeding currents which sucks them in for examination and potential demise. The deterministic chain of events that can lead to eventual capture starts before the particle is even identified, much less sensed! We will see that the feeding current reaches out far enough from the copepod that the diffusion has not decreased substantially because of the dissipation by viscous effects. This same model applies to small fish larvae (Sundby and Fossum, 1990) where visual perception replaces the feeding current.

There are tradeoffs between "ambush predation" and "actively" chasing food (Jumars, 1993). Energy expenditure is lower for the ambush mode, but its viability is limited, among other things, by the rate at which the food arrives. We will see that by using feeding currents to expand the capture radius, the copepods get more food brought in by turbulent diffusion, without having to expend the energy necessary to swim through the volume themselves.

What is the conceptual difference between food being advected towards the predator by the mean flow and food being advected to the predator by the turbulent flow? It is similar to the difference between advection and diffusion in the Reynolds' decomposition of motion into a mean and a fluctuating part. In one sense, the difference is very small since turbulent diffusion is still an advective transport of material, albeit it done with "turbulent" motions other than the "mean" currents. The decomposition depends upon a clear separation between the scales of motion for turbulence and the mean flow (Davis, 1994a,b), and that may well not exist on the scales at which copepods live and feed. However, the irregular motion of the water and the irregular swimming of the predator and prey often look more like Brownian motion and diffusion rather than the steady movement outlined in Skellam's derivation [3]. As well, the slow swimming speed of the copepod during feeding, relative to the water motion, makes a 'swept volume' model less appropriate.

ANALYSIS

How does the rate of food capture depend on the diffusion rate and the range of the feeding current? We can use a simple turbulent diffusion model for feeding. It can be modeled by a sphere of radius, r_0, with diffusion of food particles to that surface where the concentration is zero. Uniform boundary conditions simplify the problem without compromising our ability to examine the viability of the fundamental point. Setting the concentration to zero on the upper half of the sphere and the flux equal to zero on the lower half of the sphere would be more realistic but not amenable to analytic solutions.

As outlined, the problem is equivalent to heat flow into a sphere with a constant temperature (Carslaw and Jaeger, 1959). The equation for the concentration, Φ, is:

$$\frac{\partial\Phi}{\partial t} = \nabla\cdot(K\cdot\nabla\Phi), \qquad (1)$$

where K is the diffusivity and the boundary conditions are;

$$\Phi = 0 \quad \text{at } r = r_0\text{, and}$$

$$\Phi \to \Phi_\infty \text{ as } r \to \infty, \qquad (2)$$

where r represents the radial coordinate. For turbulent flow, the eddy diffusivity is proportional to the product of a velocity scale, u', and a length scale, l'(Tennekes and Lumley, 1972).

$$K \approx u'\cdot l' \qquad (3)$$

Thus the diffusivity increases with increasing spatial scale. The velocity scale, u_r, for the Kolmogorov spectral distribution of velocity (homogeneous, isotropic turbulence) at a distance r away from the origin, is,

$$u_r \approx \varepsilon^{1/3}\cdot r^{1/3}, \qquad (4)$$

where ε, is the dissipation rate for the turbulent kinetic energy. This functional relation can be seen in Rothschild and Osborn(1988, figure 1) where they plot relative velocity as a function of separation and dissipation rate. This relation holds for scales larger than those at which the viscous dissipation occurs. Combining equations (3) and (4), provides the functional form for the diffusivity relative to the particle located at the origin of the coordiante system. with A representing an unknown, but constant value,

$$K(r) = A\cdot\varepsilon^{1/3}\cdot r^{4/3}. \qquad (5)$$

With the diffusivity and the boundary conditions all spherically symmetric, the problem reduces to a differential equation in the radial coordinate only,

$$\frac{\partial\Phi}{\partial t} = \frac{1}{r^2}\cdot\frac{\partial}{\partial r}\left(r^2\cdot K(r)\cdot\frac{\partial\Phi}{\partial r}\right). \qquad (6)$$

