brief communication

Kinematics of helical motion of microorganisms capable of motion with four degrees of freedom

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ABSTRACT The kinematics of helical motion are described for an organism with four degrees of freedom, relative to the organism's frame of reference. It can rotate about any of three orthogonal axes, but can translate only in the direction of one axis. In particular, equations are developed for calculating the pitch, radius, and angular frequency of the helical path from the translational and rotational velocities of the microorganism, correcting, and expanding the analysis of Gray, J. (1955. *J. Exp. Biol.* 32:775–801).

INTRODUCTION

The motion of many free-swimming microorganisms is helical. Gray (1955) first used the mechanics of rigid body rotation to analyze helical motion. Gray assumes the organism has only three degrees of freedom relative to the organism's frame of reference (one component of translational velocity and two components of rotational velocity), and obtains two equations describing the radius and pitch of an organism's helical trajectory as functions of its speed and rate of rotation. Unfortunately, Gray does not present derivations of his equations, and the present analysis demonstrates they are incorrect.

Brokaw (1958) repeated Gray's analysis, using the same assumptions. He presents a series of equations describing an organism's translational and rotational velocities in terms of the radius, pitch, and angular frequency of its trajectory and vice versa. These equations disagree with Gray (1955), and the present analysis confirms Brokaw's results.

This paper describes the kinematics of helical motion of an organism with four degrees of freedom, relative to the organism's frame of reference: one component of translational velocity and all three components of rotational velocity. In particular, equations are developed for calculating the pitch, radius, and angular frequency of the helical motion from the rate of rotation and the speed of the organism. These equations correct Gray's equations as well as provide the additional degree of freedom. Finally, the orientations of the translational and rotational velocity vectors, with respect to the body of the organism and to the helical path, are discussed.

GLOSSARY

γ	Angular frequency of helical motion
θ	Angle between axis and tangent of helix
η	Sum of yaw and pitch ($= \omega_2\mathbf{j} + \omega_3\mathbf{k}$)
κ	Curvature
τ	Torsion
$\boldsymbol{\omega}$	Rotational velocity of organism
l	Arclength of one revolution of helix ($= \sqrt{p^2 + 4\pi^2r^2}$)
p	Pitch of helical motion
r	Radius of helical motion
s	Arclength of curve
t	Time
U	Speed ($= ds/dt = \lvert\mathbf{V}\rvert$)
$\mathbf{B}$	Unit binormal vector
$\mathbf{H}(t)$	Position vector for helical motion
$\mathbf{ijk}$	Reference frame fixed to organism
$\mathbf{IJK}$	Reference frame fixed in space
$\mathbf{K}$	Axis of helical motion
$\mathbf{N}$	Unit normal vector
$\mathbf{T}$	Unit tangent vector
$\mathbf{V}$	Translational velocity of organism.

INTRODUCTION TO HELICES

Righthand helical motion is described by the following vector function:

$$\mathbf{H}(t) = r\cos(\gamma t)\mathbf{I} + r\sin(\gamma t)\mathbf{J} + \left(\frac{p\gamma t}{2\pi}\right)\mathbf{K}, \qquad (1)$$

where **IJK** is a righthand reference frame fixed to the helix such that **K** is the axis of the helix. p is the pitch, r is the radius, and γ is the angular frequency (radians/time).[1]

Some helpful relationships emerge from the geometry of the cylinder formed by one revolution of the helix. If the cylinder is split down the side, parallel to **K**, and laid

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[1] For lefthand helical motion the sine and cosine terms are interchanged. This analysis uses the equation for a righthand helix, but the results apply equally well to lefthand helices.

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flat, the wall of the cylinder forms a rectangle. The length of the sides parallel to **K** equals p. The length of the other sides equals the circumference of the cylinder ($2\pi r$). The arc of the helix for one revolution is the diagonal, with length equal $\sqrt{p^2 + 4\pi^2 r^2}$. This quantity appears so frequently it is referred to as l. The angle θ formed by the diagonal and the side parallel to **K** also arises in later discussion. The diagonal is the arc of the helix, so θ is the angle formed by **K** and any line tangent to the helix. θ is given by

$$\tan\theta = \frac{2\pi r}{p}. \tag{2}$$

Kinematics

If the endpoint of $\mathbf{H}(t)$ is some point on an organism, and if r, p, and γ are known, the trajectory of the organism is known. These parameters can be measured by observing the motion of an organism. r, p, and γ, however, are parameters that are remote from the behavior of the organism. Of more biological interest is the organism's translational and rotational velocities (**V** and $\boldsymbol{\omega}$, respectively).

