Motility of zooplankton: fitness, foraging and predation

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The relative fitness of planktonic organisms foraging under the risk of predation is examined in terms of their swimming speed, path geometry and jump frequency. Fitness is quantified in terms of encounter and ingestion of prey, respiration and energy cost associated with swimming and mortality due to encounters with predators. It is shown that a convoluted swimming path in the form of meanders, zigzags or spirals confers greater fitness than swimming along a straight path. Optimal path configuration is such that the length-scale of the path-meanders is commensurate with an organism’s detection radius to prey, which in turn scales with the size of the organism. Optimal swimming speed for a cruise-feeding organism decreases with increasing prey concentration and increasing risk due to ambush predators. For ambush feeding on motile prey, a benefit is gained by periodically moving to a new location. The time spent swimming is largely a function of energetic costs, whereas the time spent feeding is strongly controlled by prey concentration and the risk posed, in turn, by ambush predators. These predictions are supported by observations drawn from the literature.

INTRODUCTION

As with all life, planktonic organisms are confronted with by three overarching tasks, to find food, reproduce and avoid predation. Each of these three tasks is governed by an associated encounter rate; the rate at which the organisms discovers prey, finds a mate and is itself encountered by predators. For planktonic organisms, encounter rates are in many cases strongly linked to how the organism moves through its environment. For instance, an organism waiting for prey is less likely to find food than one actively searching, and yet active searching exposes the organism to higher risk of predation. Hence, one might expect motile behaviour to reflect a trade-off between beneficial and detrimental encounters (Lima and Dill, 1990; Tiselius et al., 1997; Houston and McNamara, 1999). The fundamental significance of encounter rates suggests that there is a strong selection pressure on motile behaviour, and that the motility patterns that are witnessed in nature are in some way optimal for an individual in terms of this trade-off. Many planktonic organisms from bacteria to copepods are capable of some degree of locomotion, which is exhibited in a variety of swimming patterns. Such swimming patterns are intimately connected with the organism’s feeding strategy. An ambush feeder, for instance, is mostly stationary, but may periodically jump to a new location to “test the waters” there. Likewise, suspension feeders that produce feeding currents may alternate periods of feeding with periods of translocation. Cruise feeders display continuous swimming along relatively linear tracks with occasional changes of direction, whereas other feeders adopt a helical swimming pattern, also interspersed with occasional direction changes. Although each of these motility patterns clearly benefits a particular feeding mode, it is unavoidable that these same motility patterns expose the organism to some risk of predation.
Individual organisms are capable of a range of motility patterns; a factor reflected in the variability of motility characteristics exhibited in populations of like individuals. Some swim faster or slower, some adopt more convoluted paths than others, and time budgets devoted to different elements of their feeding behaviour may vary. In addition, motility is a flexible function of environmental conditions. For instance, swimming speed and path configuration have been shown to vary in response to food concentration [e.g. copepods (Buskey, 1984; Tiselius, 1992; Takahashi and Tiselius, 2005) and protists (Buskey and Stoecker, 1988; Fenchel and Jonsson, 1988; Bartumeus et al., 2003; Menden-Deuer and Grünbaum, 2006) and predation risk [e.g. protists (Broglio et al., 2001) and copepods (van Duren and Videler, 1996b)]. Treating these motility characteristics as adaptive traits, this work seeks to explain the underlying rules that determine which motility behaviour optimizes an individual’s fitness. At the core of this are twinned quantitative descriptions of how behaviour affects encounters with food and predators, and subsequently how these affect the net energy intake and survival of individuals.

METHOD

Encounter rates are governed by three basic components. These are the speed (v) with which an organism moves relative to its encounter partner (prey, mate or predator), the concentration (c) of its encounter partner and the encounter distance (s, i.e. the distance at which the organism detects its prey, or the distance at which the organism is detected by a predator). Indeed, a simple formulation for encounter rate \( \zeta \) can be written as \( \zeta = m^2 v c_s \), which simply states that the encounter rate is the rate of volume swept out times the concentration of encountered organisms. These parameters can be expected to be quite different for an organism’s interaction with its prey compared with its predator. More importantly, these encounter rates impact the organism’s fitness in different ways. Specifically, encounter rate with prey says something about the rate at which the organism gains energy, and hence something about its growth and reproduction rate. In contrast, encounter rate with predators says something about the organism’s mortality rate and expected life span.

Evolutionarily consistent behaviour is that which optimizes an individual’s fitness in terms of the rate at which it acquires energy for reproduction and its survival in the face of predation risk. Although there is a considerable body of work surrounding this issue (Mangel and Clark, 1988; Houston and McNamara, 1999), I will examine fitness in terms of a rather simple parameter, one that captures at least some aspect of the energy—predation trade-off. In particular, one feature of fitness can be deduced from the parameter (Gilliam and Fraser, 1987; Houston et al., 1993)

\[
g(b) = \frac{E(b)}{\mu(b)}
\]

where \( E \) is the rate at which an organism takes in energy and \( \mu \) the organism’s mortality rate. These are written as functions of behaviour, \( b \), indicating that they depend on the particular motile behaviour adopted by an organism. A simple interpretation of \( g \) is that it is the total energy gained by an organism in its expected lifetime following a given behavioural strategy. A viable behaviour is one for which \( E(b) > 0 \), at least in the long term. The behavioural strategy \( b^* \) that maximizes the parameter \( g(b) \) is optimal for an individual competing with like individuals in a stable environment for a common limiting resource.

While there are a number of behavioural optimization questions that can be addressed by this approach, I will explore three relatively general cases, namely, optimal swimming speed and path geometry for cruise feeding and the optimal jump frequency for ambush feeding. In these three cases, behaviour \( b \) can be characterized by one or two well-defined parameters that can be treated independently of each other. That is, optimal swimming speed does not affect optimal path geometry, although for other strategies this independence may be less robust. I choose, as illustrative examples, behavioural strategies of marine copepods and protists, although the underlying analysis is quite general, and can be applied equally to any number of planktonic organisms ranging from bacteria to larval fish.