Substituting equation (5) for the turbulent diffusivity

$$\frac{\partial\Phi}{\partial t}=\frac{1}{r^2}\cdot\frac{\partial}{\partial r}\left(r^2\cdot A\cdot\varepsilon^{1/3}\cdot r^{4/3}\cdot\frac{\partial\Phi}{\partial r}\right)=\frac{A\cdot\varepsilon^{1/3}}{r^2}\cdot\frac{\partial}{\partial r}\left(r^{10/3}\cdot\frac{\partial\Phi}{\partial r}\right).\qquad(7)$$

Assuming steady state:

$$0=\frac{A\varepsilon^{1/3}}{r^2}\frac{\partial}{\partial r}\left(r^{10/3}\frac{\partial\Phi}{\partial r}\right).\qquad(8)$$

Note that A and ε are both constants which can be divided out, making the steady state solution for the concentration profile independent of the dissipation and the amplitude of the diffusivity.

$$0=\frac{\partial}{\partial r}\left(r^{10/3}\frac{\partial\Phi}{\partial r}\right).\qquad(9)$$

$$\left(r^{10/3}\cdot\frac{\partial\Phi}{\partial r}\right)=\text{Constant}\qquad(10)$$

The solution for the concentration as a function of radius does not depend on the amplitude of the diffusion coefficient.

$$\Phi=\Phi_\infty\left(1-\left(\frac{r_0}{r}\right)^{7/3}\right)\qquad(11)$$

The magnitude of the gradient is:

$$\frac{\partial\Phi}{\partial r}=\frac{7}{3}\Phi_\infty\cdot r_0^{7/3}\cdot r^{-10/3}\qquad(12)$$

The flux is:

$$Flux=-K(r)\cdot\frac{\partial\Phi}{\partial r}\cdot\hat{r}=-\frac{7}{3}\Phi_\infty\cdot A\cdot\varepsilon^{1/3}\cdot r_0^{7/3}\cdot r^{-2}\cdot\hat{r}\qquad(13)$$

The integrated flux across the surface of any sphere, centered on the origin is the same:

$$\int Flux\cdot d\hat{s}=-4\pi r^2\cdot K(r)\cdot\frac{\partial\Phi}{\partial r}=-\left(\frac{28\pi}{3}\right)\cdot A\cdot\Phi_\infty\cdot\varepsilon^{1/3}\cdot r_0^{7/3}.\qquad(14)$$

The flux of food, inward towards the predator, increases as the radius to the 2.33 power. Thus, if a copepod captures food over a sphere 1 cm in radius, it gets 8.5 times as much food as it would from a sphere 4 mm in diameter! Thus we see that for a diffusive feeding procedure, the amount of food increases rapidly with the 'reach' of the predator.

In order to get a time dependent solution, we will need to use a constant diffusivity. Hence, let's compare the steady state results for variable diffusivity with the steady state solutions for a constant diffusivity, $K(r) = \kappa$. Equations (7), (9), (11), (12), (13), and (14) have the following counterparts:

$$\frac{\partial\Phi}{\partial t} = \frac{1}{r^2}\cdot\frac{\partial}{\partial r}\left(r^2\cdot\kappa\cdot\frac{\partial\Phi}{\partial r}\right) \tag{15}$$

$$0 = \frac{\partial}{\partial r}\left(r^2\cdot\frac{\partial\Phi}{\partial r}\right) \tag{16}$$

$$\Phi = \Phi_\infty\left(1-\left(\frac{r_0}{r}\right)\right) \tag{17}$$

$$\frac{\partial\Phi}{\partial r} = \Phi_\infty\cdot r_0\cdot r^{-2} \tag{18}$$

$$Flux = -\kappa\cdot\frac{\partial\Phi}{\partial r}\cdot\hat{r} = -\Phi_\infty\cdot\kappa\cdot r_0\cdot r^{-2}\cdot\hat{r} \tag{19}$$

$$\int Flux\cdot d\hat{s} = -4\pi r^2\cdot\kappa\cdot\frac{\partial\Phi}{\partial r} = -4\pi\cdot\Phi_\infty\cdot\kappa\cdot r_0 \tag{20}$$