I use three reference frames in this analysis. The first, **IJK**, is fixed in space as described for Eq. 1. The second, **ijk**, is fixed to the organism. The final reference frame, **TNB**, is one conventionally used to describe the geometry of 3D curves.

The goal of this analysis is to describe the trajectory of an organism (i.e., of **ijk**) relative to Eq. 1. This is accomplished by first describing the motion of **ijk** in terms of **V** and $\boldsymbol{\omega}$. Next, the motion of **TNB** is described in terms of r, p, and γ. The relationship between these descriptions of motion is then discussed, permitting the development of equations describing r, p, and γ as functions of **V** and $\boldsymbol{\omega}$ and vice versa.

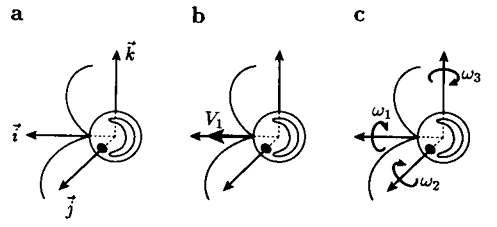

FIGURE 1 The orientation of **ijk** with respect to body axes and the components of **V** and $\boldsymbol{\omega}$. (*a*) Orientation of **ijk**. **i** is the anterior-posterior axis, pointing anteriorly. **j** is the left-right axis, pointing left. **k** is the dorso-ventral axis, pointing dorsally. (*b*) Components of velocity, relative to **ijk**. The **i** component (V_1) is the only nonzero component. (*c*) Components of rotation relative to **ijk**. ω_1 is the **i** component, ω_2 is the **j** component, and ω_3 is the **k** component.

Motion of ijk relative to IJK

ijk is fixed to the organism such that the origin of **ijk** is placed at the organism's center of mass. **i** is the anterior-posterior axis, pointing anteriorly; **j** is the left-right axis, pointing left; and **k** is the dorso-ventral axis, pointing dorsally (Fig. 1 *a*).

The motion of **ijk** relative to **IJK** is fully defined by **V** and $\boldsymbol{\omega}$ (Beatty, 1986). This analysis assumes **V** has only one nonzero component, which I arbitrarily constrain to be in the **i** direction (Fig. 1 *b*). If the organism moves with speed U, then

$$\mathbf{V} = U\mathbf{i}. \tag{3}$$

All three components of $\boldsymbol{\omega}$ are assumed to be nonzero, thus

$$\boldsymbol{\omega} = \omega_1\mathbf{i} + \omega_2\mathbf{j} + \omega_3\mathbf{k}, \tag{4}$$

where $\boldsymbol{\omega}$ has units of radians/time (Fig. 1 *c*).[2] Therefore, if U, ω_1, ω_2, and ω_3 are known, the motion of the organism is defined by Eqs. 3 and 4.

Motion of TNB relative to IJK

TNB is a reference frame used in differential geometry (Gillett, 1984, ch. 16.2) and the kinematics of a particle (Beatty, 1986, ch. 1). **T** is the unit tangent vector; **N** is the unit normal vector, and **B** is the unit binormal vector. The orientation and motion of **TNB** relative to **IJK** can be calculated from Eq. 1. I present only the relationships needed in later discussion.

$$\mathbf{T} = \frac{\mathrm{d}\mathbf{H}/\mathrm{d}s}{|\mathrm{d}\mathbf{H}/\mathrm{d}s|} \tag{5}$$

$$\mathbf{N} = \frac{\mathrm{d}\mathbf{T}/\mathrm{d}s}{|\mathrm{d}\mathbf{T}/\mathrm{d}s|} \tag{6}$$

$$\mathbf{B} = \mathbf{T} \times \mathbf{N} \tag{7}$$

$$U = \left|\frac{\mathrm{d}\mathbf{H}}{\mathrm{d}t}\right| = \frac{\gamma l}{2\pi} \tag{8}$$

$$\kappa = \left|\frac{\mathrm{d}\mathbf{T}}{\mathrm{d}s}\right| = \frac{4\pi^2 r}{l^2} \tag{9}$$

$$\tau = \left|\frac{\mathrm{d}\mathbf{B}}{\mathrm{d}s}\right| = \frac{2\pi p}{l^2}, \tag{10}$$

where s is the arclength, κ is the curvature, and τ in the torsion of the curve.