RESULTS

Speed of swimming

For a cruising predator such as a ciliate or a copepod, increasing its swimming speed will impact its fitness in three ways; it will increase contact with food (positive), require greater energy expenditure (negative), and increase predation by higher contact rates with predators (negative). For such an organism, the rate at which it encounters immobile prey is \( \zeta_{prey} = \pi R^2 v C \) where \( R \) is the prey detection distance, \( v \) the organism’s swimming speed and \( C \) the prey concentration. Given that the organism spends a finite time \( h \) handling prey, the
ingestion rate is then

\[ I = \frac{\pi R^2 C_v}{1 + \pi R^2 C_{oh}} \]  

(2)

which is consistent with a Hollings type II functional response. Tacit assumptions in equation (2) are that effects of turbulence are negligible and that all encounters lead to a successful capture. This, of course, is not always the case, although I maintain these simplifications throughout. The rate of intake of energy is thus \( I \), where \( e \) is the per-capita energy content of prey that can be assimilated. Swimming however has an energetic cost (Vlymen, 1970); the faster the speed, the greater the power required to propel the organism forward. Assuming Stokes’ law (appropriate when the Reynolds number \( \text{Re} < 1 \), cf. Table I), the power required is \( W = q v^2 \), where, for brevity, \( q \) is a parameter depending on various hydro mechanical factors (see Table I for details). An important factor in calculating \( q \) is \( e \), the efficiency with which internal energy is converted to forward locomotion. Although estimates of this vary greatly (Minkina, 1981; Morris et al., 1985; Buskey, 1996), I use here a value \( e = 1\% \). The net rate of energy intake is thus

\[ E = \frac{esC_v}{1 + \hbar C_v} - m - qv^2 \]  

(3)

where \( m \) is the base metabolic cost of the organism, and cross-sectional search area is written \( s = \pi R^2 \). The maximum gross rate of energy intake is \( E_{\text{max}} = e/h \), a condition set by the maximum ingestion rate \( I_{\text{max}} = 1/h \). Energy expenditure in the form of base metabolism and swimming costs cannot exceed \( E_{\text{max}} \). That is, in order for swimming behaviour to be viable, its speed must be such that

\[ v < \left( \frac{1}{q} \frac{e}{h} - m \right)^{1/2} \]

Swimming at speed \( v \), the organism also has an encounter rate with its predators

\[ \zeta_{\text{prey}} = \pi X^2 P(v^2 + a^2)^{1/2} \]  

(4)

where \( X \) is the distance at which a predator can detect the organism, \( u \) the predator swimming speed and \( P \) the concentration of predators. Assuming that each encounter has a fixed probability of capture, this gives mortality rate \( \mu \propto \zeta_{\text{prey}} \). For an ambush predator, \( u = 0 \) so that the swimming speed of the organism becomes all important in its predation risk. For visual ambush predators, \( \zeta_{\text{prey}} \propto v \). In contrast, for a rheotactic predator relying on hydro mechanical signals to alert it to the presence of prey, the detection distance scales as \( X \approx a (v/\sigma)^{1/2} \) where, as before, \( a \) and \( v \) are the size and swimming speed of the organism under consideration and \( \sigma \) the sensitivity (threshold speed) that the predator can detect (Visser, 2001). This is based on the

\begin{table}[h]
\centering
\caption{Glossary of terms}
\begin{tabular}{|c|c|}
\hline
Symbol & Description \\
\hline
\hline
\( a \) & Equivalent spherical radius of an organism \\
\( A \) & Amplitude of a helical or sinusoidal path \\
\( B \) & Pitch of a helical path \\
\( C \) & Concentration of prey \\
\( D \) & Diffusivity, for random motility, \( D = v \lambda / \beta \) \\
\( d \) & Translocation distance for ambush feeding \\
\( \epsilon \) & Per capita energy content of a prey cell that can be assimilated \\
\( E \) & Network rate of energy acquisition due to a specific motile behaviour \\
\( F \) & Feeding duration for ambush feeding \\
\( g \) & Ratio of net rate of energy gain to intrinsic mortality rate \\
\( h \) & Handling time \\
\( p \) & Predation factor that scales the risk due to a specific behaviour to the background mortality rate \\
\( P \) & Concentration of predators \\
\( Q \) & Rate of energy intake for cruise feeding \\
\( q \) & A hydro mechanical parameter (dimensions \( M T^{-1} \)) relating power expended to swimming velocity, specifically \( q = 6\pi r^2 \) as a low Reynolds number regime \\
\( R \) & The detection distance at which an organism detects its prey \\
\( r \) & Radius of encounter sphere, set to \( R \) for foraging and \( X \) for predation \\
\( \text{Re} \) & Reynolds number: \( \text{Re} = \pi R^2 \) \\
\( S \) & Swimming duration for ambush-feeding translocation \\
\( T \) & Duration of a feeding-translocation cycle for ambush feeding, \( T = F + S \) \\
\( u \) & Swimming speed of an organism’s predator \\
\( \nu \) & Swimming speed of organism under consideration \\
\( V \) & Generally, the volume swept out by a spherical ball following a specific trajectory \\
\( X \) & The detection distance at which an organism is detected by its predator \\
\( Z \) & Encounter rate \\
\( \Omega \) & Cross-sectional area of a helical tube perpendicular to the helical axis \\
\( \alpha \) & Net energy required for an organism to reproduce one offspring \\
\( \delta \) & Path efficiency for helical swimming, \( \delta(a,A,B) = \Omega(r,A,B) \sin [\theta(\pi)^2] \) \\
\( \epsilon \) & Efficiency of swimming: ratio of power expended by organism to power used in overcoming viscous drag, take to be 1% \\
\( \gamma \) & Path efficiency for a random walk, \( \gamma(A,r) = 4A/[4A + 3r] \) \\
\( \eta \) & Viscosity of water, taken to be \( 1.3 \times 10^{-3} \text{ m}^2 \text{s}^{-1} \) \\
\( \lambda \) & Correlation length of a random walk \\
\( \mu \) & Net mortality rate including that due to a specific behaviour \\
\( \mu_0 \) & Background mortality rate \\
\( \theta \) & Pitch angle of a helical path, \( \theta = \tan^{-1}(B/2\pi A) \) \\
\( \rho \) & Density of water, taken to be \( 1028 \text{ kg m}^{-3} \) \\
\( \tau \) & Correlation time of a random walk \\
\hline
\end{tabular}
\end{table}
hydromechanical signal generated by a self-propelled body, and basically states that a faster swimming organism is more conspicuous than one that swims at a lower speed. In this case, $k_{\text{predator}} \propto v^2$.

