

The fluid mechanics of copepod feeding in a turbulent flow: A theoretical approach

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Abstract – An important area of biodynamics research is the interaction between predator and prey in nature. Several scales are significant for interactions between predator and prey over the life cycle of each organism. A key factor is the encounter probability (group and individual). On the basis of physical considerations, the group encounter probability depends upon the respective patch sizes (on the order of 10s of km) and their relative dispersion (or aggregation) rates in turbulent systems. The encounter probability at the individual level is affected by the relative motion of the predator and the prey and is controlled by the velocity spectrum. In addition, at the individual level, the striking distance of a predator will depend on motility and perception of the prey. Here we address the mechanics of copepod predation on phytoplankton and the coupling with the physics of turbulent fluid motions. Our aim is to review pertinent fluid dynamics, on scales of less than a few metres, to provide a framework in which to consider the role of fluctuating fluid velocities on copepod feeding.

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1. INTRODUCTION – COPEPOD FEEDING PROBLEMS

The general problem of understanding turbulent particle motion has led to a variety of particle dynamics research with applications to chemical reactions and combustion (ABBAS, KOUSSA and LOCKWOOD, 1981), sediment transport (MIDDLETON and SOUTHARD, 1978), atmospheric aerosols (MAXEY and CORRSIN, 1986), etc. Another stimulus for research on this topic is the use of particles for tracers of fluid flow (e.g. DICKEY and MELLOR, 1979; DICKEY and MELLOR, 1982). A few laboratory studies with rather limited dynamical ranges have been devoted to sediment settling velocities in oscillating and turbulent flows (FIELD, 1968; MURRAY, 1970). In addition, wind tunnel experiments have used particles of varying density and sizes (SNYDER and LUMLEY, 1971; WELLS and STOCK, 1983). Nonetheless, our understanding of particle motion in oscillating and turbulent flows is still quite limited (CLIFT, GRACE and WEBER, 1978; MAXEY and CORRSIN, 1986). One of the more relevant studies was recently done by GRANATA and HORNE (1985), who examined the horizontal dispersion rates of two diatoms (one large and one relatively small). They found the two rates to vary significantly and hypothesized that this variance was caused by the difference in the sinking rates. It is likely that many of these experimental approaches could be useful to researchers studying predator-prey patch interactions on the scale of metres and less.

This paper reviews four separate areas of fluid mechanics relevant to feeding in a turbulent flow. For our purposes, a copepod (length scale $O(1\text{mm})$)¹ is the predator and a diatom $O(10^{-2}\text{mm})$ is the prey. In Section 1, we examine the forces acting on a fluid and the organisms it contains, then show how to evaluate these forces quantitatively and how to determine resulting particle dynamics. In Section 2 we discuss turbulent primary flows and non-turbulent secondary flows (such as the feeding and swimming motions generated by copepods). Finally in Section 3, we consider secondary flows superimposed upon the turbulent flow to determine the relative motion of predator and prey and consider the effects of turbulence on: 1) boundary layers about both the predator and the prey; 2) chemodetection of prey by predators; 3) encounter rates of predators with prey; and 4) Reynolds numbers and length scales pertinent to the feeding problem.

A review of the literature on copepod feeding strategy and predation theory is beyond the scope of this paper. For readers interested in the theories and strategies of general zooplankton predation, the following collection of symposia papers is recommended: 1) KERFOOT (1980); 2) KERFOOT and SIH (1987); and 3) PAFFENHOFER and PRICE (1987). Readers specifically interested in swimming and feeding behavioral modifications of marine copepods in response to food are directed to papers by BUSKEY (1984), POULET and GILL (1988), POULET and OUELLET (1982), and WONG, RAMCHARAN and SPRULES (1986). For freshwater zooplankton predation behavior, recent studies have been done by RAMCHARAN and SPRULES (1989), SCHULZE and FOLT (1989), and YOUNG and GETTY (1987). It is our opinion that turbulent motions of predator and prey will be important for prey capture regardless of which strategy or theory is supported.

1.1 Forces acting on a particle

Plankton and the fluid in which they reside are acted upon by both body forces and surface forces which determine the direction and magnitude of motion. For our purposes the only significant body force is gravity. Surface forces acting on a particle are normal stresses (pressure) and tangential stresses (friction) both of which may be important depending on flow conditions (i.e. turbulent, laminar, or creeping flow).

¹ $O()$ is an abbreviation for "on the order of".

Newton's second law states that the sum of the forces acting on a body is equal to the product of its mass (m) and its acceleration (a). The vertical component of the forces may be written as:

$$\Sigma F_z = ma_z \quad (1)$$

A vertical force balance on a plankter may be expressed as an inertial force balanced by the sum of a buoyancy force, F_B (a body force), and a drag force, F_D (a surface force):

$$ma_z = F_B - F_D \quad (2)$$

The buoyancy force is:

$$F_B = (\rho_p - \rho)V_p g \quad (3)$$

where ρ_p and ρ are the densities of the plankton particle and of the fluid, V_p is the particle volume and g is gravitational acceleration. The vertical drag force, F_D , can be represented using the empirical relationship:

$$F_D = C_D \rho A_p \frac{w_p^2}{2} \quad (4)$$

C_D is the shape and size dependent drag coefficient, A_p is the projected area of the particle and w_p is the vertical component of the particle velocity.

In nature, plankton live in a fluid environment that is usually turbulent on scales of tens of metres down to millimetres. On scales less than the order of 1mm, however, the fluid adjacent to a plankter is non-turbulent. The Reynolds number for an organism provides a convenient way to characterize flow conditions experienced by the organism. The Reynolds number is defined as:

$$Re = \frac{\text{inertial forces}}{\text{viscous forces}} = \frac{uL}{\nu} \quad (5)$$

where u is the fluid velocity relative to the organism (in an arbitrary direction), L is some nominal length scale of the organism and ν is the kinematic viscosity of the fluid ($\approx 1\text{mm}^2\text{s}^{-1}$ for seawater).

As Reynolds numbers increase beyond values of 1, inertial forces begin to dominate and are balanced by pressure and viscous forces. For Reynolds numbers less than 1, inertial forces are negligible and viscous forces balance pressure forces. For most geophysical flows, turbulent fluid motion must be considered along with predator-prey motions such as sinking velocity, swimming speed, and feeding current (see Section 3.0, Turbulence and Predator-Prey motion).