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[2] ω_1 is sometimes called "roll"; ω_2 is "pitch" (not to be confused with the pitch of the helix), and ω_3 is "yaw".

Relationship between the motions of ijk and TNB

I proceed from here in two steps. First, I describe the orientation of **ijk** relative to **TNB**. Next, I describe the relationship between the rate of rotation of **ijk**, which is given by ω, and the rate of turning of **TNB**, which is given by κ and τ.

The center of mass of the organism is the point that is being tracked. The origin of **ijk** is the organism's center of mass, so this point traces the trajectory. The origin of **TNB** also traces the trajectory, so the origin of **ijk** is the origin of **TNB**.

The speed of **ijk** is the same as the speed of **TNB**, the latter given by Eq. 8. The velocity of **ijk** has only one component, which is in the **i** direction, so from Eq. 5,

$$\mathbf{T} = \mathbf{i}. \tag{11}$$

N, given by Eq. 6, is, therefore,

$$\mathbf{N} = \frac{d\mathbf{i}/ds}{|d\mathbf{i}/ds|}. \tag{12}$$

Because **i** does not change direction with respect to the organism's body, $d\mathbf{i}/dt$ is simply $\boldsymbol{\omega} \times \mathbf{i}$, thus,

$$\frac{d\mathbf{i}}{ds} = \frac{d\mathbf{i}}{dt}\frac{dt}{ds} = \frac{1}{U}\frac{d\mathbf{i}}{dt} = \frac{\boldsymbol{\omega} \times \mathbf{i}}{U}. \tag{13}$$

This relationship can be simplified by using a second rotation vector

$$\boldsymbol{\eta} = \omega_2\mathbf{j} + \omega_3\mathbf{k}. \tag{14}$$

$\boldsymbol{\eta} \times \mathbf{i} = \boldsymbol{\omega} \times \mathbf{i}$ because the **i** component of the rotation does not affect **i**. Therefore,

$$\frac{d\mathbf{i}}{ds} = \frac{\boldsymbol{\eta} \times \mathbf{i}}{U}, \tag{15}$$

and

$$\mathbf{N} = \frac{\boldsymbol{\eta} \times \mathbf{i}}{|\boldsymbol{\eta} \times \mathbf{i}|}. \tag{16}$$

This can be simplified further using the relationship

$$|\boldsymbol{\eta} \times \mathbf{i}| = |\boldsymbol{\eta}||\mathbf{i}|\sin\psi = |\boldsymbol{\eta}|, \tag{17}$$

where ψ, the angle between $\boldsymbol{\eta}$ and **i**, is 90°. Inserting this into Eq. 16 yields

$$\mathbf{N} = \frac{\boldsymbol{\eta} \times \mathbf{i}}{|\boldsymbol{\eta}|} = \frac{\boldsymbol{\eta}}{|\boldsymbol{\eta}|} \times \mathbf{i}. \tag{18}$$

From the cross-product relationships of the axes of right-hand coordinate systems ($\mathbf{N} = \mathbf{B} \times \mathbf{T} = \mathbf{B} \times \mathbf{i}$), it follows from Eq. 18 that

$$\mathbf{B} = \frac{\boldsymbol{\eta}}{|\boldsymbol{\eta}|}. \tag{19}$$

Eqs. 11, 18, and 19 describe the orientation of **ijk** relative to **TNB**.