The mortality rates of organisms are partly due to risky behaviour (such as high speed swimming) and partly due to other effects such as disease, parasites or background predation not due to a specific behavioural strategy (e.g. due to a cruise predator with $a >> v$). To include all effects, net mortality rate can be written

$$\mu = \mu_0(1 + p_0 v^a)$$ (5)

where $n = 1$ or $2$ for visual and rheotactic ambush predation, respectively. Here, $\mu_0$ is the mortality rate independent of swimming and $p_0$ coefficients expressing the increase in predation risk due to motility. In general, the fitness parameter can thus be written as

$$g(v) = \frac{[\epsilon C_f/(1 + h s C_f)] - m - q v^2}{\mu_0(1 + p_1 v + p_2 v^2)}.$$ (6)

As an illustrative example, let us look at the fitness in terms of swimming speed for a generic calanoid copepod with prosome length 600 $\mu$m (e.g. Temora longicornis), feeding on a typical prey item Thalassiosira weissflogii (carbon content 260 pg C cell$^{-1}$, $\epsilon = 6 \times 10^{-6}$ J cell$^{-1}$). Parameter values are listed in Table II. The handling time is assumed to be $h = 4$ s, corresponding to a maximum ingestion rate of 900 cell h$^{-1}$ or 5 $\mu$g C day$^{-1}$, a value consistent with laboratory observations (e.g. Takahashi and Tiselius, 2005) and others reported in Mauchline (Mauchline, 1998). Based on formulas given in Mauchline (1998), the respiration rate of $T. longicornis$ at 15°C is $3.3 \times 10^{-2}$ $\mu$L O$_2$ h$^{-1}$ which corresponds to a base metabolic rate of $m = 1.8 \times 10^{-7}$ W. The equivalent spherical radius of the copepod is $a = 0.14$ mm [based on volume, also from relationship found in Mauchline (Mauchline, 1998)]. Assuming a swimming efficiency $\varepsilon = 1\%$, this gives a hydrodynamic swimming cost coefficient $q = 3.6 \times 10^{-2}$ W s$^{-2}$ m$^{-2}$.

For the detection distance, we set $R = 600 \mu$m (Tiselius and Jonsson, 1990) to give a prey cross-sectional search area of $s = 1.1 \times 10^{-6}$ m$^2$.

Background mortality rate is taken as $\mu_0 = 0.1$ day$^{-1}$, or about $10^{-6}$ s$^{-1}$. This mortality rate is typical for a range of marine copepods, even in the absence of direct predation, that is due solely to parasites and disease (Mauchline, 1998; Tang et al., 2006), and may be deemed a reasonable estimate when behaviour independent predation (e.g. fast swimming cruise predators) is included. On top of this is added a behaviour specific mortality rate due to swimming. While the variation of this contribution to mortality will be examined later, for the moment, I choose parameters such that the total mortality increases by 25% at a swimming speed of 1 mm s$^{-1}$ (about 1 body length per second). This gives coefficients $p_1 = 2.5 \times 10^5$ s m$^{-1}$ and $p_2 = 2.5 \times 10^5$ s$^2$ m$^{-2}$ for visual and rheotactic predation, respectively. These coefficients are somewhat arbitrary and essentially reflect the abundance of visual and rheotactic predators, respectively. For instance, the value given for $p_1$ is consistent with a larval fish (visual) predator with detection distance $X = 3$ mm, 100% capture efficiency and abundance $P = 10$ m$^{-3}$.

Given these parameter settings, Fig. 1 plots the fitness parameter $g$ as a function of swimming speed for various prey concentrations. This is plotted for the three cases: (i) behaviour independent mortality; (ii) rheotactic ambush predation and (iii) visual ambush predation. At low swimming speeds, fitness is constrained by $\epsilon / h \mu_0$ (high prey concentration) and $-m / \mu_0$ (at low concentration), the latter being non-viable. The effect of hydrodynamic cost becomes apparent at high swimming speeds, particularly in case (i) where predation is independent of swimming speed. Somewhere between $10^7$ and $10^6$ cells m$^{-3}$, all swimming speeds become non-viable. The prey concentration at which this happens is independent of the predation risk.

Summary plots of the optimal swimming speed (derived numerically) are given in Fig. 2 for all the three cases; Fig. 2A for variable prey concentration and Fig. 2B for variable predation risk. Optimal swimming speed in general is a decreasing function of concentration; the more prey is available, the slower an organism can afford to swim. By and large, predation has a strong influence on optimal swimming speed. This can be seen in the order of magnitude difference between