One fundamental question concerning the motion of a particle relative to a steady, uniform fluid flow relates to shape and size effects on drag. This problem has been considered extensively for the idealized case of a sphere with varying diameter or Reynolds number (BATCHELOR, 1970; CLIFT, GRACE and WEBER, 1978). The very low Reynolds number case ($Re \ll 1$) gives a Stokes' law form ($C_D = 24/Re$); however, for greater Reynolds numbers, appreciable departure from Stokes' Law occurs (Fig.1) and more complicated Re dependent empirical forms must be used (see Table 1). Unfortunately, few studies have been devoted to non-spherical shapes (CLIFT, GRACE and WEBER, 1978; KOMAR and REIMERS, 1977; MIDDLETON and SOUTHARD, 1978).

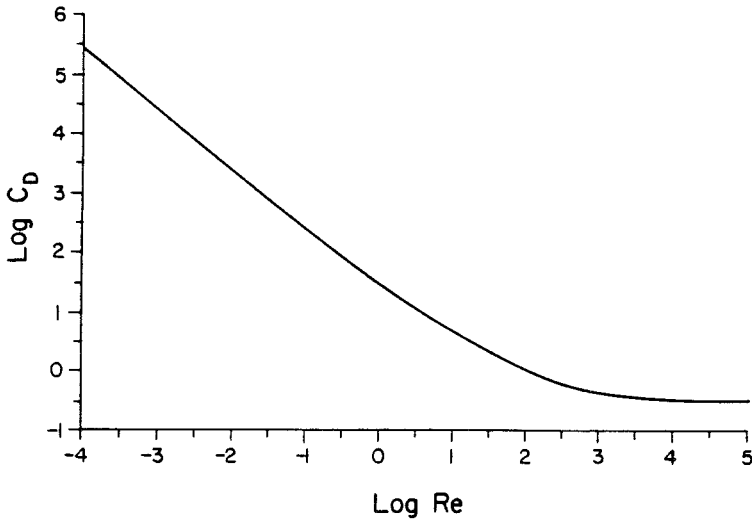


FIG. 1. \log_{10} of the Reynolds number ($Re=uL/v$) of a particle versus \log_{10} of C_D , the drag coefficient of the particle (calculated from the recommended equations in Table 1).

TABLE 1. Recommended equations for drag coefficients

$\beta = \log_{10} Re$ and $Re = uL/v$

Range	Correlation
(A) $Re < 0.01$	$C_D = 3.16 + 24/Re$
(B) $0.01 < Re \leq 20$	$C_D = 24/Re(1 + 0.1315Re^{(0.82-0.05\beta)})$
(C) $20 \leq Re \leq 260$	$C_D = 24/Re(1 - 0.1935Re^{0.6305})$
(D) $260 \leq Re \leq 1500$	$C_D = 10^{(1.6435 - 1.1242\beta + 0.1558\beta^2)}$

From CLIFT, GRACE and WEBER (1978).

The Reynolds number varies as a function of size (e.g. the organism's length), shape (which affects the drag coefficient), and swimming (or sinking) speed. Most plankton are non-spherical, varying in size and shape, though many are bilaterally symmetric. Further, the drag coefficient varies widely with an organism's Reynolds number. Small organisms such as diatoms and copepod larvae have small vertical velocities and large drag coefficients. Larger, adult copepods have higher velocities and reduced drag coefficients.

As a result of the dependence of Reynolds numbers on the size, shape, and velocity of an organism, relative speeds between predators and prey can vary by several orders of magnitude, even excluding motility. Clearly, relative speed is an important factor in determining encounter rates of predators and prey.

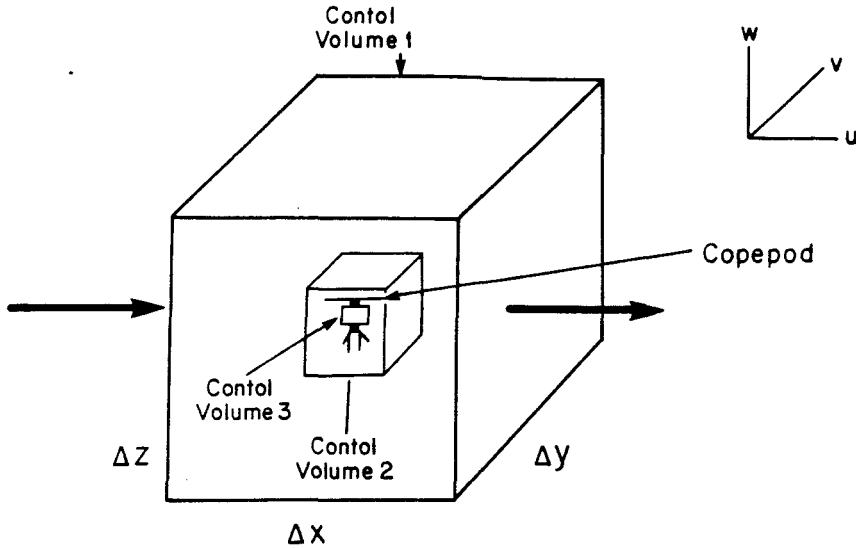


FIG.2. Control volumes about a copepod. Control volume 1 is the volume enclosing all primary fluctuations; control volume 2 encloses the animals boundary layer; control volume 3 encloses the feeding and swimming appendages.

1.2 Quantitative analysis of flow relative to a predator

A standard approach used in analyzing fluid flow is to evaluate fluxes of various quantities through a control volume of known dimensions. Three parameters are of particular importance: mass, momentum, and energy. A mass balance, for instance, can be used to determine the amount of prey removed from the control volume as well as the removal rate (per unit time).

A control volume, V , can be defined as any arbitrary volume in space that is completely enclosed by a surface area, S . An example of a control volume is the cube shown in Fig.2.

