

A review of two recent predation-rate models: the dome-shaped relationship between feeding rate and shear rate appears universal

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Two predation-rate models are reviewed: one, a stochastic model by MacKenzie *et al.* (1994) applies to the scales of intermediate and fully turbulent deformation; the other, a deterministic model by Jenkinson and Wyatt (1992) applies to the scales of laminar shear. Both models predict that predation rate should be a dome-shaped function of deformation rate. This is because, above a given deformation rate, some of the prey entering the model predator's perception zone (reactive field) is carried out of perception distance (reactive distance) again before the predator can catch it. Using the concept of the Deborah number, it is shown that both models agree well at the interface between their respective domains. This adds credibility to both models and suggests that the dome-shaped function applies across all scales.

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Introduction

The Deborah number, De , was borrowed from Rheology, the study of deformation in continua (Reiner, 1964).

$$De = \lambda/t \quad (1)$$

where t is the characteristic time of deformation of the supporting medium and λ is the characteristic time of the process under consideration. De was proposed by Jenkinson and Wyatt (1992) (JW) as an aid to thought in plankton ecology. They illustrated this aid with three models. In one model, of feeding by a pelagic predator with a "wait-and-chase" strategy, the amount of prey perceived (i.e. encountered) is directly proportional to the shear rate. One finding was that, when shear rates exceed a critical value, not all the prey perceived can be attained. The amount of prey attainable (and thus available as potential food) was found to show a dome-shaped relationship with shear rate (JW's Table 1). This model is deterministic and thus cannot be applied to the stochastic, intermediate sub-range of turbulence.

MacKenzie *et al.* (1994) (MMCL) independently developed a stochastic model of predator-pursuit success, applicable to the intermediate and fully turbulent scales. When combined with Rothschild's and Osborn's (1988) encounter-rate model, MMCL also indicated a

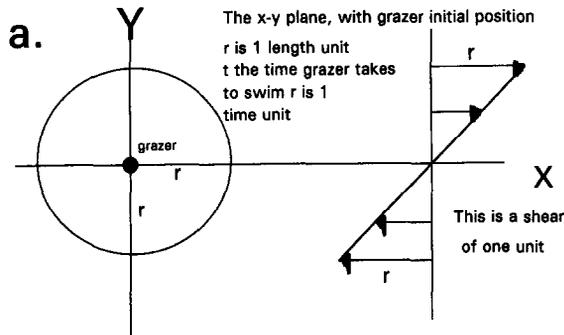
dome-shaped relationship between overall feeding rate probability and turbulence.

The present article further develops the JW model and explores its interface with the one proposed by MMCL.

Methods

JW's model, initially developed in *Basic*, has been reformulated for the present article using the *Mathcad* (Mathsoft, Inc.) electronic scratch-pad. A motile predator is centred in a spherical perception sphere (PS) in simple, steady, shear flow (Fig. 1). An encounter occurs when an immotile prey is brought into any part of the PS by the shearing water. The predator starts swimming directly towards it. As the direction of the prey changes, the predator changes course to keep swimming towards it. The radius of the perception sphere is defined as one length unit and the time the predator takes to swim this distance through still water is one time unit. Because of this scaling, De is here the same as the scaled shear rate. It turns out that water flow through the whole perception sphere $F = 4 \cdot De \cdot \int_0^1 |y| \cdot \sqrt{1-y^2} \cdot dy = 4 \cdot De/3$. A time step, δt , of 0.01 was used, corresponding to predator reaction-time. It is assumed that prey density is low, so that no correction has been made for the effect of perceiving two or more prey organisms simultaneously.

Perception sphere and 1 unit of "simple" planar shearing



Perception sphere in y-z plane. This is the circular area impinged by perceivable prey

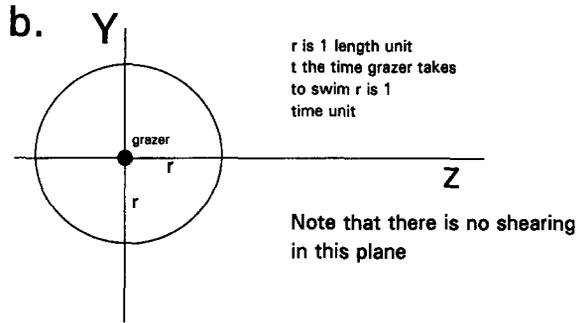


Figure 1. The spatial coordinates used by JW's model. a. The x and y dimensions; b. the z and y dimensions. Note that x, y, and z are defined in relation to a field of simple, steady shearing, and not to the vertical or horizontal.