### Table II: List of coefficient values used for the illustrative example of optimal swimming speed

<table>
<thead>
<tr>
<th>Coefficients derived for an adult $T. longicornis$</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Metabolic cost ($m$)</td>
<td>$1.8 \times 10^{-7}$ W</td>
</tr>
<tr>
<td>Swimming cost coefficient ($q$)</td>
<td>$3 \times 10^{-4}$ W s$^{-2}$ m$^{-2}$</td>
</tr>
<tr>
<td>Handling time ($h$)</td>
<td>4 s</td>
</tr>
<tr>
<td>Search cross section area ($s$)</td>
<td>$2.8 \times 10^{-7}$ m$^2$</td>
</tr>
<tr>
<td>Base mortality ($\mu_0$)</td>
<td>$10^{-8}$ s$^{-1}$</td>
</tr>
<tr>
<td>Coefficients derived for prey item: Thalassiosira weissflogii</td>
<td>$6 \times 10^{-6}$ J cell$^{-1}$</td>
</tr>
<tr>
<td>Predation enhancement coefficients:</td>
<td></td>
</tr>
<tr>
<td>Visual predator ($p_1$)</td>
<td>$\mu_0 \times 2.5 \times 10^2$ s m$^{-1}$</td>
</tr>
<tr>
<td>Rheotactic predator ($p_2$)</td>
<td>$\mu_0 \times 2.5 \times 10^5$ s$^2$ m$^{-2}$</td>
</tr>
</tbody>
</table>

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the behaviour independent mortality case (Fig. 2A), and those where mortality has linear or quadratic dependence on swimming speed. For the former case, the level of predation risk has no effect on the optimal swimming speed, but it does for the behaviour dependent case (Fig. 2B). Here, the predation factor $\phi$ is taken as multiples of the predation coefficient given above. That is, the increase in predation risk over background mortality is $\phi \times 25\%$ at $1 \text{ mm s}^{-1}$. Essentially, $\phi$ represents variable abundances of different types of predators. For the cases where swimming speed contributes to mortality, as with predation by visual or rheotactic ambush predators, optimal swimming speed is a decreasing function of predation risk.

Typical swimming speeds for *T. longicornis* adults range between 10 and $2 \text{ mm s}^{-1}$ (van Duren and Videler, 1996a; Mauchline, 1998), consistent with the estimates here. Further, female *T. longicornis* are seen to decrease their swimming speed from $\sim 5 \text{ mm s}^{-1}$ at prey concentrations of $10^8$–$10^{10}$ cells m$^{-3}$ to $\sim 2 \text{ mm s}^{-1}$ at $10^{11}$ cell m$^{-3}$ (van Duren and Videler, 1996a). Likewise, van Duren and Videler (van Duren and Videler, 1996b) also show a decrease in average swimming speed (50–20%) of *T. longicornis* in response to perceived predation risk (in this case, the presence of chemical exudates from fish). Although these changes in swimming speed are not as dramatic as those predicted here for optimal swimming speed, they nonetheless confirm the general trend—swimming speeds should decrease as both prey concentration and predation risk increase.
Meanders, zigzags and spirals

An organism swimming in a straight-line path presents the most efficient means of searching for prey while also exposing itself to maximum predation risk. It can mitigate its predation risk by the simple expedient of introducing a degree of curvature to its path in the form of meanders, zigzags or spirals. Executing a convoluted path, the organism is doubling back over volumes of space where it has already exposed itself to risk, and that it has evidently found “safe”. Moreover, since search distance is generally smaller than the exposure distance, a moderate degree of curvature may significantly decrease exposure to risk while having a barely perceptible effect on its foraging efficiency. This is illustrated in Fig. 3 for a sinusoidal swimming path. For simplicity, this is illustrated for a two-dimensional search following a sinusoidal path. As the detection distance increases, so too does the overlap volume. In general, an overlap in the volume swept out becomes significant when the detection distance exceeds the radius of curvature of the path. For the sinusoidal path illustrated in Fig. 3, this happens when \( R > \frac{v^2}{(4A\omega^2)} \) where \( A \) is the amplitude of the sinusoidal path and \( \omega \) its frequency. In what follows, I consider two motility patterns commonly exhibited by planktonic organisms: helical swimming and random walk motility and how these swimming paths affect the fitness of organisms that execute them.

Helical swimming

Helical swimming is a common mode of locomotion exhibited by plankton including bacteria (Berg, 1992), protists (Fenchel and Jonsson, 1988) and copepods (Titelman, 2001). Mechanistically, it arises due to an axial rotation together with forward propulsion and enables organisms to “average out” asymmetries in their morphology and/or propulsive thrust and achieves a degree of net forward motion rather than continually swimming in circles (e.g. Fenchel, 2001). Organisms are able to alter the amplitude and rate of rotation (thus pitch) of their helical paths independently of each other (Fenchel, 2001; Machemer, 2001). Some organisms appear to alter their rate of rotation in response to local chemical concentrations, providing an effective and efficient chemotactic ability (Grenshaw, 1996; Thar and Fenchel, 2001). In light of the above, it may also be deemed possible that helical swimming has an advantage over straight-line swimming in that it potentially decreases the exposure volume of the organism to predation risk.

A helical path can be characterized by its amplitude \( A \), pitch \( B \) and speed \( v \) (Fig. 4). The volume swept out by a spherical absorber (radius \( r \)) following a helical path, increases linearly with time as

\[
V(t) = \Omega(r, A, B)ut
\]

where \( \Omega(r, A, B) \) is the area “cut” by the spherical absorber through a plane perpendicular to the axis of the helix and \( u \) the along axis swimming speed. The latter is given by \( u = v\sin\theta \), where \( \theta \) is the pitch angle given by \( q = \tan^{-1}(B/2\pi r) \). The volume \( V(t) \) is the volume of a helical tube of height \( ut \). It turns out that the cut area \( \Omega \) is rather tricky to calculate, and this is done numerically.

The “efficiency” of the helical path is the ratio of the new (net) volume searched, or exposed to, to the gross volume. That is,

\[
\delta(r, A, B) = \frac{\Omega(r, A, B)}{\pi r^2} \sin\theta
\]

Fig. 3. Illustration of how a curved path (dotted line) decreases predation risk. The exposure volume (bounded by dashed lines) is decreased with respect to a straight swimming path due to overlaps (shaded area). The volume searched for prey (bounded by the solid lines) however remains the same as for a straight path.
and tangential speed $v$ whose centre travels along this path, traces out a helical tube. $\Omega$ is the cross sectional area of the tube in a plane perpendicular to the axis of the helix, and the volume of the tube increases in time as $\Omega = \Omega u t$ where $u = v \sin \theta$. In (B), an overlap in the volume traced out first occurs when $B = 2r$ or $L = 2r$ where $L^2 = (2A^2 + B/2)^2$.

with $r$, the overlap becomes large, and the path efficiency approaches zero. When $B = 0$, the path is a closed torus, and $\delta = 0$.