I can now relate ω of **ijk** to κ and τ of $\mathbf{H}(t)$. Eq. 9 gives κ. $d\mathbf{T}/ds$ ($=d\mathbf{i}/ds$) was derived in Eq. 15, so κ is known:

$$\kappa = \left|\frac{d\mathbf{T}}{ds}\right| = \left|\frac{\boldsymbol{\eta} \times \mathbf{i}}{U}\right| = \frac{|\boldsymbol{\eta}|}{U}. \tag{20}$$

Substituting Eq. 19 into Eq. 10 yields

$$\tau = \left|\frac{d}{ds}\left(\frac{\boldsymbol{\eta}}{|\boldsymbol{\eta}|}\right)\right| = \frac{1}{U}\left|\frac{d}{dt}\left(\frac{\boldsymbol{\eta}}{|\boldsymbol{\eta}|}\right)\right|. \tag{21}$$

The derivation of the last term is given in Appendix A, yielding the result

$$\tau = \left(\frac{1}{U}\right)\left[\omega_1 + \left(\frac{\omega_2\omega_3' - \omega_2'\omega_3}{|\boldsymbol{\eta}|^2}\right)\right]. \tag{22}$$

In summary, this equation describes the rate of change of direction of $\boldsymbol{\eta}$ in **IJK** space. $\boldsymbol{\eta}$ changes direction with respect to **IJK** both when **ijk** changes orientation in **IJK** space and when $\boldsymbol{\eta}$ changes direction with respect to **ijk**. The term ω_1/U is the rate of change of direction of $\boldsymbol{\eta}$ due to the organism rotating around its anterior-posterior axis. The rest of this equation describes the change of direction of $\boldsymbol{\eta}$, with respect to **ijk**. If the direction of $\boldsymbol{\eta}$ with respect to **ijk** is constant, this term equals zero, leaving

$$\tau = \frac{\omega_1}{U}. \tag{23}$$

The direction of $\boldsymbol{\eta}$ remains constant if $\omega_2 = 0$, $\omega_3 = 0$, or $\omega_2 = \alpha\omega_3$ for some constant α. Each of these conditions effectively leaves the organism with only two degrees of rotational freedom: ω_1 and one component perpendicular to ω_1.

Relating *r*, *p*, and γ to *U* and $|\omega|$

It is now possible to obtain equations for r, p, and γ in terms of U, ω_1, ω_2, and ω_3. Equating eq. 9 with eq. 20 and equating 10 with 22 yields

$$p = \frac{2\pi U(\omega_2^2 + \omega_3^2)[\omega_1(\omega_2^2 + \omega_3^2) + \omega_2\omega_3' - \omega_2'\omega_3]}{(\omega_2^2 + \omega_3^2)^3 + [\omega_1(\omega_2^2 + \omega_3^2) + \omega_2\omega_3' - \omega_2'\omega_3]^2} \tag{24a}$$

$$r = \frac{U(\omega_2^2 + \omega_3^2)^{5/2}}{(\omega_2^2 + \omega_3^2)^3 + [\omega_1(\omega_2^2 + \omega_3^2) + \omega_2\omega_3' - \omega_2'\omega_3]^2} \tag{24b}$$

$$\gamma = \frac{[(\omega_2^2 + \omega_3^2)^3 + (\omega_1(\omega_2^2 + \omega_3^2) + \omega_2\omega_3' - \omega_2'\omega_3)^2]^{1/2}}{(\omega_2^2 + \omega_3^2)}. \tag{24c}$$

There are too many unknowns in Eq. 24a–c to derive explicit expressions for ω_1, ω_2, and ω_3 in terms of r, p, and

γ. However, if the direction of η with respect to **ijk** is constant, as discussed after Eq. 22, then the derivatives in Eq. 24a–c drop out, leaving

$$p = \frac{2\pi U\omega_1}{(\omega_1^2 + |\eta|^2)} = \frac{2\pi U\omega_1}{|\omega|^2} \tag{25a}$$

$$r = \frac{U|\eta|}{(\omega_1^2 + |\eta|^2)} = \frac{U|\eta|}{|\omega|^2} \tag{25b}$$

$$\gamma = \sqrt{\omega_1^2 + |\eta|^2} = |\omega|. \tag{25c}$$

Again, I must emphasize that if the direction of η is constant with respect to **ijk**, then the organism effectively has only two degrees of rotational freedom.

Eq. 8, which gives U in terms of r, p, and γ, now can be combined with Eq. 25a–c to obtain expressions for ω_1 and $|\eta|$ in terms of r, p, and γ:

$$\omega_1 = \frac{p\gamma}{l}, \tag{26a}$$

$$|\eta| = \frac{2\pi r\gamma}{l}. \tag{26b}$$

Thus, if r, p, and γ are known, then U, ω_1, and $|\eta|$ are known.