The control volume does not deform and is permeable to matter. The mass within control volume 1 is given by $m = \rho V_{\text{fluid}} + \rho_{\text{pred}} V_{\text{pred}} + \rho_{\text{prey}} V_{\text{prey}}$, where ρ is the density of the fluid, ρ_{pred} is the density of the predator, and ρ_{prey} is the density of the prey. The volumes occupied by the fluid, predator, and its prey are V_{fluid} , V_{pred} , and V_{prey} , respectively. A mass density for the control volume can be defined as:

$$\rho_{\text{cv}} = \frac{m}{V} = \frac{\rho V_{\text{fluid}} + \rho_{\text{pred}} V_{\text{pred}} + \rho_{\text{prey}} V_{\text{prey}}}{V} \tag{6}$$

For the volume in Fig.2, the mass balance may be written as:

$$\dot{m}_{\text{in}} - \dot{m}_{\text{out}} = - \iint_S (\rho U_{\text{fluid}} + \rho_{\text{pred}} U_{\text{pred}} + \rho_{\text{prey}} U_{\text{prey}}) \cdot \mathbf{n} \, dS \tag{7}$$

Assuming that the fluid, predator, and prey masses are the major mass components, the difference between the mass flow rates into and out of the control volume may be written as $\dot{m}_{\text{in}} - \dot{m}_{\text{out}}$. U_{fluid} , U_{pred} , and U_{prey} are the velocity vectors for the fluid, predator, and prey. The directional unit vector (positive outward) is $\mathbf{n} = \mathbf{n}(x, y, z)$.

For steady-state conditions, biological reactions of predator and prey, such as production (P) or grazing (G), in the control volume must be balanced by the total change in mass of the control volume or:

$$[(P_{\text{pred}} - G_{\text{pred}}) + (P_{\text{prey}} - G_{\text{prey}})] = \dot{m}_{\text{in}} - \dot{m}_{\text{out}} \quad (8)$$

For prey alone, the mass balance may be written as:

$$- \iint_S (\rho_{\text{prey}} \mathbf{U}_{\text{prey}}) \cdot \mathbf{n} \, dS = P_{\text{prey}} - G_{\text{prey}} \quad (9)$$

Assuming $P_{\text{prey}} \ll G_{\text{prey}}$, for the small time steps, equation 9 reduces to:

$$- \iint_S (\rho_{\text{prey}} \mathbf{U}_{\text{prey}}) \cdot \mathbf{n} \, dS = - G_{\text{prey}} \quad (10)$$

That is, the grazing rate of the predator on the prey can be measured based on the prey mass density flux through the control volume.

To analyze forces within the control volume, a momentum (M) equation can be derived from Newton's second law using an approach analogous to that used for the mass balance. Similarly, energy can be computed using the control volume formulation.

Figure 2 illustrates more specifically how the control volume concept can be used to study predator-prey relationships. The selection of a control volume (that is, where to define the boundaries) depends on the scale of the process under investigation. To study the effects of turbulent flow on predation, for instance, the control volume would be chosen to include the predator, its prey and the main stream (undisturbed) flow (control volume 1). If the boundary layer about the animal were of interest, the control volume would be selected to be the volume from the predator to, but not including, the main stream flow (control volume 2). To consider the energetics of appendage motion associated with feeding and swimming, the pertinent control volume would be the volume about the appendages (control volume 3). Once the control volume is defined, appropriate equations can be written to describe the flux of any parameter through surfaces of the fluid volume.

To use the control volume approach, optical techniques currently exist for analyzing: 1) copepod appendage motion during feeding in control volume 3 on time scales of tens of microseconds and spatial scales of tens of microns (STRICKLER, 1985); 2) swimming and sinking motions of predator and prey in control volume 2 on time scales of hundreds of milliseconds and spatial scales of millimetres (MARRASE, COSTELLO, GRANATA and STRICKLER, 1990); and 3) turbulent flow fields and plankton motions in control volume 1 on time scales of hundreds of milliseconds and spatial scales of centimetres (DICKEY, HARTMAN, HURST and ISENGLE, 1984).

2. PLANKTON AND FLOW REGIMES

2.1 Conceptualization of flow conditions around a particle

Figures 3a-d depict flow about a particle. We can visualize particle motion in a Lagrangian reference frame, where the particle trajectory is viewed relative to the fluid. When flow becomes turbulent, a particle's trajectory will be irregular in direction and speed, and the particle's orientation will vary as the particle rotates in the velocity gradient.

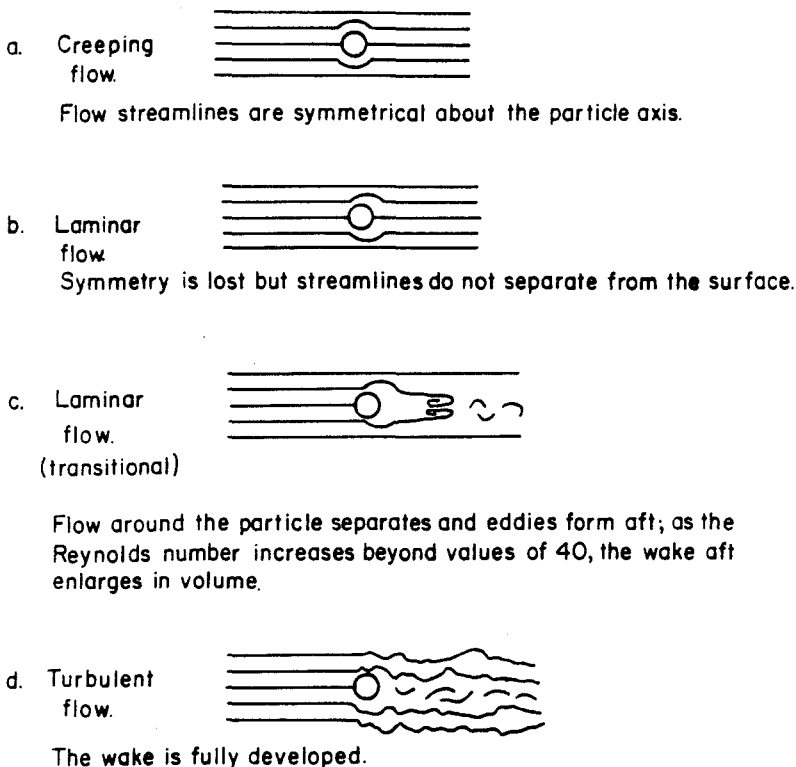


FIG.3. Streamlines about a spherical particle, which could be a predator or a prey, for: a) creeping flow, $Re \leq 0.1$; b) beginning laminar flow, $Re = 1$; c) laminar-transitional flow, $20 \leq Re \leq 100$; and d) transition from laminar to turbulent flow, $100 < Re < 400$.