The gradient is much steeper for the variable diffusivity (figure 1). For comparison consider the difference between the two cases if the diffusivities are the same at the surface of the sphere, i.e. if $\kappa = A\cdot\varepsilon^{1/3}\cdot r_0^{4/3}$. The variable diffusivity produces a flux of $\frac{28}{3}\pi\cdot\Phi_\infty\cdot\kappa\cdot r_0$ while the constant diffusivity would produce a flux of $4\pi\cdot\Phi_\infty\cdot\kappa\cdot r_0$. The difference is due to the larger gradient at the surface of the sphere in the case with the variable diffusivity. The larger gradient at the surface arises because the diffusivity is greater away from the sphere and hence, it replenishes the region near the sphere faster. The gradient is greater for the variable diffusivity only for a short distance away from the surface. Equating the two steady state gradients, equations (12) and (17):

$$\Phi_\infty \cdot r_0 \cdot r^{-2} = \frac{7}{3}\Phi_\infty \cdot r_0^{7/3} r^{-10/3} \tag{21}$$

$$r^{4/3} = \frac{7}{3} \cdot r_0^{4/3} \tag{22}$$

$$r = 1.89 \cdot r_0 \tag{23}$$

In the case with the variable diffusion, the predator depletes the food in the nearby water. The concentration is a 80% of Φ_∞ at $r = 2 \cdot r_0$. With a constant diffusivity, the copepod depletes the food concentration over a much greater range, with the concentration reaching 80% of Φ_∞ at $r = 5 \cdot r_0$.

There is a problem with the steady state solutions. The amount of material that must be consumed by the predator starting from a uniform concentration and eating until the steady state distributions is established is infinite, for either functional form of the diffusivity.

For the constant diffusivity

$$\iiint (\Phi_s - \Phi_\infty) dv = \int_{r_0}^{\infty} \Phi_\infty \cdot \frac{r_0}{r} \cdot 4\pi \cdot r^2 \cdot dr = 4\pi \cdot \Phi_\infty \cdot r_0 \cdot \int_{r_0}^{\infty} r \cdot dr \to O\left(r^2\right) \to \infty \tag{24}$$

and for the variable diffusivity

$$\iiint (\Phi_s - \Phi_\infty) dv = \int_{r_0}^{\infty} \frac{7}{3} \cdot \Phi_\infty \cdot \left(\frac{r_0}{r}\right)^{7/3} \cdot 4\pi \cdot r^2 \cdot dr =$$

$$4\pi \cdot \Phi_\infty \cdot r_0^{7/3} \cdot \int_{r_0}^{\infty} r^{-1/3} \cdot dr \to O\left(r^{2/3}\right) \to \infty \tag{25}$$

Thus, rather than consider the steady state solution one should examine the time dependent problem. Unfortunately, there is no simple solution for the time dependent problem with the variable diffusivity. Therefore, let us look at some of the characteristics of the time dependent solution for constant diffusivity, the solution to equation (15), which has a similarity solution available (Carslaw and Jaeger, 1969).

$$\Phi = \Phi_\infty\left(1-\left(\frac{r_0}{r}\right)\right)+\Phi_\infty\cdot\left(\frac{r_0}{r}\right)\cdot erf\left[\frac{(r-r_0)}{2\sqrt{\kappa\cdot t}}\right] \qquad (26)$$

The first term is the steady state solution and the second is a decaying, time dependent term. the flux per unit area is:

$$-\kappa\cdot\frac{\partial\Phi}{\partial r}\cdot\hat{r} = -\kappa\cdot\Phi_\infty\cdot\left(\frac{r_0}{r^2}-\frac{r_0}{r^2}\cdot erf\left(\frac{(r-r_0)}{2\sqrt{\kappa t}}\right)+\frac{r_0}{r}\cdot\left(\frac{1}{\sqrt{\pi\cdot\kappa\cdot t}}\right)\cdot exp\left(\frac{(r-r_0)^2}{4\cdot\kappa\cdot t}\right)\right)\cdot\hat{r}(27)$$

At $r = r_0$, the flux integrated over the surface of the sphere is:

$$Flux = -4\pi\cdot\kappa\cdot\Phi_\infty\left(r_0+\left(\frac{r_0^2}{\sqrt{\pi\cdot\kappa\cdot t}}\right)\right) \qquad (28)$$

At t=0, the time dependent term is infinitely large, but it decays rapidly (figure 2) and its time integral is finite. When $t = t' = \left(\frac{r_0^2}{\pi\kappa}\right)$, the time dependent term has decreased to the same value as the steady state term. Figure 3 shows the development of the concentration distribution (equation 26) as a function of t'. By the time $t = 4\cdot t'$, the time dependent concentration for the constant diffusivity case is lower than the steady state solution for the variability diffusivity almost all the way to $r = 3\cdot r_0$.