Orientation of V and ω with respect to H

Eqs. 8, 25c, and 26a and b give the magnitudes of **V** and $\boldsymbol{\omega}$. They do not give their directions. If, however, the orientation of the organism (i.e., of **ijk**) is known with respect to the helical path (i.e., with respect to **IJK**) then the directions of **V** and $\boldsymbol{\omega}$ can be determined.

The direction of **V** is given by Eqs. 3 and 11 which say that **V** of an organism located at some point P on the helix points in the direction of **T** at P.

$\boldsymbol{\omega}$ is a rotation, so both the axis of rotation and the sense of rotation must be determined. This discussion uses conventional righthand rotation. Appendix B demonstrates that the axis of the helix **K** is parallel to $\boldsymbol{\omega}$. Therefore, from Eq. 25c,

$$\boldsymbol{\omega} = \pm\gamma\mathbf{K}. \tag{27}$$

The sense of $\boldsymbol{\omega}$ is given by the handedness of the helix. For a righthand helix, $\boldsymbol{\omega}$ is positive. For a lefthand helix, $\boldsymbol{\omega}$ is negative.

If we consider the plane formed by **V** and $\boldsymbol{\omega}$, some interesting relationships arise. **V** is tangent to the helix, and $\boldsymbol{\omega}$ is parallel to **K**. Therefore, **V** and $\boldsymbol{\omega}$ define a plane that is both tangent to the helix and parallel to **K**. This is the "rectifying plane" used to describe 3D curves (Fig. 2). By definition, **B** lies in the rectifying plane, so from Eq. 18, η also lies in this plane. **N** is perpendicular to the rectifying plane (Fig. 2 *b*), so **N** is perpendicular to **K** and parallel to $\boldsymbol{\omega} \times \mathbf{V}$ (and to $\eta \times \mathbf{V}$, a result also obtained by Eq. 18). This means the point at which $\boldsymbol{\omega} \times \mathbf{V}$ emerges from the body of the organism faces the axis of the helix. If the direction of $\boldsymbol{\omega} \times \mathbf{V}$ does not change, one side of the organism always faces the axis of the helix.

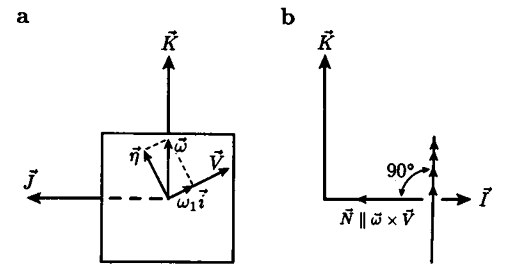

FIGURE 2 The rectifying plane of the helix and its relationship to **V** and $\boldsymbol{\omega}$. The rectifying plane is parallel to **K** and tangential to the cylinder formed by the helix. *a* and *b* present two orthogonal views. **V**, $\boldsymbol{\omega}$, and η all lie in the rectifying plane. **N** (which is parallel to $\boldsymbol{\omega} \times \mathbf{V}$) is perpendicular to the rectifying plane, points towards **K**, and is perpendicular to **K**.

The direction of **V**, with respect to **ijk**, is constant (Eq. 3). Therefore, the direction of $\boldsymbol{\omega} \times \mathbf{V}$ can change in only four ways. (*a*) **V** changes sign. If $\boldsymbol{\omega}$ does not change sign, the direction of $\boldsymbol{\omega} \times \mathbf{V}$ is reversed, and the handedness of the helix is the same. (*b*) $\boldsymbol{\omega}$ changes sign. In this case the direction of $\boldsymbol{\omega} \times \mathbf{V}$ is reversed, and the helix changes handedness. (*c*) η changes sign, but not direction. In this case, the direction of $\boldsymbol{\omega} \times \mathbf{V}$ is reversed, and the handedness of the helix is unchanged. (*d*) η changes direction with or without changing sign. For example, if $\omega_2 > 0$ and $\omega_3 = 0$, then **j** is parallel to η, and $-\mathbf{k}$ is parallel to **N**, i.e., the ventral side of the organism faces **K** (Fig. 3). If $\omega_2 = 0$ and $\omega_3 > 0$, then **k** is parallel to η, and **j** is parallel to **N**, i.e., the lefthand side of the organism faces **K** (Fig. 4). If $\omega_2 > 0$ and $\omega_3 > 0$ then η lies somewhere between **j** and **k** in the **jk** plane. Finally, if ω_2 and ω_3 can change sign, η can rotate 360° in the **jk** plane.