In terms of fitness, an organism should tailor its path so as to maintain a high efficiency with respect to its search for prey ($\delta(R, A, B) \to 1$) while at the same time keeping its exposure to predation as low as possible ($\delta(X, A, B) \to 0$); $R$ and $X$ being the prey and predator detection distances, respectively. The corresponding fitness function can be written as

$$g(A, B) = \frac{e^{\pi R^2 C_0 \delta(R, A, B)} - \tilde{m}'}{\mu_0 (1 + p \delta(X, A, B))}. \quad (9)$$

In this case, $\tilde{m}'$ is the net metabolic cost including that due to swimming and $p$ the increased mortality due to an increase in the number of ambush predators. While there may be some energetic costs associated with swimming along a specific helical path (e.g. pitch is determined by axial rotation rate which in turn requires energy expenditure to overcome viscous torque), $\tilde{m}'$ is treated as being behaviourally independent. Provided the metabolic cost is small compared with the rate of energy intake $Q = e^{\pi R^2 C_0}$, the relevant functional form reduces to

$$g(A, B) = \frac{Q}{\mu_0} \frac{\delta(R, A, B)}{\delta(X, A, B)}.$$

Figure 6A traces $\delta(R, A, B)$ and $\delta(X, A, B)$ for a given fixed helical pitch ($\theta = 0.16$, equivalent to $A/B = 1$), prey detection distance ($R$) and predator detection distance ($X = 10R$) for varying helical amplitude $A$. The ratio $X/R = 10$ is consistent with general predator, prey size ratios (Hansen et al., 1994), and the observation that detection distance often scales with body size. The corresponding fitness function is given in Fig. 6B for a variety of predation pressure factors. For this configuration, the optimum amplitude appears to be independent of predation pressure, and is located where the foraging efficiency first approaches 1 (Fig. 6A).

Geometric considerations (cf. Fig. 4B) suggest that the overlap is zero (i.e. efficiency is 1) when both $B/2 \geq R$ and $L/2 = (A^2 + B^2/4)^{1/2} \geq R$. This can be seen by considering the overlap of cross-sectional search areas at half (the latter) and a full (the former) orbital periods. For the example of the path configuration considered above ($A = B$), the former condition is limiting so that $A^* = B^* = 2R$.

Is this a global optimum though? The organism may after all be able to vary both amplitude and pitch independently. First, it can be noted that the path efficiency with respect to the predator (detection distance $X$) should be as low as possible, and lie in the lower left hand corner of Fig. 5. That is, $A/X \leq 1$ and $B/A \leq 1$. On the other hand, the foraging efficiency should be as close to 1 as possible; a condition met for $B^* \approx 2R$. 

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**Fig. 4.** A helical swimming path (A) is defined by amplitude $A$ and pitch $B$, or pitch angle $\theta = \tan^{-1}(B/2\pi A)$. A spherical shell, radius $r$ and tangential speed $v$ whose centre travels along this path, traces out a helical tube. $\Omega$ is the cross sectional area of the tube in a plane perpendicular to the axis of the helix, and the volume of the tube increases in time as $\Omega = \Omega u t$ where $u = v \sin \theta$. In (B), an overlap in the volume traced out first occurs when $B = 2r$ or $L = 2r$ where $L^2 = (2A^2 + B/2)^2$.

**Fig. 5.** Contours of the efficiency of a helical path (amplitude $A$ and pitch $B$) for a search/exposure radius $r$. The lines $B = 2r$ (dotted line) and $A = B$ (dashed line) are plotted for reference.
This can be seen in Fig. 5 where the line $B = 2R$ is plotted and is coincident with the contour $\delta = 1$ in the region where $B/A \leq 1$. Combining these conditions, we thus have the condition

$$X \geq A^* \geq B^* \approx 2R.$$  

This suggests that for helical swimming, optimal geometry should conform to a spiral with a shallow pitch; i.e. the amplitude should be of the same order or larger than the pitch.

Although there are no specific observations of helical swimming under the dual pressures of foraging efficiency and predation risk, some corroboration can be found in observations of nauplii swimming patterns. Titelman and Kiørboe (Titelman and Kiørboe, 2003b) show typical swimming tracks of late stage Centropages typicus and Acartia tonsa with pitch $B = 300–500 \mu m$ and amplitude $A = 250–500 \mu m$, that is $A \approx B$. Given that these organisms have an equivalent spherical diameter $a \approx 100 \mu m$, their detection radius to their prey is a few times their body radius, i.e. $R \approx 200 \mu m$, it appears that $B \approx 2R$, which is consistent with the condition stated above.

**Random walk**

The volume swept out by a spherical shell that is moving through space following a random walk trajectory, conforms to a mathematical entity known as the “Wiener sausage” [Fig. 7, named after the celebrated mathematician Norbert Wiener (1894–1964)]. This turns out to be a useful measure to number of real world processes in physics, chemistry and communication (e.g. Oshanin et al., 1994; Yang et al., 2000; Kesidis et al., 2003), as well as for the searching strategies of planktonic organisms (Levandowsky et al., 1988; Viswanathan et al., 1999).

A random walk trajectory can be characterized by a swimming speed $v$ and a correlation time scale $\tau$. That is, $\tau$ is a measure of how long the path has directional persistence, and can be related to the correlation length scale $\lambda = v\tau$. For brevity, we will term $\lambda$ the motility length scale and $\tau$ the motility time scale. Although I have illustrated this in Fig. 7 as a sequence of straight-line segments interrupted by discrete turn events, a zigzag path, the treatment is formally identical for a continuous random walk (Taylor, 1921), a meandering path. If we consider an organism executing a random walk motility with search (or exposure) radius $r$, then its search (or exposure) volume equates to a Wiener sausage. The pertinent question with regards fitness is how the characteristics of the Wiener sausage vary as a function of the motility length scale relative to both the search and exposure radii.