Initial conditions for a quarter sphere with y and z positive (the other three quarters are congruent):

$$\left\{ \begin{array}{l} t=0; \text{ define } \delta t \\ \text{Define } py_0, pz_0, \text{ such that } (py_0^2 + pz_0^2) \leq 1 \\ px_0 = \sqrt{1 - py_0^2 - pz_0^2} \end{array} \right\} \quad (2)$$

$$\{gx_0=0, gy_0=0, gz_0=0, h=1\} \quad (3)$$

Subsequent iterations:

$$\left\{ \begin{array}{l} px_{t+\delta t} = px_t + (De \cdot py_t \cdot \delta t) \\ py_{t+\delta t} = py_t \\ pz_{t+\delta t} = pz_t \end{array} \right\} \quad (4)$$

$$\left\{ \begin{array}{l} gx_{t+\delta t} = gx_t + [\delta t \cdot |px_t - gx_t| \cdot (px_t - gx_t)/h_t^2] + (De \cdot gy_t \cdot \delta t) \\ gy_{t+\delta t} = gy_t + [\delta t \cdot |py_t - gy_t| \cdot (py_t - gy_t)/h_t^2] \\ gz_{t+\delta t} = gz_t + [\delta t \cdot |pz_t - gz_t| \cdot (pz_t - gz_t)/h_t^2] \\ h_{t+\delta t} = \sqrt{(px_t - gx_t)^2 + (py_t - gy_t)^2 + (pz_t - gz_t)^2} \end{array} \right\} \text{ until } gy_t \leq py_t \quad (5)$$

$$t = t + \delta t \quad (6)$$

(where gx_t, gy_t, gz_t is the three-dimensional position of the predator (grazer) at time t , px_t, py_t, pz_t is the immobile prey's position, and h_t is predator-prey distance).

Results

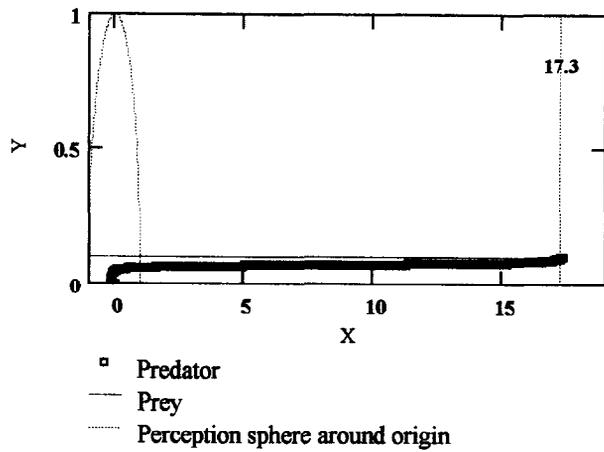
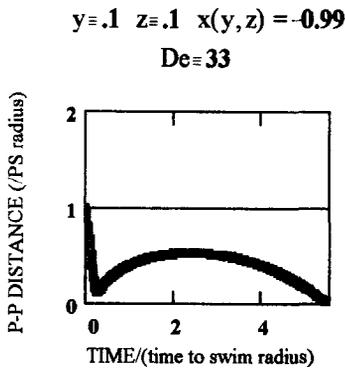
For all prey entry positions and values of De , the predator-prey distance, h , initially decreases with time, but in some cases h then increases again. At each point, y, z , by which prey can enter the perception sphere, a value of De exists (which will be called $Demax_{y,z}$) above which h increases to exceed the perception distance, and the prey is considered lost. In those parts of the PS in which $De > Demax_{y,z}$, the prey which enters is thus encountered (i.e. perceived), but remains unattainable.