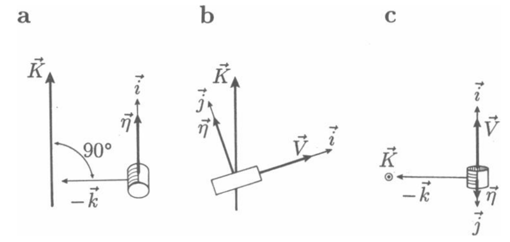

FIGURE 3 The orientation of an organism with respect to **K** when $\omega_2 > 0$ and $\omega_3 = 0$. When $\omega_3 = 0$, $\eta = \omega_2\mathbf{j}$. Therefore, the ventral side of the organism faces **K**. The "organism" in this picture has stripes on its anterior end and its ventral side. *a–c* present three orthogonal views of the organism.

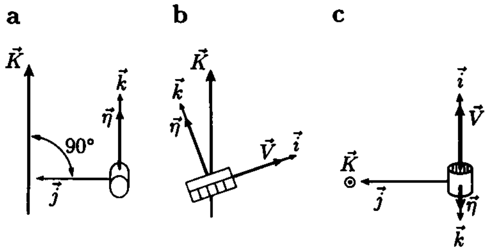

FIGURE 4 The orientation of an organism with respect to **K** when $\omega_2 = 0$ and $\omega_3 > 0$. When $\omega_2 = 0$, $\eta = \omega_3\mathbf{k}$. Therefore, the lefthand side of the organism faces **K**. The "organism" in this figure has the same markings as in Fig. 3. *a–c* present three orthogonal views of the organism.

DISCUSSION

Eq. 24a–c disagree with those of Gray (1955). Gray assumed that ω_3 equals zero and that ω_2 is constant and obtained

$$\omega_1 = \gamma, \quad r = \frac{U\omega_2}{\omega_1^2}, \quad p = \left(\frac{2\pi U}{\omega_1^2}\right)\sqrt{\omega_1^2 - \omega_2^2}, \tag{28}$$

in the present notation. The formula for p requires that ω_2 be less than ω_1, unless p is a complex number, neither of which is correct. I can only obtain Gray's equations by incorrectly defining τ as $|\mathrm{d}\mathbf{N}/\mathrm{d}s|$.

Brokaw (1958) repeated Gray's analysis. Assuming $\boldsymbol{\omega} = \gamma\mathbf{K}$, Brokaw used an approach different to the present analysis, and reported

$$\omega_1 = |\omega|\cos\theta, \quad \omega_2 = |\omega|\sin\theta \tag{29a}$$

$$|\omega| = \gamma, \quad r = \frac{U\omega_2}{|\omega|^2} \tag{29b}$$

$$p = \frac{2\pi U\cos\theta}{|\omega|}, \tag{29c}$$

in the present notation. Substitution of Eqs. 29a into 29c yields 25a. Eqs. 29b are Eq. 25b and c for $\omega_3 = 0$. Therefore, the present analysis agrees with Brokaw.

Keller and Rubinow (1976) analyze the motion of an organism that propagates helical waves down a single flagellum. They calculate **V** and $\boldsymbol{\omega}$ from the moments on both the flagellum and the body of the organism. They present equations for r, p, and U in terms of the **V** and $\boldsymbol{\omega}$ (their p. 158). They calculate that ω_2 and ω_3 are small relative to ω_1 for such an organism. If this result is substituted into Eq. 28a and b, and if the assumption $V_2 = V_3 = 0$ is substituted into their equations, we obtain the same result.

The present results also agree with various equations presented by Naitoh and Sugino (1984), Fenchel and Jonsson (1988), and Sugino and Naitoh (1988).

Eqs. 25–27 can be easily used to determine $\boldsymbol{\omega}$ and **V** of microorganisms moving with constant r, p, and γ (Crenshaw, 1989*a*). However, if r, p, and γ are not constant, then these equations can be applied only if the organism moves with two degrees of rotational freedom.