At large times ($t \gg \tau$) and in the diffusive limit ($r \gg \lambda$), the expectation value of the volume of a Wiener sausage (i.e. new volume scanned) is linear in time, and can be written as $V[t] = 4\pi \lambda^3 t/3$ (Berezkovskii et al., 1989; Kesidis et al., 2003). This can

![Fig. 7. The Wiener sausage; the volume traced out by a spherical shell whose trajectory follows a random walk. Run lengths $\lambda_i$ are exponentially distributed, and turn angles $\theta_i$ are uniformly random.](https://academic.oup.com/plankt/article-abstract/29/5/447/1498407)
be compared to the gross volume swept out \( V(t) = \pi r^2 \mu t \).
That is, the ratio of net to gross volume swept out goes as \( \lambda /r \), so that the efficiency is relatively small for large \( r \).
This analysis is not particularly revealing, however, as it relies on the diffusive assumption that the search radius is much larger than the motility length scale. In contrast, it appears that the motility length scale exhibited by a planktonic organism is larger than its detection distance for prey while being of the same order as the distance at which a predator detects it (Visser and Kiørboe, 2006).

A full and rigorous examination of the characteristics of the Wiener sausage over the relevant parameter space (i.e. as the motility length-scale varies with respect to the detection distance from \( \lambda < r \) to \( \lambda \gg r \)) is beyond the scope of this work. As an indication, however, we can examine the asymptotic limits. For \( \lambda \ll r \), the diffusive limit can be assumed to apply, giving

\[
\beta_{\text{diff}} = \frac{4}{3} \pi r \lambda v \quad (10)
\]

where \( \beta \) is the rate of change of the Wiener sausage, i.e. maximum clearance rate. At the other extreme where \( \lambda \gg r \), the ballistic limit applies

\[
\beta_{\text{ball}} = \pi r^2 v. \quad (11)
\]

A simple relationship connecting the two for all ranges of \( \lambda \) and \( r \) is

\[
\beta(\lambda, r) = \frac{4\lambda}{4\lambda + 3r} \pi r^2 v. \quad (12)
\]

Although the argument supporting this is somewhat circumstantial, a similar (albeit more complex) expression was more rigorously derived by Harris (Harris, 1982) for the flux of Brownian particles into a perfectly absorbing sphere, a problem closely related to the volume of the Wiener sausage. In Fig. 8, I give a comparison of the expression given here, and the corresponding form based on Harris (Harris, 1982). The two follow very similar trends, although the formulation given here better captures the diffusive limit. Given this similarity and the rule of parsimony, I will use equation (13) to describe the volume of the Wiener sausage.

The fitness of an organism in terms of its motility length scale can thus be written as

\[
g(\lambda) = \frac{\epsilon C \beta(\lambda, R) - m}{\mu_0 (1 + p \gamma(\lambda, X))}
\]

where \( \gamma(\lambda, r) = 4\lambda/(4\lambda + 3r) \) is the path efficiency. Figure 9A traces the path efficiency for foraging \( \beta = R \) and predation \( \beta = X = 10R \) as a function of varying motility length scale. The relative fitness of different motility length scales are plotted in Fig. 9B, again assuming that the predator detection distance \( X \) is 10 times the foraging detection distance \( R \). These are plotted for different predation risk factors \( p \), representing the relative risk due to encounters with ambush predators, to general background (behaviour independent) mortality risk. Essentially, \( p \) can be thought of as scaling with the abundance of ambush predators. These plots show a marked maximum, particularly at intermediate values of \( p \). The maximum shifts towards smaller motility length scales as the behaviourally dependent predation risk increases.

The optimal motility length scale for an organism executing a random walk lies between its detection distance to its prey and the distance at which it in turn is detected by its predators (Fig. 10). For high risk of ambush predation \( p \approx 10 \), \( \lambda^* \) tends to the prey detection radius \( R \), whereas at low risk \( p \approx 0.3 \), \( \lambda^* \) tends to the predator detection radius \( X \). This is consistent with results found by Visser and Kiørboe (Visser and Kiørboe, 2006), which showed, for a range of
planktonic organisms (bacteria, flagellates, ciliates, nauplii and adult copepods), a distinct relationship between the motility length scale and the size of the organisms itself. Specifically, \( \lambda \approx 15a \) where \( a \) is the equivalent spherical radius of the organism. Typically, the prey detection distance is a few times the radial size of the organism (e.g. Lenz and Yen, 1993), so that \( \lambda \approx 5R \) is roughly the optimum found for an ambush predation risk of \( p = 1 \), i.e. where half the net mortality rate is due to risky behaviour.

### Diffusion, depletion and jumps

Ambush predators, such as nauplii of marine copepods (Buskey et al., 1993; Titelman, 2001), rely on the motility of their prey to bring about encounters. If the prey’s motility conforms to a random walk, then the underlying encounter process is diffusive in nature [provided run length to encounter distance is small (Visser and Kiørboe, 2006)]. Starting from an initially undisturbed prey field, the organism’s encounter rate with prey is initially high but falls off with time as the local prey field becomes depleted. That is, the encounter rate becomes diffusion limited. To alleviate this, the organism can move to a new, undisturbed part of the prey field where its encounter rate is again high (Titelman and Kiørboe, 2003b). Each relocation, however, will expose the organism to some elevated risk of predation (Titelman and Kiørboe, 2003a). Functionally, this is very similar to the classic problem of optimal foraging on patches (Charnov, 1976) when predation risk is taken into account (Gilliam, 1990).