Figure 2 illustrates two predator and prey pathways for different entry points and values of De , over a quarter of a circle in the y-z plane, and Figure 3 shows the values of $Demax_{y,z}$ obtained for different points of entry (y, z) into the perception zone. Values were a little lower than those obtained by JW. When $y=0$,

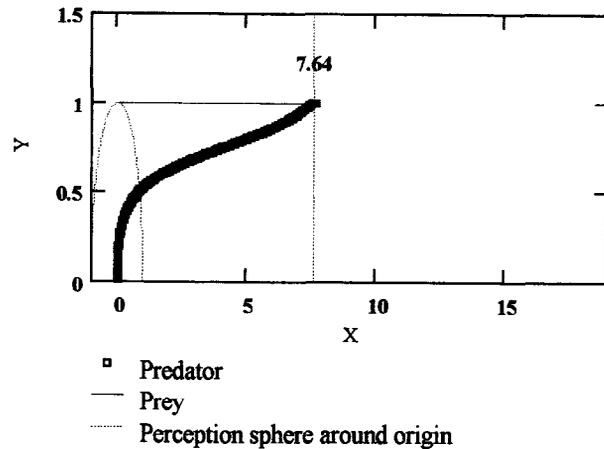
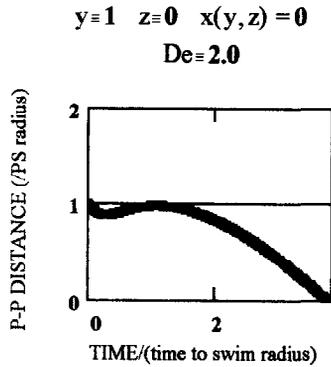
$Demax_{y,z} = \text{infinity}$, and so the contouring has been terminated at $y=0.05$.

By summing water flow ($\text{area} \cdot De \cdot y$) over all values of y, z for which $De < Demax$, and repeating this for different values of De , the volume of water flowing through the attainable zone F_a was determined as a function of De . The results are shown in Figure 4. When $De \leq 2.05$, all the PS is attainable, so F_a is directly proportional to De (and so also to the shear rate). But above this value, F_a increases more slowly, reaches a peak when $De \approx 3$, and then declines.

Rothschild and Osborn (1988) and Yamazaki *et al.* (1991) proposed that encounter rate is proportional to shear rate. This is shown by JW's model to be true. The rate of encounter with attainable prey is also proportional to shear rate up to $De=2.05$. Above this value, however (under the conditions used to define JW's



$last(h) \cdot \delta t = 5.57$ **i.e. when**
 $max(gx) = 17.391$ **i.e. where (x)**



$last(h) \cdot \delta t = 3.82$ **i.e. when**
 $max(gx) = 7.641$ **i.e. where (x)**

Figure 2a, b. Running JW's model for two combinations of prey-entry site (y, z) and De . The figures illustrate how predator-prey distance, h (left-hand diagrams) and predator and prey x - y coordinates (right-hand diagrams) change with scaled time. Although the z dimension is not illustrated, it is modelled.

model), the relationship is dome-shaped. In addition to flow through the attainable zone, the model also gives the time taken to catch the prey. As swimming speed of the model predator is constant, this time represents energy. Some attainable prey may not be worth the time and energy necessary to catch them. The trade-offs are likely to depend on the mix of abundance and quality of the different prey organisms perceived. At high prey densities, the effect of perceiving more than one prey at a time would flatten the top of the dome somewhat.

Interface with the feeding model of MacKenzie, Miller *et al.*

Table 1 gives some equivalences in terminology between the two models. MMCL's model shows a similar dome

shape in ingestion rate versus turbulent shear rate in the turbulent regime. If MMCL's model and JW's are both valid, they ought to give similar results at the interface between their respective domains of application, namely turbulent and laminar (or sub-Kolmogorovian).

MMCL (1994, Figs 3, 4) predicted, from surface wind speed, the turbulent velocity, ω , at a depth of 20 m. They then applied this to a model fish larva, having values of reactive distance (perception distance), $R=6$ mm, and of swimming speed, $v=2$ mm s⁻¹, typical for cod larvae. In their set-up, De can be defined as (shear rate) \times (time taken to swim reactive distance), i.e. $(\omega/R) \times (R/v) = \omega/v$ (see also JW's Table 1). It can then be seen in their Figure 4 that maximum feeding rates for the fish larvae, I_{MAX} , occur at De values of 3.2, 1.6, and 1.0 for pursuit times of 0.9, 1.7, and 2.6 s (0.3, 0.6, and 0.9 time units),