As discussed previously, changes in the shape of an organism will alter flow conditions and Fig.3 only depicts various flow conditions around a spherical particle. For the purposes of illustrating the types of flow, however, a planktonic organism is presumed to roughly approximate a spherical particle. If $Re \leq 0.1$, viscous forces dominate and streamlines (which are the paths of the fluid about the particle) are symmetrical forward and aft of the particle (CLIFT, GRACE and WEBER, 1978; Fig.3a). This condition is designated as creeping flow. As Re increases to values greater than 1 (Fig.3b), inertial forces become important and symmetry is lost as streamlines stretch – a condition of laminar flow. For $20 \leq Re \leq 100$, streamlines separate from the particle's surface producing eddies aft of the particle (Fig.3c). A transition from laminar to turbulent flow for a sphere occurs for $100 < Re < 400$ when the wake becomes chaotic (Fig.3d).

As the streamlines diverge about the particle, the fluid velocity is increased. At the surface of the particle the tangential fluid velocity is zero (a condition of no-slip). Outward from the particle's surface, the velocity increases until the free-stream velocity is reached. That is, at a certain distance from the particle's surface, the streamlines are not affected by the presence of the particle. This distance is the boundary layer thickness of the fluid about the particle. For $Re \gg 1$, a streamlined particle shape can reduce the boundary layer and the effects of drag.

For low Reynolds numbers, a streamlined organismal shape has no effect on pressure drag but does increase the viscous drag because the surface area of the particle is increased. At higher Reynolds numbers, a streamlined shape can reduce the tendency for flow to separate from the surface thereby reducing the pressure drag. Therefore, from a fluid mechanics perspective, copepod larvae ($Re < 1$) would not benefit from streamlining while an adult copepod ($Re > 1$) might. Additionally, turbulence may affect drag on a particle by modifying the flow field around a particle. The effect of a boundary layer on predation is discussed more fully in section (2.3).

2.2 Turbulent flow – a condition of nature

A turbulent flow field has the following general qualitative attributes: 1) it is diffusive and dissipative, 2) it is irregular and its vorticity (a measure of the local rate of fluid rotation) fluctuates, 3) it is intermittent and patchy, and 4) its Reynolds number is high (greater than 100). A copepod in high Reynolds number flow can be exposed to eddies of various sizes (Fig.4). Size scales of turbulent eddies, pertinent to copepod predation, can be characterized by control volume 1 in Fig.2.

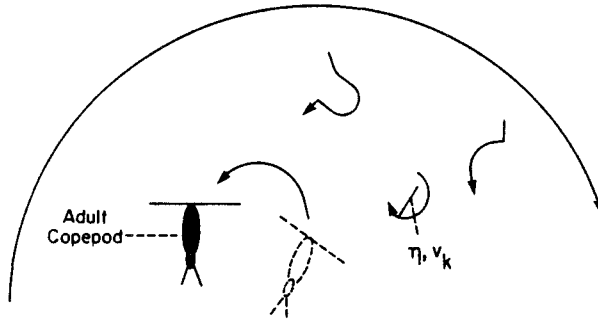


FIG.4. A time lapse diagram representing eddy length scales relative to the size of an adult copepod. The smallest eddies have a length scale η and a velocity of v_k .

The smallest eddies have a mean length scale η (Kolmogorov length scale) which is dependent upon the rate at which turbulent kinetic energy is dissipated, ϵ , such that $\eta = (v^3/\epsilon)^{1/4}$. It should be noted that η represents the length at which inertial forces balance viscous forces. The scale of the smallest eddies at the viscous cut-off may vary by at least an order of magnitude.

If η is less than the length of a copepod, turbulence will not significantly contribute to fluctuations in the copepod's motion, however, eddies larger than the copepod will generally cause fluctuations proportional to the fluctuating fluid velocities.

A technique such as laser anemometry can be used to generate a time series of instantaneous velocity (e.g. horizontal component) as depicted conceptually in Fig.5. A record such as this can be represented as an energy spectrum in frequency. This frequency spectrum can be transformed into a spatial spectrum using Taylor's frozen turbulence hypothesis (e.g. TENNEKES and LUMLEY, 1973) so length scales pertinent to predator-prey interactions can be analyzed. Several important scales are represented in the spatial turbulence energy spectrum illustrated in Fig.6. The transition from turbulent to laminar motion is marked by the Kolmogorov length scale, η , or the Kolmogorov wavenumber k_d ($k_d = 2\pi\eta^{-1}$). The larger scale turbulent eddies (smaller wavenumbers) depend on the conditions of the generation of the turbulence; however, as the energy cascades to the smaller scale eddies, the energy spectrum becomes universal.

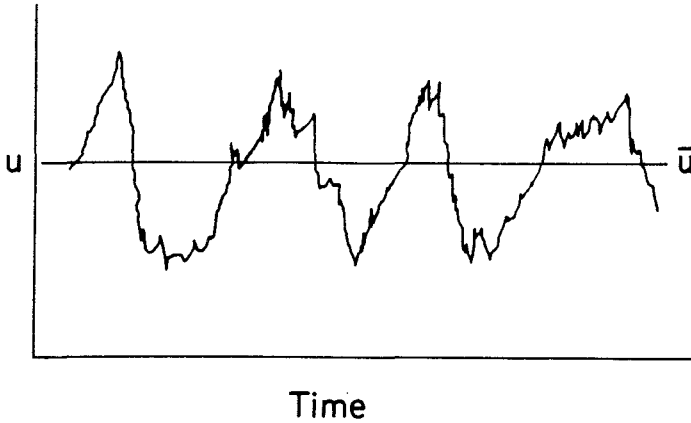


FIG.5. A conceptual velocity time series for a flow with eddies as depicted in Fig.4 where u , u' , and \bar{u} are the instantaneous, fluctuating, and mean velocities which may be related as: $u = u' + \bar{u}$. The root mean square of the fluctuating velocity, $(\overline{u'^2})^{1/2}$, is referred to as the turbulent intensity.