By the time $t = 16\cdot t'$, the time dependent solution for constant diffusivity has lower concentration than the steady state solution for variable diffusivity all the way to $r = 6.5\cdot r_0$. The time dependent constant diffusivity case sets a limit on the development of the variable diffusivity distribution. What does the time scale, $t' = \left(\frac{r_0^2}{\pi\kappa}\right)$, correspond to in the ocean. Using a value of 1 cm for r_0, and a value of 0.1 cm²/s for κ, makes the time scale, t', on the order of 3 seconds. The value for κ represents the mean vertical diffusivity in the ocean and is lower than the coefficient derived from lateral diffusive processes. Nevertheless, the time scale is appropriate to the feeding events and processes of copepods and fish larvae.

What is the relative contribution of the two terms to the total flux up to that time?

$$\int_0^{t'}\cdot 4\pi\cdot\kappa\cdot\Phi_\infty\left(r_0+\left(\frac{r_0^2}{\sqrt{\pi\cdot\kappa\cdot t}}\right)\right)dt = 4\pi\cdot\kappa\cdot\Phi_\infty\cdot\left(r_0\cdot t'+\left(\frac{2\cdot r_0^2\cdot\sqrt{t'}}{\sqrt{\pi\cdot\kappa}}\right)\right)$$

$$= 4\pi \cdot \kappa \cdot \Phi_\infty \cdot \left(\frac{r_0^{\,3}}{\pi \cdot \kappa} + \left(\frac{2 \cdot r_0^3}{\pi \cdot \kappa} \right) \right) = 12 \cdot \Phi_\infty \cdot r_0^{\,3} \qquad (29)$$

This amount is about 3 times the amount of food that was in the volume of radius $r = r_0$, when the copepod arrived, which in our model disappears (but is not eaten) at the moment the copepod arrives. By the time $t = 16 \cdot t'$, the total has climbed to $96 \cdot \Phi_\infty \cdot r_0^{\,3}$, with two-thirds from the steady state flux and one-third from the transient term.

DISCUSSION

What would constrain a copepod from developing an ever increasing sphere of dining influence? The volume over which the feeding current ranges is limited by the size of the copepods appendages and presumably, there are constraints that limit the size of copepods based on their anatomical and physiological strategies (McGowan, 1994). Too large a copepod would be an appealing target for the larger fishes. The forms that seems most consistent with benefiting from the turbulent diffusion of food are the jellyfish, which cover a large volume with little mass. Thus they get significant diffusion with little appeal to predators of the appropriate size scale due to their low density of edible matter.

Is there some consideration which forms a criterion for setting a minimum range for the feeding current of a copepod? Below a certain scale, dependent on the local turbulent intensity, turbulent eddies are dissipated and the relative velocity is due to a viscous shear of eddies of larger scale. At these scales the diffusive flux of food particles decreases rapidly with decreasing separation. Thus, it is appropriate to expect the feeding current should reach out, as close as possible, to the scale where the characteristics of the turbulent diffusion changes. Figure 1 in Rothschild and Osborn shows Δu as a function of r for different values of the dissipation rate, ε. For all but the highest dissipation rates, the complete transition to the $\Delta u_r \approx \varepsilon^{1/3} \cdot r^{1/3}$ regime occurs at scales of 3 to 10 cm, greater than the copepods feeding current radius. The effect is to reduce Δu, and by equation (3) the diffusivity $K(r)$, by up to a factor of 3 below the value it would have if the turbulence continued to the 1 cm scale. Thus, it appears that the limit on copepod size precludes it from taking full advantage of the present levels of oceanic turbulence. It may be that the predators cure this shortcoming by jittering around their central location. It is possible for the predator to increase the value of r_0 by moving around the origin, along as the wandering keeps the surface concentration on the expanded sphere at zero. A. Brooks (personal communication) notes that many of Strickler's pictures show several predators in a group. Such a congregation would have an r_0 significantly larger than the range of one individuals feeding current. Testing such ideas will require detailed observations with realistic situations.