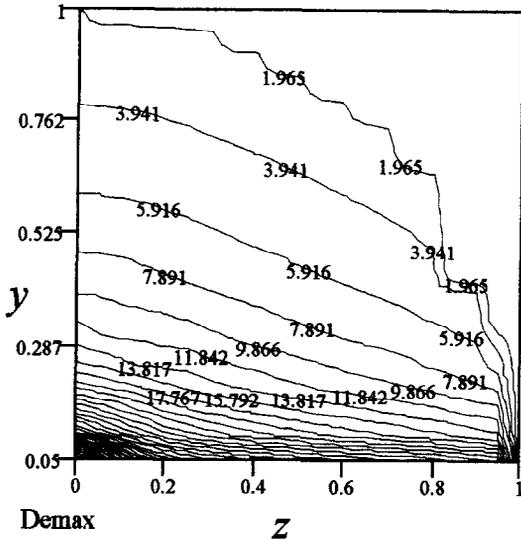


Figure 3. The y-z plane through the perception sphere showing the attainable zone for different values of Deborah number. The 1.965 contour represents the outline of the perception sphere. Other contours represent the part of the perception sphere attainable for a given value of De. Near y=0 (the x-z plane), Demax approaches infinity.

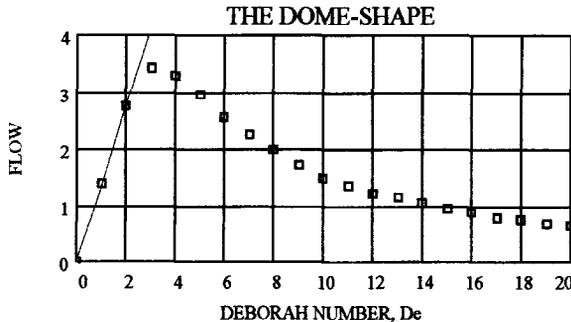


Figure 4. For different values of De, here defined as (shear rate) × (time taken for predator to swim its perception distance), the straight line shows F, the water flow [units: (perception distance)³/(time to swim perception distance)] through the whole perception sphere. The small squares show F_a, the water flow through the attainable part of the perception sphere. Note that encounter (i.e. perception) rate = F × prey concentration. Note also that for values of De between 0 and ≈2.5, F_a = F (i.e. all prey perceived is attainable), but that for higher values of De, F_a < F. (Derived by running JW's model.)

respectively. At very small pursuit times, I_{MAX} would be expected to occur at values of De, here taken as (rms shear rate)/(time for predator to swim reactive distance), i.e. a little higher than 3.2. The De values at which I_{MAX} occurs in the stochastic model of MMCL (1.0 to 3.2) are similar to that given by JW's deterministic one (≈3). Unlike MMCL's model, JW's does not take account of any handling time, and loss of prey is not stochastic but is an "on-off" function of initial prey position and De. Determinist or stochastic functions for predator (or even

Table 1. Equivalences in terminology between MMCL's model (MacKenzie *et al.*, 1994) and JW's (Jenkinson and Wyatt, 1992; present paper).

MMCL	JW
Encounter	Perception
Reactive distance	Perception distance
Reactive field	Perception or detection zone or sphere
Turbulent velocity, ω, over a given distance	(Shear rate over a given distance) × (the distance)
Minimum pursuit time	[Reaction time before predator starts chase]

prey) behaviour or water flow would be easy to incorporate, but few realistic values seem yet to be available for the laminar regime.

The results of JW and MMCL together strongly suggest that the dome-shaped relationship is universal, applying across the viscous, intermediate, and fully turbulent regimes. The dome-shaped relationship also concurs with the idea, illustrated by Margalef's (1978) idea of a field ploughed every week, that "... excess energy cannot be utilised by a system ...". The dome shape may also complement the dispersion of phytoplankton patches by turbulence as an explanation for the Lasker Effect (Lasker, 1975).