The most accessible approach to include time budgets and time dependent energy intake into the analysis is to introduce a more general formulation of Gilliam’s fitness parameter:

\[
g(b, t) = P_{\text{f}}(b, t) \int_0^\infty E(b, s) \, ds. \tag{13}\]

Here, \( P_{\text{f}}(b, t) \) is the probability of an organism surviving to time \( t \) while executing behaviour \( b \) and the integral is the net energy acquired in the same interval. This is the basis of the analyses introduced by Mangel and Clark (Mangel and Clark, 1988), and it can be noted that for the case where the rate of energy acquisition and survival are time independent, and taking into account that the appropriate integration time scale is the expected life span of the organisms (i.e. \( \mu^{-1} \)), the expression in equation (14) reduces (to within a constant factor) to the fitness parameter in equation (1).

For an ambush predator, its encounter rate with motile prey is given by

\[
\zeta(t) = 4\pi DR C \left(1 + \frac{R}{\sqrt{\pi D t}}\right). \tag{14}\]
where \( D = w\lambda/3 \) (e.g., Berg, 1992) is the diffusivity of its randomly moving prey, which swim at speed \( w \) and with a motility length scale \( \lambda \). Other parameters are as already given and defined in Table I. The total energy acquired follows

\[
\Sigma(t) = e^{\int_0^t \gamma(s) \, ds} = 4e \pi DRCt \left( 1 + \frac{2R}{\sqrt{\pi Dt}} \right)
\]

which is initially rapid \((t < R^2/D)\) but falls off with time. If this were the only consideration, then an optimal foraging time could be derived in a manner directly analogous to Charnov’s marginal value problem. However, here, we recognize that there are in addition to energetic costs in moving from place to place, and that the predation risk may differ when swimming and feeding. The fitness for a single jump-feeding bout cycle of duration \( t = F + S \) is given by

\[
g_{\text{cycle}} = \left[ \Sigma(F) - \left( mT + \frac{qd^2}{S} \right) \right] \exp(-\mu_s S - \mu_f F)
\]

where \( S \) is the time spent swimming, \( F \) the time spent feeding and \( \mu_s \) and \( \mu_f \) the mortality rates while swimming and feeding, respectively. The distance \( d \) is the length scale of the depletion zone beyond which the organism should move. However, fitness per cycle (or for any fixed time interval) is not the same as lifetime fitness. With regard to the latter, the question of how many cycles can be accommodated in an expected life span also becomes an issue. In particular, the fitness after \( n \) cycles is

\[
g_{n\text{cycle}} = n \left[ \Sigma(F) - \left( mT + \frac{qd^2}{S} \right) \right] \exp(-\mu_s n S - \mu_f n F)
\]

from which it can be deduced that the number of cycles in an expected life span is

\[
n = \frac{1}{\mu_s S + \mu_f F}.
\]

Thus, to within a constant, the lifetime fitness is given by

\[
g(F, S) = \frac{\Sigma(F) - (mT + \frac{qd^2}{S})}{\mu_s S + \mu_f F}
\]

and is consistent with that derived by (Gilliam, 1990). Finally, predation while swimming depends on swimming speed, so that \( \mu_s \propto \bar{v} = d/S \). Thus, swimming fast will incur a greater mortality rate, but it will be sustained for a shorter period so that risk, \( \mu_s S \), is independent of swimming duration. Equation (20) thus becomes

\[
g(F, S) = \frac{\Sigma(F) - (mT + \frac{qd^2}{S})}{\mu_0(F + \bar{p})}
\]

where \( \mu_0 \) is the mortality rate while feeding and \( \mu_0 \bar{p} \) the mortality associated with traversing the distance \( d \). That is, the mortality associated with traversing the distance \( d \) is equivalent with feeding for \( \bar{p} \) seconds.

Solving equation (21) for \( \partial g/\partial S = 0 \) and \( \partial g/\partial F = 0 \) gives the optimal swimming and feeding durations as being

\[
S^* = \frac{d \sqrt{\frac{2}{m}}}{F^*}.
\]

\[
F^* = \left( \frac{\beta(1 - m') - k + (\beta(1 - m') - k^3 + \mu_0^2)^{1/2}}{\alpha} \right)^2
\]

where \( k = 2d(qm)^{1/2}, \alpha = R(\pi D)^{-1/2} \) and \( m' = m/\left(4\pi RDC\right) \). The optimal swimming duration is independent of either prey concentration or predation risk.

Copepod nauplii provide an illustrative example of how these functions. Nauplii (e.g. early stages of A. tonsa, T. longicornis and Calanus helgolandicus) often exhibit jump-sink behaviour with jump frequencies ranging from 1 min\(^{-1}\) to 3 s\(^{-1}\); a behaviour thought to be associated with ambush feeding on motile prey (Titelman and Kiørboe, 2003b). Figure 11 shows the optimal feeding duration \( F^* \) and optimal fitness \( g(S^*, F^*) \) follow equation (21) using parameters (Table III) consistent with a nauplius feeding on a motile protist (e.g. Balanion comatum) with motile diffusivity \( 3 \times 10^{-9} \, \text{m}^2 \, \text{s}^{-1} \) (Visser and Kiørboe, 2006) at different levels of predation risk and prey concentration. The optimal swimming (jump) duration calculated from equation (22) for this example is \( S^* = 0.14 \, \text{s} \), and is independent of predation risk and prey abundance. At high prey concentration, optimal feeding duration \( F^* \) increases markedly with predation risk—the benefit of moving beyond the diffusive boundary layer becomes negligible compared with the risks involved. The maximum cell concentration plotted in Fig. 11A is \( 10^5 \) cells m\(^{-3}\), although it should be noted...
that higher concentrations follow very nearly the same line. As cell concentration is decreased, the effect of predation risk is decreased, until at $10^7$ cells m$^{-3}$ the optimal feeding duration is very nearly independent of risk. That is, the net energy intake is so small that any increase in predation risk is of marginal impact. At prey concentrations a little less than $10^7$ cells m$^{-3}$, the fitness function becomes negative and ambush feeding becomes non-viable. At intermediate values of the predation risk factor, and for a broad range of cell concentrations, the optimal feeding duration for these parameters range between 0.1 and 10 s. These values of $F^*$, and that for $S^*$, calculated above compare favourably with observed values (Titelman, 2001) for early stage nauplii of $A. tonsa$ (0.6 ± 0.4 s and 0.08 ± 0.02 s), $C. helgolandicus$ (7 ± 3 s and 0.12 ± 4 s) and $T. longicornis$ (11 ± 4 s and 0.12 ± 1 s).