How can we test the hypotheses that feeding currents serve to increase the flux of a 'diffusive' transport of food? Two types of measurements would shed some light on the question. First we should look and see what the effect of a predator is upon the distribution of prey. Does a predator decrease the concentration of food particles at some distance in front (diffusive case) or does it just appear to eat its way through the water? In the latter case, the concentration behind the predator will be more depressed than the concentration in front. In the diffusive case the reverse would happen. Second, we can also examine the path of particles which are eaten. Do they move (diffuse) toward the predator or are they just grabbed by the predator as it goes by?

Where should such studies be performed? Probably not in laboratory experiments - as useful as they have been and still are! The turbulent spectra are incorrect. At large Reynolds number, such as we find in the ocean, the peak of the dissipation spectrum is at a wavelength about 30 times Kolmogorov scale, $L_k = \left(\nu^3/\varepsilon\right)^{1/4}$(Tennekes and Lumley, 1972; Gargett et. al., 1984). Laboratory experiments (e.g. Hill et. al., 1992) are at relatively low Reynolds number and therefore have a small range of wavenumbers between the scale of energy input and the scale of dissipation processes. In these small tanks, the turbulent kinetic energy occurs at spatial scales that are little separated (if at all) from the scales at which the dissipation occurs. In such cases, it is inappropriate to contemplate an inertial subrange or use any of the formulas based on such assumptions. Oceanic turbulence has a separation of the scales, so that the energy containing eddies are often distinctly larger than those at which dissipation occurs. It is the larger scales which are diffusing the food so rapidly that the deficit appears only in the region very near the predator. Thus, if the larger scales are missing from the flow the distribution of prey will be different.

Another problem with earlier laboratory experiments involves the 'tethering' of the copepod. While this procedure makes the data gathering much easier, an untethered copepod "sees" a different velocity spectrum with considerably less low frequency energy than a tethered copepod which is restrained and must face whatever comes. A free floating copepod drifts with the large scale eddies and escapes the buffeting. Also, when tethered, the food is advected past by the low frequency eddies while free floating predators are not aided by the mean current and the low frequency eddies which move them also. Fortunately, the experimental technology (and unfortunately the complexity) is advancing and it is now possible to follow untethered copepods.

Understanding the feeding process will require detailed oceanic measurements and visualization of the processes, the distribution of prey and the changes with time. These measurements are within the realm of the new instrumentation that is being developed. The important parameters include 1) the range at which the prey is entrained by the feeding currents, 2) the local prey concentration, 3) the distribution of predators and prey as a function of time, and 4) the intensity of the turbulence; all measured in relation to the encounter rate. Future modeling efforts will need to include significant improvements on the motion of finite size particles in a turbulent field. Treating predators and prey as simple points is not adequate for quantitative predictions.

CONCLUSIONS

1) Copepod feeding can be considered as turbulent diffusion of the food in towards the region where the feeding currents serve to capture the food well before it is identified.

2) The behavior of the copepods is such that they benefit significantly from the turbulent processes which enhance their encounter with prey. Specifically, the feeding currents generated by copepods are on appropriate scales to act in concert with turbulent diffusion of prey.

3) Laboratory measurements show many aspects of the process but cannot realistically model the oceanic turbulence over a range of scales, even when matching the intensity in terms of the dissipation rate.

4) Measurement programs should determine the range at which prey is entrained and the flux of prey as a function of local concentration and turbulent intensity. The critical measurements appear to be the distribution of the prey relative to the predator as a function of time through the feeding process. If the copepods are eating in a swept-volume manner, the prey will be depleted in the area behind them. If diffusion is the process, the depression in concentration will be more in front of them.