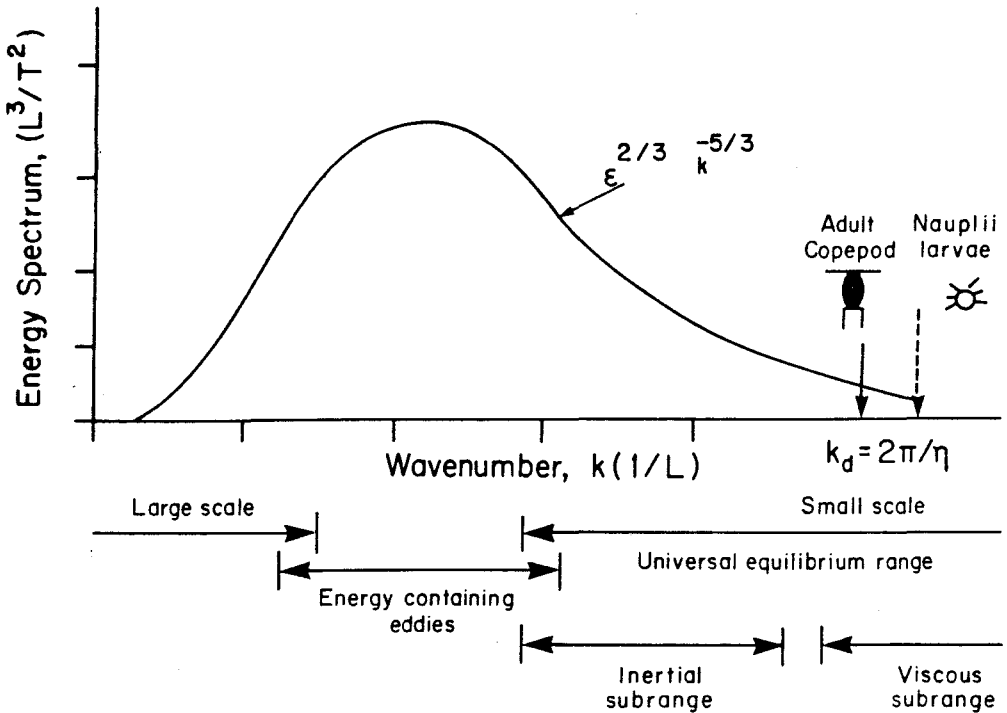


FIG.6. A graph of a typical energy spectrum of a turbulent environment. The Kolomogorov wavenumber is $k_d(k_d=2\pi\eta^{-1})$.

In the universal range, energy is not lost but is transferred into smaller eddies, until inertia in these small eddies is no longer dominant and viscous dissipation of energy occurs. The peak in the spectrum indicates the scale of the most energetic eddies. For progressively larger wavenumbers, the inertial subrange and finally the viscous subrange are encountered (see Fig.6).

Large scale (small wavenumber) physical forcing in the ocean generates turbulence as it adds kinetic energy to the fluid. The input of this kinetic energy is reflected in the low wavenumber portion of the energy spectrum and is related to the length scale of the physical forcing event. On small scales (say the size of an adult copepod), an increase in kinetic energy would cause an increase in the turbulent intensity (the magnitude of the fluctuating fluid velocity) resulting in an increase in the mixing rate and the rate of momentum flux. More importantly, η decreases (as $\eta \propto \epsilon^{-1/4}$) as kinetic energy increases (ROTHSCHILD and OSBORN, 1988).

2.3 Organismal motility and boundary layers

Plankton can, in some cases, regulate their positions and distributions in the water column by generating their own forces through buoyancy and/or motility. For instance, copepods have a wide range of swimming velocities and can generate feeding currents that allow the animals to scan a moderate volume of water in search of food.

A boundary layer of thickness δ next to a copepod arises when the fluid adjacent to the animal resists motion (that is $u=0$ at the boundary) relative to the fluid about the animal. The boundary layer can be characterized by using control volume 2 in Fig.2. For a natural (turbulent) flow, the velocity of the organism relative to the fluid must be considered thus:

$$\delta = \left(\frac{vL}{|u_\infty - u_p|} \right)^{1/2} = \left(\frac{vL}{u'} \right)^{1/2} \quad (11)$$

where u_∞ is the free stream velocity (primary motions), u_p is the particle velocity (secondary motions) and the velocity relative to the particle is $u' = |u_\infty - u_p|$ (SCHLICHTING, 1955). A dimensionless boundary layer thickness can be defined as:

$$\frac{\delta}{L} = \left(\frac{v}{u'L} \right)^{1/2} = Re^{-1/2} \quad (12)$$

From Eq(12) we can see that the boundary layer around a particle of size L will be large if the relative velocity is small. Conversely, large velocity differences reduce the boundary layer.

For a copepod, the boundary layer thickness will depend on the scales of turbulence that are experienced, the swimming speed, the velocity of the feeding current and the length scale of the animal. Larval copepods probably follow most scales of turbulent motion while adults may diverge from the smaller scale motion and reflect only the motion on the larger scales. Also, larvae have lower swimming speeds than adults. Both effects would decrease the relative velocity of the larvae, compared to an adult. Consequently, the larger adults $O(1\text{mm})$ would have thinner boundary layers per unit body length than the smaller nauplii larvae $O(10^{-1}\text{mm})$. As larvae begin to grow, the boundary layer may immediately decrease in thickness depending on the interaction of L and u' .

Copepod feeding currents result from slow swimming motions of the organism. STRICKLER (1985) reported the maximum fluid velocity generated by a feeding current to be 10mm s^{-1} , producing a Reynolds number of approximately 1. KOEHL and STRICKLER (1981) measured maximum velocities of a feeding appendage to be 22mm s^{-1} and estimated the boundary layer next

to the appendage to be 0.018mm thick (or roughly $L/50$). Based on these measurements, the boundary layer next to the copepod should always be laminar, providing turbulence does not penetrate into the boundary layer.