In the absence of turbulence, ambush predators are ultimately dependent on the motility of their prey to bring about contacts, and not all prey are equally obliging. When the concentration of motile prey becomes low, it may benefit an organism to abandon ambush feeding all together and switch to another feeding mode (suspension or cruise). Indeed, treating feeding mode as an adaptive behaviour (in this case cruise versus ambush) and the prey species as being either stationary or motile but otherwise similar, we can see how food selectivity emerges as an optimization property. Ambush feeding is low cost, low risk and preferentially selects for motile prey. Cruise feeding is high cost, high risk but is relatively neutral in selectivity. As the relative ratio of stationary to motile prey increases, fitness is optimized by ambush feeding initially, but switches to cruise feeding as the proportion of stationary prey increases. The switch in mode is accompanied by a switch in potential selectivity with 100% of the diet composed of motile prey before, to roughly the same ratio as ambient after the switch.

**DISCUSSION**

By whatever mode they are achieved, and in whatever way they are realized, planktonic behaviour has emerged from evolutionary processes. Specifically, evolution has equipped planktonic organisms with a repertoire of behaviours and capabilities so as to optimize the fitness of individuals with respect to fundamental life processes in the face of varying environmental conditions. If credible conjectures as to how these life processes are influenced by environmental conditions, and these conjectures can be cast in terms of quantifiable mechanisms, then optimal behaviour can be predicted. Indeed, optimal behaviour as an emergent property of adaptive trait analysis has been promoted as a cornerstone of individual based ecology (Grimm and Railsback, 2005). Such analysis has only recently been applied to questions of planktonic behaviour. The concept of optimization, as invoked by individual based ecology, is extremely simple yet extremely
powerful (Sutherland, 2005), and is of course the driving principal behind evolution. It is therefore somewhat surprising that it has not found greater currency in marine sciences.

In this work, I have concentrated on only one aspect of fitness: namely net energy gain versus predation over an expected lifetime. Other aspects of the energy–predation trade-off, may be cast in different formulations (e.g. Abrahams and Dill, 1989; Abrams, 1993; Houston et al., 1993). Further, this may not be the pertinent aspect at all times during a plankter’s life cycle. At times, optimizing the number of mating encounters may be more relevant (Kiørboe, 2006); at other times, it may be the protection of offspring (Kiørboe and Sabatini, 1995). Predation also changes through the lifetime of an organism, both in that the spectrum of predators arrayed against it changes, but also in that its capacity to detect and escape from predators may develop. In general, predation risk for later life stages is lower than that for earlier life stages. Furthermore, while few, the marine pelagic environment does present some refuges from predation. Seeking out deep dark depths during daylight hours as a refuge against visual predation is a clear example (Zaret and Suffern, 1976). More complex are behaviourally mediated indirect interactions where an organism’s predator and prey can strike up a mutually beneficial relationship; the predator finding an “attractor” and the prey finding a refuge (Dill et al., 2003; Kaartvedt et al., 2005). Finally, there is the issue of environmental variability. In the work presented here, I have assumed a uniform, well-mixed, stable environment. Such conditions select against variability in adaptive traits; variability in behavioural characteristics will result in sub-optimal performance. The environment, however, varies both in time and space. In this case, variability is a positive attribute, allowing organisms to explore their local fitness landscape, balancing occasional sub-optimal behaviour against a flexibility to adapt to changing conditions.

Despite the simple mechanisms considered in this work, there are some general conclusions that can be drawn:

(i) Optimal swimming speed for a cruise predator decreases with increasing prey concentration and increasing risk due to ambush predators.

(ii) A convoluted swimming path in the form of meanders, zigzags or spirals confers greater fitness to an individual than swimming along a straight path. Optimal path configuration is such that the length-scale of the path-meanders (pitch for a helical path, motility length scale for a random walk) scales with the organisms detection radius to prey, which in turn scales with the size of the organism.

(iii) For an ambush predator feeding on motile prey, the time spent swimming is largely a function of energetic costs, whereas the time spent feeding is strongly controlled by prey concentration and the risk posed by ambush predators.

These conclusions may be expected to hold up irrespective of the precise details of the formulation used. The encounter volume with respect to predator or prey or both might not be spherical, the Reynolds number might exceed unity requiring a different drag formulation, or the statistics of the random walk might be other than Gaussian (e.g. a Lévy walk) so that the characteristics of the “sausage” are not the same as for the Wiener sausage. Whatever the details of the energy–predation trade-off may be, the approach used here allows fitness to be quantified, and subsequently, optimal behaviour to be estimated in an evolutionarily consistent way.

These general conclusions can have far reaching consequences as to how vital rates are parameterized in zooplankton models. For instance, optimal swimming speed is a function of both predator and prey abundance, *v*(*C*, *P*). If we assume that in nature, where predator and prey abundances vary, organisms adopt their optimal swimming speed, then the functional form of realized ingestion rates and mortality rates will be other than that commonly assumed. For instance, mortality rate will not be linearly dependent on predator abundance (Abrams, 1993). As predator abundance (and hence predation risk) increases, optimal swimming speed decreases, thus reducing actual mortality rates. Likewise, the actual functional response curve may not follow a Hollings II functional response even though the underlying predator–prey interactions are consistent with the Disk equation (Hollings, 1959). Because optimal swimming speed decreases with increasing prey concentration—an organism can afford to move at a more leisurely pace when food is abundant—encounter rates and thus clearance rates decrease with increasing prey concentration. Although this effect may be of negligible consequence at saturating food concentrations, it may significantly alter the functional response at low and intermediate food concentrations.

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