Discussion

To determine which feeding-rate model to use, it is desirable to know the length scales of turbulence. The value of the ratio, A, between the actual size of the dissipation-eddies and a calculated "Kolmogorov" length was proposed by Kolmogorov (1941a, b) to be a constant close to unity. Later, Oboukhov (1962) was still suggesting that A might be only a weak function of the origin of the turbulence. It now seems clear, however, that A is strongly variable, and at times nearer to 50 than to 1 in the sea (Jenkinson, 1986; Yamazaki *et al.*, 1991), but has also been found as small as 0.5 (Gibson *et al.*, 1970). Parallel to fundamental studies on turbulence, it may be necessary to proceed, for the time being, by obtaining large amounts of data on ocean turbulence at scales relevant to feeding, particularly to determine empirically how A varies *in situ*. Research should also concentrate much more than at present on the "statistically unimportant" (in terms of energy dissipation) but volumetrically (Brasseur and Lin, 1991) and, no doubt, biologically dominant zones surrounding the intermittent "events". Consideration must also be given to the structures of turbulence (Yamazaki, 1991), which represent some potential predictability (to organisms), at present ignored by current, stochastic models.

MMCL's model involves primarily the feeding by fish larvae at scales around the Kolmogorov length. The authors acknowledge that the smallest turbulent eddies are frequently bigger than the Kolmogorov length, and that, as a result, this feeding should often take place within, rather than across turbulence-dissipation eddies. Nevertheless, they consider that the feeding processes would still be influenced by the strong turbulent fluctuations, found by Hill *et al.* (1992) embedded in the shear, even within dissipation eddies.

JW's deterministic model is likely to be more appropriate at scales smaller than the Kolmogorov length (Table II in JW), including the feeding scales of fish larvae at low turbulent-energy dissipation, as well as when turbulence is damped by density stratification or slime; it is likely to apply to copepod feeding in all but the most vigorous turbulence, and protozoan feeding everywhere (Wyatt and Jenkinson, 1993). Stochastic effects caused by Brownian motion embedded in the laminar shear field may be relevant also at the scales of prey-encounter by very small protozoa and motile bacteria. In large-scale shear fields, such as occur in tideways and rivers, laminar, deterministic models may also be appropriate to hunting by large fishes and aquatic mammals, although the embedded turbulence may once more require stochastic and deterministic elements to be combined in the same model.

The good interface between the stochastic and deterministic feeding models gives hope that differences in the feeding-rate/shear-rate relationship occurring between the turbulent and laminar regimes might validly be ignored in provisional models of feeding by single species. Regardless of which model is used, it might prove possible to tune it to differences in turbulent regime using empirically derived functions. Models of multi-species environments should take into account that feeding and reproduction in different predator species, even at similar rms shear rates, are likely to be favoured more by one regime or the other, leading in time to different species dominating. Furthermore, some plankton organisms appear actively to select preferred shear regimes (Crawford and Purdie, 1992; Mackas *et al.*, 1993), while others have been shown to be good at switching feeding mode when the ambient flow regime is changed (Kiørboe and Saiz, 1995).

JW suggested that grazers with the ability to use "dead reckoning" navigation in shear fields would have a competitive advantage. Under both laminar and turbulent conditions, they would be able to catch their prey more quickly by using indirect swimming routes, and would be able to assess where the prey should be during periods when it is carried out of perception range. Such behaviour might be more dominant in organisms with more highly developed nervous systems.

From recent, but rather limited, experimental data, it seems that plankton organisms are generally well

adapted to the conditions of turbulence where they occur naturally (Kiørboe and Saiz, 1995). This strongly suggests that one of the dominant selection pressures acting on plankton organisms is behavioural adaptation to ambient turbulence. We should not be surprised if plankton predators and prey "know" (in the evolutionary and behavioural sense) much more about marine turbulence than we do.

For different key predators and prey, observations should be made to determine size and shape of perception zones, swimming speeds and hunting behaviour including the cues used for navigation and the employment of dead reckoning.

Phytoplankton slime and fibres can either increase or decrease De . For instance, Adriatic diatom mucus can show copepod swimming (Malej and Harris, 1993), thus increasing De , and must increase the energy and the time necessary for copepods to catch their prey. Mucus sheaths, in contrast, and mucus aggregates dramatically reduce local deformation rates, and thus De . *A priori*, this reduction in shearing might help grazers unless (1) the mucus is thick enough to slow penetration; or (2) it is toxic or retains either toxins or mimics of toxins. The concept of De simplifies the conceptualization of these partially opposing effects.

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