TABLE 2. Reynolds numbers for swimming and feeding copepods based on $Re_e = \frac{L_b U}{\nu}$.

	Stage	L_b (mm)	U (mm s ⁻¹)	Re_s
Swimming	Adult	1-10	1-100	1-1000
	Larvae	0.1-1	0.1-1	0.01-1
Feeding	Adult	1-10	1-10	1-100
	Larvae	0.1-1	0.1-1	0.01-1

The Reynolds number and the swimming velocity of a copepod increase several orders of magnitude with length of the organism (Table 2). In general, the swimming velocities of most organisms increase with the length scale of the organisms. A range of swimming Reynolds numbers, Re_s , has been defined by OKUBO (1987) as:

$$Re_s = \frac{U_s L_b}{\nu} \quad (13)$$

where U_s is the animal swimming speed and L_b is the body length. An empirical fit of data results in the following relationships:

$$Re_s = 3.71 L_b^{1.86} \quad (14)$$

and

$$U_s = 0.371 L_b^{0.86} \quad (15)$$

where L_b is in mm and U_s is in mm s⁻¹ (Fig. 7).

The swimming speed of an adult copepod is 1 to 100mm s⁻¹ (STRICKLER, 1977), with swimming Reynolds numbers between 4 and 271 (for $1\text{mm} \leq L_b \leq 10\text{mm}$). For larvae, Re_s would be approximately 10^{-2} (based on $L_b = 10^{-1}\text{mm}$) or less. Thus, based on swimming behavior, Reynolds numbers vary by as much as 4 orders of magnitude as our predator grows.

3. TURBULENCE AND PREDATOR-PREY MOTIONS

Unless there are large relative velocity differences between the animal and the turbulent fluid, the predator's swimming and feeding currents will determine the thickness of the boundary layer. If the animals are large enough, turbulence will transfer more momentum into the boundary layer, reducing the boundary layer thickness. Feeding currents may also transfer momentum and vorticity into the animal boundary layer. Suction, created by copepod appendages, advects vorticity toward the copepod, confining it to a thin region in the boundary layer. As the suction or feeding is increased, vorticity is confined to thinner layers about the organism (BATCHELOR, 1970). Vorticity and momentum fluxes are probably unsteady since swimming and feeding behavior (and thus velocity) changes temporally, as a function of the turbulent flow regime. For

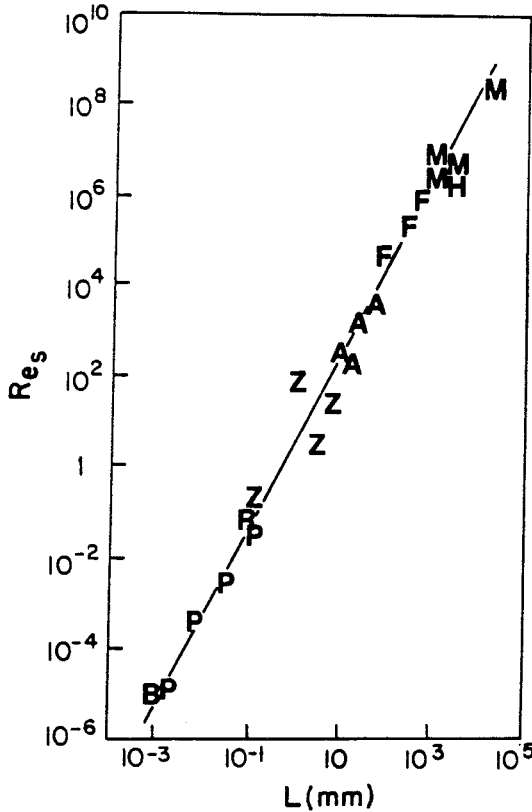


FIG.7. A $\log_{10}\text{-}\log_{10}$ plot of the Reynolds number characterizing organismal motion versus the length, L_o , of the organism. Letters designate the type of organism: H for humans, M for other mammals, F for fish, A for amphipods, Z for zooplankton, P for phytoplankton, and B for bacteria. After OKUBO (1987).

instance, turbulent intensity beyond a critical value can elicit a reduction of copepod swimming speed (COSTELLO, MARRASE and STRICKLER, 1990). Reduced swimming motion equates to a reduced energy output, presumably while energy intake is enhanced by turbulence as a result of increased prey encounter (MARRASE, COSTELLO, GRANATA and STRICKLER, 1990). The animal's energy output can be quantified by measuring the energy dissipated per unit volume and time in the boundary layer (i.e. control volume 2, Fig.2) as:

$$\epsilon_{bl} = \frac{1}{2} \rho \frac{\partial}{\partial x_0} \int_0^{\infty} u(y)(u_{\infty}^2 - u(y)^2) dy \tag{16}$$

where u_{∞} is the main stream velocity, $u(y)$ is the velocity a perpendicular distance y from the animal's surface, and x is the horizontal distance along the surface (SCHLICHTING, 1955).

STRICKLER (1985) has suggested that small scale perturbations of feeding currents by turbulent flows can affect the capture of food by animals such as calanoid copepods. The interactions of feeding currents and turbulent water motion of various scales and intensities, however, is not well understood.

3.1 Relative motion between predator and prey

The relative velocity of a copepod depends not only on its swimming speed but also upon the amount of "slippage" resulting from the scale of turbulent motion contributing to the animal's fluctuating velocity. Slippage occurs when a particle does not follow the motion of the fluid.