The present analysis is limited. First and foremost, it describes the motion of an organism with only one degree of translational freedom. For many microorganisms, though, the assumption that **V** has only one component appears correct. If $V_2 = V_3 = 0$, the organism (*a*) always moves with one axis of its body tangential to the helix, i.e., one part of its body always faces forward during forward locomotion, and (*b*) one point on the cell always faces the axis of the helix if r, p, and γ are constant. Most microorganisms appear to move in this manner (Jennings, 1904; Bullington, 1925; Kamiya and Witman, 1984; Rüffer and Nultsch, 1985).

The second limitation of this analysis is that Eqs. 24a–c, 25a–c, and 26a and b are only correct to the extent that the organism's center of mass does not change position within the organism's body. The present analysis presents the trajectory of the center of mass, which is the origin of **ijk**. A living organism is not a rigid body. It deforms, so the center of mass moves within the organism. The trajectory described by this analysis, therefore, is not the trajectory of a single point in the organism. However, the center of mass for most free-swimming organisms probably does not change position greatly, so this analysis errs only slightly.

The third limitation is that the restriction required to produce Eq. 25a–c from 24a–c (the direction of η remains constant) is quite severe. As discussed earlier, this restriction effectively limits the organism to two degrees of rotational freedom. Analyses of the flagellar beat of *Chlamydomonas reinhardtii* indicate $\boldsymbol{\omega}$ is variable in these cells (Kamiya and Witman, 1984; Omoto and Brokaw, 1985; Rüffer and Nultsch, 1985, 1987). The flagellate *Dunaliella bioculata* changes $\boldsymbol{\omega}$ (Schoevaert et al., 1988). Ciliates change $\boldsymbol{\omega}$ by altering the direction of ciliary beat (Naitoh and Sugino, 1984; Sugino and Naitoh, 1988; Machemer and Sugino, in press). Furthermore, a large body of evidence, beginning with Gray (1955), documents changes in $\boldsymbol{\omega}$ of spermatozoa with changes in flagellar beat (Rikmenspoel et al., 1960; Brokaw, 1979; Brokaw et al., 1974; Goldstein, 1977; Okuno and Brokaw, 1981). The kinematics of motion with varying r, p, and γ (and thus **V** and $\boldsymbol{\omega}$) are addressed elsewhere (Crenshaw, 1989*b*; Crenshaw, H. C., and L. Edelstein-Keshet, manuscript in preparation).

APPENDIX A

Derivation of $\left|(\mathrm{d}/\mathrm{d}t)/(\eta/|\eta|)\right|$:

By the quotient rule:

$$
\begin{aligned}
\frac{\mathrm{d}}{\mathrm{d}t}\frac{\eta}{|\eta|} &= \frac{|\eta|\eta' - \eta|\eta|'}{|\eta|^2} \\
&= (\omega_2^2 + \omega_3^2)^{-1}[(\omega_2^2 + \omega_3^2)^{1/2}(\omega_2'\mathbf{j} + \omega_2\mathbf{j}' + \omega_3'\mathbf{k} + \omega_3\mathbf{k}') \\
&\quad - (\omega_2\mathbf{j} + \omega_3\mathbf{k})(\omega_2^2 + \omega_3^2)^{-1/2}(\omega_2\omega_2' + \omega_3\omega_3')] \\
&= (\omega_2^2 + \omega_3^2)^{-3/2}[(\omega_2^2 + \omega_3^2) \\
&\quad \{\omega_2'\mathbf{j} + \omega_3'\mathbf{k} + [\omega_2(\omega \times \mathbf{j})] + [\omega_3(\omega \times \mathbf{k})]\} \\
&\quad - (\omega_2\mathbf{j} + \omega_3\mathbf{k})(\omega_2\omega_2' + \omega_3\omega_3')] \\
&= (\omega_2^2 + \omega_3^2)^{-3/2}[(\omega_2^2 + \omega_3^2)[\omega_2'\mathbf{j} + \omega_3'\mathbf{k} + (\omega \times \eta)] \\
&\quad - (\omega_2\mathbf{j} + \omega_3\mathbf{k})(\omega_2\omega_2' + \omega_3\omega_3')] \\
&= (\omega_2^2 + \omega_3^2)^{-3/2}[\omega_2^2\omega_2'\mathbf{j} + \omega_2^2\omega_3'\mathbf{k} + \omega_2^2(\omega \times \eta) \\
&\quad + \omega_2'\omega_3^2\mathbf{j} + \omega_3^2\omega_3'\mathbf{k} + \omega_3^2(\omega \times \eta) - \omega_2^2\omega_2'\mathbf{j} \\
&\quad - \omega_2\omega_3\omega_3'\mathbf{j} - \omega_2\omega_2'\omega_3\mathbf{k} - \omega_3^2\omega_3'\mathbf{k}] \\
&= (\omega_2^2 + \omega_3^2)^{-3/2}[(\omega_2^2 + \omega_3^2)(\omega \times \eta) \\
&\quad + (\omega_2\omega_3' - \omega_2'\omega_3)(\omega_2\mathbf{k} - \omega_3\mathbf{j})] \\
&\quad \left[\text{Note: } \frac{\omega_1}{\omega_1}(\omega_2\mathbf{k} - \omega_3\mathbf{j}) = \frac{\omega \times \eta}{\omega_1}\right] \\
&= (\omega_2^2 + \omega_3^2)^{-3/2}(\omega \times \eta)\left[(\omega_2^2 + \omega_3^2) + \frac{1}{\omega_1}(\omega_2\omega_3' - \omega_2'\omega_3)\right]
\end{aligned}
$$