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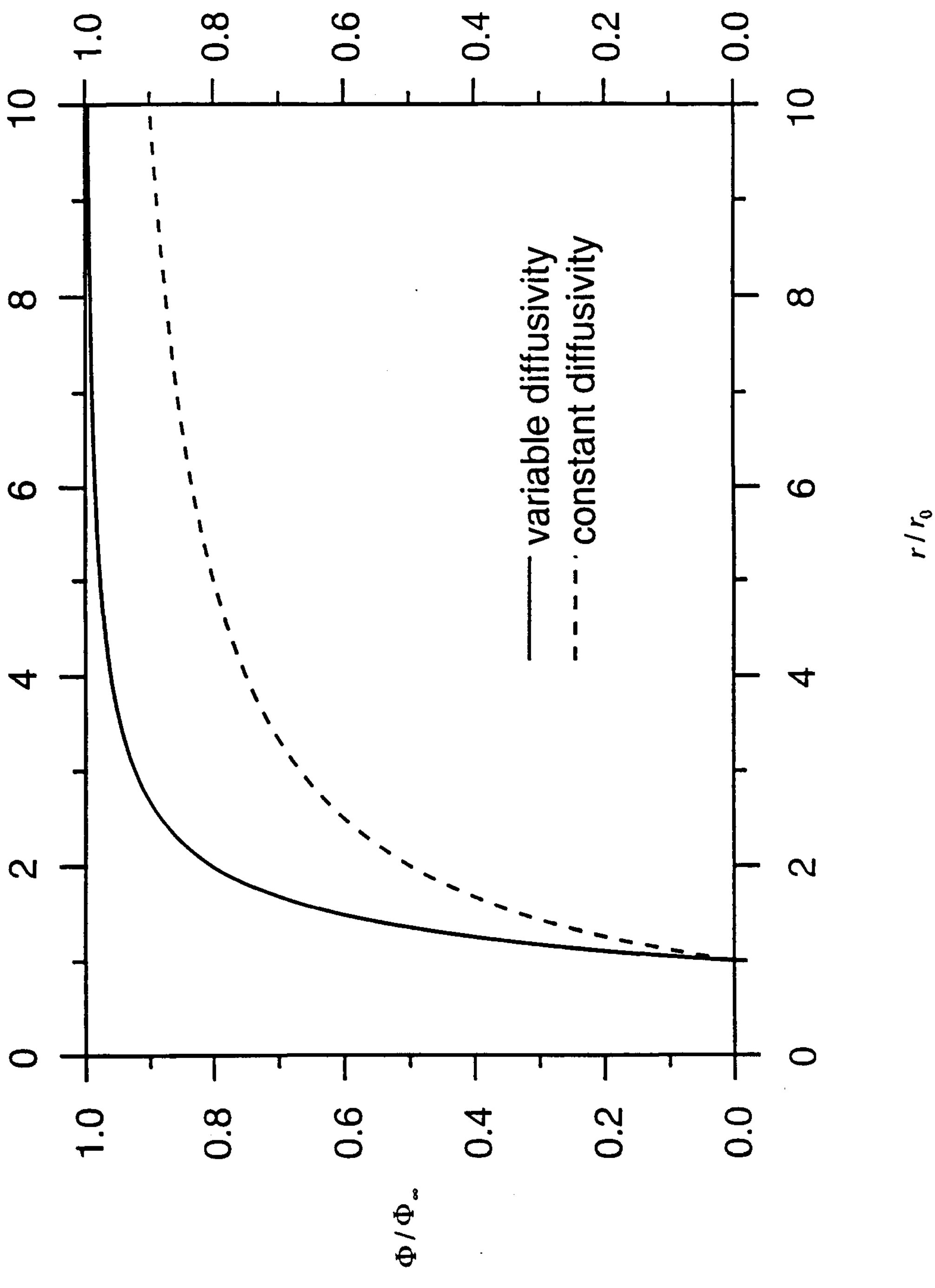

Figure 1

Concentration of prey as a function of radial distance from the predator. The left curve represent the solution (equation 11) for the variable diffusivity given in equation (5). The curve to the right represents the solution for a constant diffusivity (equation 17). The radial coordinate is in units of r_0.