A fundamental problem of particle dynamics has been addressed by MAXEY and RILEY (1983), who have formulated, in detail, the equation of motion for a small rigid sphere in non-uniform flow. Generally, large, dense particles deviate from the fluid motion. Two extremely important terms in the nonlinear equation are the "added mass" and the Basset history terms. Added mass accounts for the acceleration of the particle's mass relative to the fluid displaced by the moving particle. The Basset history term accounts for the past motion of the particle, a calculation commonly neglected but often significant at high frequencies. For small particles, the mean motion is not drastically affected by the history; however, the fluctuation is affected. Particle fluctuation and fluid turbulence can be represented spectrally or in terms of a Fourier integral (CLIFT, GRACE and WEBER, 1978):

$$u' = \int_0^{\infty} A_{\omega} \omega \cos(\omega t + \phi_{\omega}) d\omega \quad (17)$$

where ω is the angular frequency, A_{ω} is the amplitude, and ϕ_{ω} is the phase shift. One way to determine whether a particle will follow the fluid motion is to compare the relaxation time, τ , of the particle within a flow with the particle's oscillation period, τ_o . The relaxation time is given by $\tau = a^2((2\rho_p/\rho)+1)/9\nu$ and the particle's oscillation period is $\tau_o \propto 1/\omega$, where ρ_p is the particle density, ρ is the fluid density, a is the nominal particle radius, and ω is the particle oscillation frequency resulting from fluid motion. For small particles (low Re), the particle path will follow the fluid path if $\tau_o \gg \tau$, or

$$\frac{\nu}{\omega a^2} \gg \frac{(2\rho_p/\rho) + 1}{9} \quad (18)$$

Using this criterion, small particles such as diatoms and copepod larvae, with nominal lengths equal to or less than 10^{-1} mm, densities similar to the fluid, and $\omega > 10s^{-1}$, should follow the fluid motion. This is not necessarily true for adult copepods. For an adult copepod with lengths greater than 1 mm and densities greater than the fluid ($\rho_p/\rho \approx 1.5$), and for $\omega > 10s^{-1}$, we would expect particle slippage to occur. Since Eq.(18) applies only to "small" particles that follow the fluid flow (and small is not well defined), it is important to determine the effects of the phase shift and the amplitude of the oscillations for small larvae and larger adult copepods. A particle's oscillation frequency, amplitude and phase shift can all be determined experimentally using laser Doppler velocimetry or by applying the solution of the MAXEY and RILEY (1983) equation for specific flow conditions (steady or oscillatory) and particle properties (density and shape).

3.2 Effects of turbulence on sensory perception of prey

The work of several investigators (ALCARAZ, PAFFENHOFER and STRICKLER, 1980; ANDREWS, 1983; BUSKEY, 1984; KOEHL and STRICKLER, 1981; PAFFENHOFER and PRICE, 1987; ROSENBERG, 1980; STRICKLER, 1982, 1985; VANDERPLOEG and PAFFENHOFER, 1985) suggests that organisms such as copepods are capable of sensing food at a distance of 1 mm or less (either visually or chemically), of orienting themselves with respect to a non-turbulent flow field, and of setting up

optimal feeding currents. Turbulence may affect copepod feeding by disrupting the velocity field associated with feeding currents, by interfering with the animal's physical and chemical sensory systems, and by reducing or removing the chemical signal through advection and diffusion.

ANDREWS (1983) has modelled chemoreception in relation to feeding currents. This aspect is important in that the sphere of influence of the predator along with its prey may be significantly affected (PRICE, PAFFENHOFER and STRICKLER, 1983; PRICE and PAFFENHOFER, 1984). Turbulence could reduce the gradient of the prey's chemical signal. If the concentration of the signal were below the concentration detectable by the copepods, the prey might escape capture.

The mechanoreception of prey may also be important to prey capture (LEGIER-VISSER, MITCHELL, OKUBO and FUHRMAN, 1986). STRICKLER (1985) reported that an adult copepod spends $O(10s)$ searching for food, $O(1s)$ to capture food and only $O(0.1s)$ to handle individual food particles. Turbulence could adversely affect mechanical food capture if the particles were advected past the copepod at rates faster than the animal's reaction time.

Another problem a copepod may encounter, caused by large, ephemeral fluctuating velocities, is the change in its spatial orientation resulting from rotation in a shear field. Copepods that are unable to compensate for this rotation, may become disoriented and feed inefficiently. This type of motion would occur within control volume 1 in Fig.2.

3.3 Encounter rates

A key predator-prey interaction is food capture which is a function of predator encounters with prey. Particle encounter probabilities (encounter rates) can be defined using control volume 3 in Fig.2. Encounter rates have been modelled by GERRITSEN and STRICKLER (1977). Their model was modified for turbulent flow conditions by ROTHSCHILD and OSBORN (1988) using fundamental information derived from first principles involving relative predator-prey motion and the prey concentration (number per unit volume). The ROTHSCHILD and OSBORN model shows that the frequency of prey particles encountered by predators increases with increasing turbulent intensity and decreasing relative organismal velocities. This indicates that, from a purely physical perspective, increased turbulence enhances predator-prey encounters.

In contrast, encounter rate could be reduced if the predator and prey patches disperse at different rates. For instance, if a prey patch disperses faster than a smaller predator patch, the centroids of the two patches would not overlap (GRANATA and HORNE, 1985). From the predator's perspective, this would result in a decrease in the maximum concentrations of prey and thus a decrease in encounter rate. However, increases in momentum flux and fluctuating velocities could enhance the encounter rate between predator and prey, which might offset patch dispersion (ROTHSCHILD and OSBORN, 1988).

Preliminary observations for tethered copepod feeding in turbulent and laminar flows (COSTELLO, MARRASE and STRICKLER, 1990; MARRASE, COSTELLO, GRANATA and STRICKLER, 1990) indicate that turbulence enhances algal encounter rates, measured as the number of algae passing through a unit volume per unit time, compared to laminar flow conditions. However, there have been no studies with free swimming animals in a well defined turbulent flow field. There have been a few numerical and laboratory studies devoted to particle trajectories and the dispersion of particles (DICKEY and MELLOR, 1982; WELLS and STOCK, 1983). Although Lagrangian time scales of particles with differing properties in various controlled turbulent flow conditions have been determined by several investigators, only limited parameter ranges have been examined. Nonetheless, this type of data should be useful for modellers.

3.4 Reynolds numbers and length scales of pertinence

Thus far, we have focused primarily upon fluid flow on the scale of the organism. Larger scales of motions directly affect advection and diffusion (collectively called dispersion) of planktonic individuals and populations (patches). Several Reynolds numbers have already been presented for plankton in laminar and creeping flow conditions but not for plankton entrained in turbulent flows. One important parameter used to characterize turbulence that can be obtained from ocean measurements is the dissipation rate of turbulent kinetic energy, ϵ . There is a considerable amount of information now available on dissipation of turbulent kinetic energy in the upper ocean (GARGETT, STANFORD and OSBORN, 1979; GRANT, STEWART and MOLLIET, 1962; LUECK and OSBORN, 1982; LUECK and REID, 1984; OAKEY and ELLIOT, 1982). A few representative ranges of values of ϵ are presented in Table 3. From these data, we have calculated the corresponding Kolmogorov length scale, η , and the Kolmogorov velocity scale, $v_k = (\nu\epsilon)^{1/4}$.