$$
\begin{aligned}
\left|\frac{\mathrm{d}}{\mathrm{d}t}\left(\frac{\eta}{|\eta|}\right)\right| &= (\omega_2^2 + \omega_3^2)^{-3/2}\left[(\omega_2^2 + \omega_3^2) + \frac{1}{\omega_1}(\omega_2\omega_3' - \omega_2'\omega_3)\right]|\omega \times \eta| \\
&= (\omega_2^2 + \omega_3^2)^{-3/2}\left[(\omega_2^2 + \omega_3^2) + \frac{1}{\omega_1}(\omega_2\omega_3' - \omega_2'\omega_3)\right] \\
&\quad \cdot \omega_1(\omega_2^2 + \omega_3^2)^{1/2} \\
&= \omega_1 + \frac{(\omega_2\omega_3' - \omega_2'\omega_3)}{(\omega_2^2 + \omega_3^2)} = \omega_1 + \frac{(\omega_2\omega_3' - \omega_2'\omega_3)}{|\eta|^2}.
\end{aligned}
$$

APPENDIX B

Let ϕ be the angle between V and ω and let θ be the angle between T and K. I will demonstrate that ω is parallel to K by showing that (*a*) V is parallel to T, (*b*) ϕ equals θ, and (*c*) ϕ and θ behave similarly.

First, T is parallel to V by definition (Eq. 11).

Second, θ, which is constant for a helix of constant radius and pitch, is given by Eq. 2 as $\tan\theta = 2\pi r/p$. In the following equations I demonstrate that $\tan\phi$ also equals $2\pi r/p$:

$$
\cos\phi = \frac{\mathbf{V} \cdot \omega}{|\mathbf{V}||\omega|}, \quad \sin\phi = \frac{|\omega \times \mathbf{V}|}{|\mathbf{V}||\omega|}
$$

$$
\begin{aligned}
\tan\phi &= \frac{|\omega \times \mathbf{V}|}{\mathbf{V} \cdot \omega} = \frac{|\omega \times U\mathbf{i}|}{U\mathbf{i} \cdot \omega} \\
&= \frac{|\omega \times \mathbf{i}|}{\mathbf{i} \cdot \omega} = \frac{|\eta \times \mathbf{i}|}{\mathbf{i} \cdot \omega} = \frac{|\eta|}{\omega_1}.
\end{aligned}
$$

Substituting Eq. 26a and b into this last equation yields $\tan\phi = 2\pi r/p$, so $\phi = \theta$.

Finally, the two angles behave similarly. When $\phi = 0°$, the organism rotates around V, resulting in a path that is a straight line, which is a helix with $r = 0$, so $\theta = 0°$. When $\phi = 90°$, the organism rotates around an axis perpendicular to V, resulting in a path that is a circle, which is a helix with $p = 0$, so $\theta = 90°$.

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