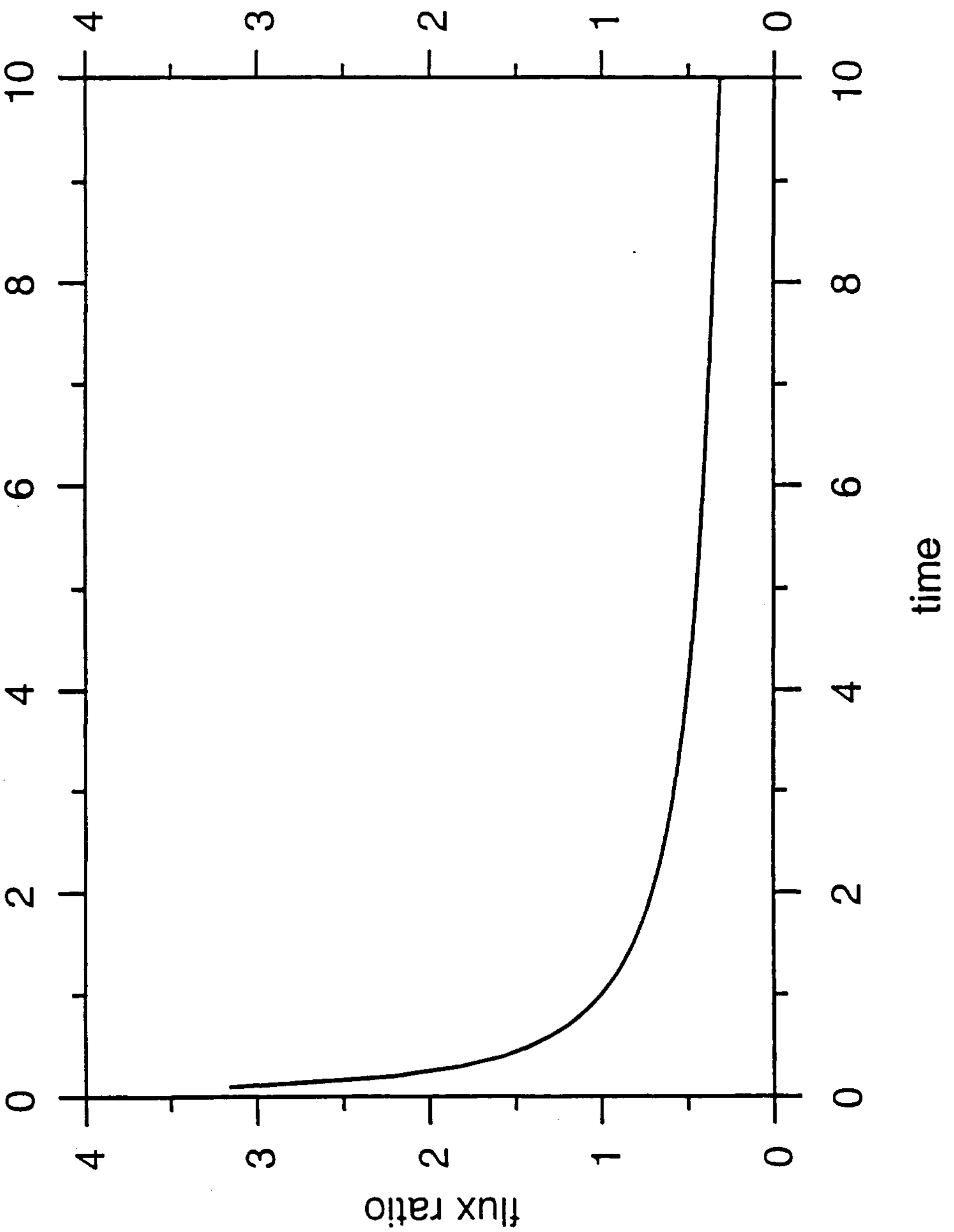

Figure 2

The ratio of the time transient flux to the steady state flux, calculated from equation(28). Time is plotted in units of $t' = \left({r_0^2}/{\pi \cdot \kappa} \right)$.