TABLE 3. Reynolds number for particles in turbulent flows

Region	$\epsilon(\text{mm}^2\text{s}^{-3})$	$\eta(\text{mm})$	$v_k(\text{mm s}^{-1})$	$Re=v_k L/\nu$		
				Adult ($L=1.0\text{mm}$)	Larvae ($L=0.1\text{mm}$)	Prey ($L=0.01\text{mm}$)
North Pacific ¹	.0001-1	10-1	0.1-1	0.1-1	0.01-0.1	0.001-0.01
Sargasso Sea ²	.001-1	6-1	0.1-1	0.1-1	0.01-1	0.001-.01
Scotia Shelf ³	0.1-1	2-1	0.6-1	0.6-1	0.06-0.1	0.006-.01
Seymour Narrows ⁴	0.1-100	2-0.3	0.6-3	0.6-3	0.06-.3	0.006-.03

¹LUECK and OSBORN (1982)

²GARGETT, SANFORD and OSBORN (1979)

³OAKEY and ELLIOT (1982)

⁴GRANT, STEWART and MOLLIET (1962)

We have computed Reynolds numbers for passive copepods (adult and larvae) and diatoms using the Kolmogorov velocity scale and the approximate sizes of the organisms along with the kinematic viscosity, ν . Characteristic Reynolds numbers based upon the small scale (Kolmogorov scale) flow are quite small $O(1)$ or less and the Reynolds numbers of the zooplankton are two orders of magnitude greater than those of the diatoms, depending on the developmental stage of the copepod (Table 3). Again, η and v_k values represent mean estimates and may vary by at least an order of magnitude, thus the Reynolds number would scale up or down accordingly. Nevertheless, mean Reynolds numbers are informative. Reynolds numbers in Table 3, which range from 10^{-3} for prey up to ~ 1 for adult copepods, should be compared with Swimming Reynolds numbers in Table 2 which vary from 10^{-2} to 10^3 . One important point here is that Reynolds numbers, relevant to predator feeding, vary by as much as 6 orders of magnitude. Furthermore, the drag coefficient is rapidly varying over this range of Reynolds numbers (Fig. 1 and Table 1). On this basis alone, the motion of the adult would be expected to differ from that of prey and thus a relative motion should exist.

DAVIES (1972) has noted that large particles will follow the large scale motions only; however, if the particles are of the same size as the smallest scales of motion, they will follow these scales. It can be seen from Table 3 that the diatoms are generally two orders of magnitude smaller than the Kolmogorov scale while the adult copepods are within an order of magnitude of the Kolmogorov scale; this implies that copepods may or may not satisfy DAVIES' general requirement. Thus, it is likely that the predator-prey interaction process takes place in a transitional regime.

At what point in time and space the transition from non-turbulent to turbulent flow should occur cannot be predicted because temporal and spatial characteristics are dependent on nonlinear, coupled equations. The interaction of a non-turbulent ambient flow with animal generated disturbances could trigger an ambient turbulent flow since small perturbations can produce large effects as energy cascades through turbulent systems. In atmospheric science, this dynamic response is referred to as the Butterfly Effect (LORENZ, 1963). In the ocean, an analogy could be that major variabilities could result from small perturbations induced, for instance, by the flap of a copepod appendage. Both are examples of chaotic processes.

4. SUMMARY - WHAT IS IMPORTANT TO COPEPODS?

The motion of particles in a turbulent flow depends upon the characteristics of the particles and of the flow field. Particles generally respond to turbulent fluctuations on scales larger than the particle length (or some other pertinent length scale). Particles much larger than the scale of turbulent motion show little effect of small scale velocity fluctuation. Conversely, particles smaller than the smallest fluctuating scales respond to these fluctuating velocities. The cut-off size between large and small particles has yet to be determined.

Small scale turbulence must be treated separately (SAWFORD, 1985) because the equations for turbulence are restricted to time and space scales much greater than the Kolmogorov scale. In the space domain, this means that the standard Lagrangian correlation function, which has an exponential form, cannot be used for low Re because it does not have a viscous cutoff at large wavenumbers (TENNEKES, 1979). The ambient flow field relevant to the individual predator-prey interaction is in the small scale range. In a study related to the interpretation of particle tracer turbulence data, DICKEY and MELLOR (1979) rederived the Kolmogorov $r^{2/3}$ law using high wavenumber spectra. They presented a formulation for a flow based Reynolds number dependent upon velocity correlation functions which may be applicable to small scale turbulence and copepod encounter.

It is likely that future predator-prey studies will entail matching the flow and particle field information obtained in the laboratory with relevant longer time scales obtained from the Lagrangian models. For instance, the $r^{2/3}$ model can be used to relate smaller scale information to physical, optical, and biological field observations on larger spatial scales.

The flow conditions associated with copepod feeding span a wide range of Reynolds numbers. Copepod larvae predominantly experience creeping flow because of their small size and low swimming speeds. Often larval Reynolds numbers do not differ from those of their prey, suggesting that both follow the same scales of motion. As the animal grows, behavior and feeding patterns change (HAURY and PIEPER, 1988) perhaps in response to the flow conditions. As the size of the organism increases so does the Reynolds number, the organism's relative velocities, and the drag forces on the organism.

Turbulence increases the mixing rate in the fluid and, as a consequence, places more momentum into the boundary layer around an entrained particle. For adult copepods, increased

mixing would result in increased relative velocities and increased encounter rates, which could result in higher ingestion rates, provided turbulence does not detrimentally affect prey capture. Finally, an increased encounter rate has been connected with behavioral changes in swimming and feeding patterns that may require lower energy output by the animal when feeding in a turbulent environment. All of these issues illustrate the importance of the interrelationships between behavior, development, and energetics of copepod feeding in a turbulent flow.

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