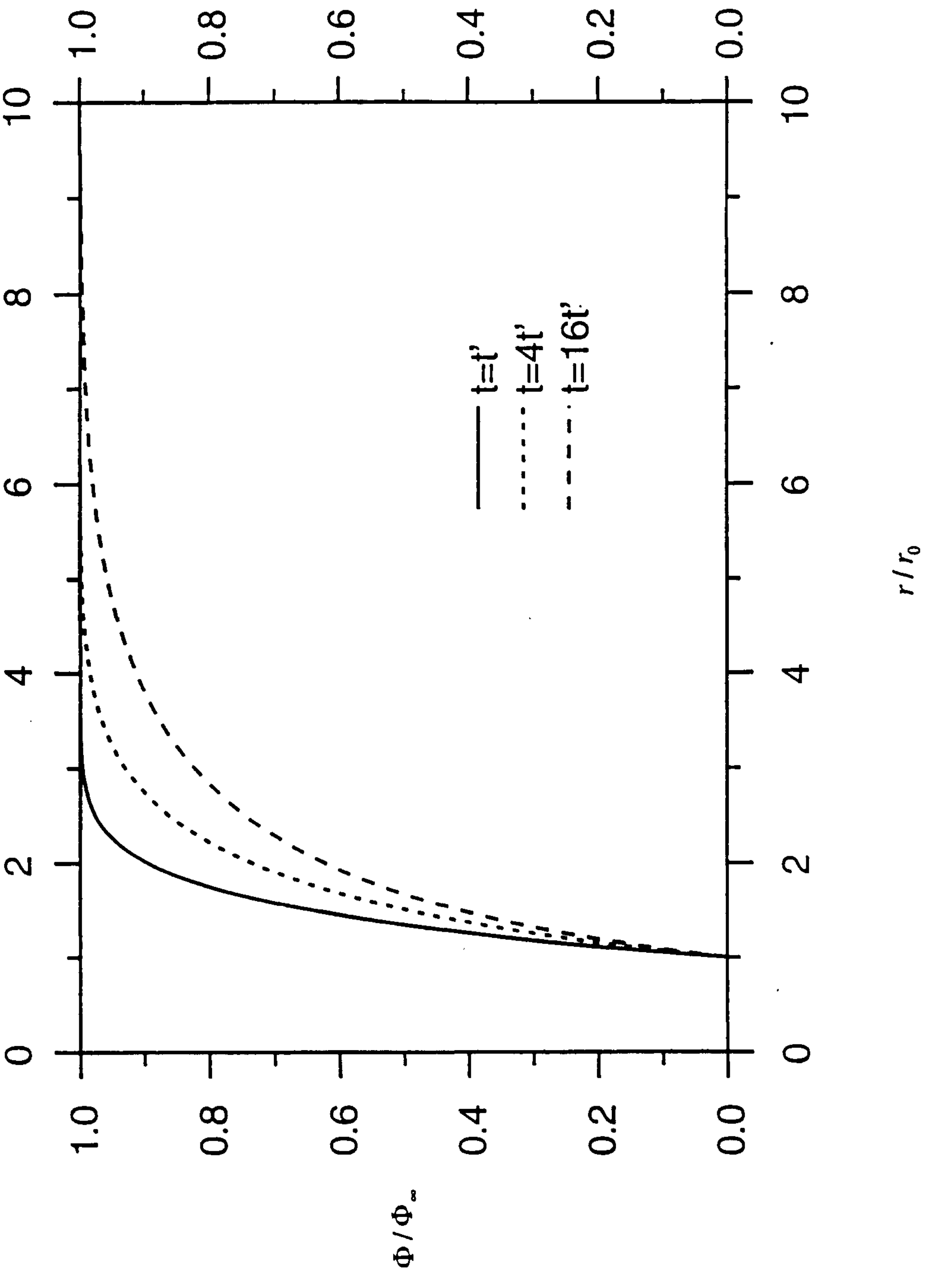

Figure 3

The progression with time of the concentration profile in the case with constant diffusivity. The curves show the distribution of Φ/Φ_∞ at time $t = t'$, $t = 4 \cdot t'$, and $t = 16 \cdot t'$, where $t' = \left(r_0^2 / \pi \cdot \kappa \right)$ is the time at which the time dependent contribution to the flux has decayed to equal the steady state value, i.e. when the total flux has decreased to twice the steady state value. The radial coordinate is in units of r_0.