# Analysis of efficient strokes for multi-legged microswimmers

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*Abstract*— **We consider efficient controls for swimming with multiple rigid legs at low Reynolds number. We derive equations governing the translation and rotation of a general class of multi-legged swimmers, and we formulate energy-efficient controls of symmetric swimmers as a problem in geometric control theory. We then focus on the case of symmetric swimmers with multi pairs of legs. In the framework of sub-Riemannian geometry, abnormal geodescics are analyzed and shown to depend on the number of pairs of legs. Inspired by larval copepods possessing three pairs of legs, we compute various swimming strokes and explore optimal controls in that specific situation. We also compare our results to experimental measurements of larval copepod.**

## I. INTRODUCTION

Tiny marine organisms display diverse shapes and locomotion strategies that are strikingly different from those of larger organisms. For example, tiny crustaceans such as copepods, arguably the most abundant group of animals on Earth, swim by moving their numerous appendages or legs like the oars of a boat, except that the leg movements are not synchronized [1]. Given that swimming is critical to their survival, for instance to find food particles and escape from predators, one might expect the thriving copepod species to be efficient swimmers following millions of years of evolution. To test whether nature's solutions to efficient swimming are optimal, it is helpful to approach the problem from the perspective of geometric control theory. This approach of finding optimal controls also helps to identify suitable design principles for tiny swimming robots in future medical, oceanography, and technological applications.

Various different models of tiny swimmers and associated optimization problems have been analyzed in the past. A relatively well studied model is the minimal design consisting of three linked rods known as Purcell's swimmer [2] [3]. Here we analyze a recent model [4] inspired by larval copepods possessing three pairs of legs [1]. In fact, only two pairs of rigid legs are needed for locomotion along a straight line, and optimal strokes have been recently found [5]. However, larval copepods curiously possess three pairs of legs (Figure 1) and that number can increase as they develop into adulthood. The number varies across species and developmental stages of other crustaceans. Of interest is a general mathematical framework for analyzing optimal strokes of an arbitrary number of legs. In [6] the authors use the maximum principle combined with numerical methods to compute energy optimal periodic strokes for the so-called Purcell Three-link swimmer and in [5] a similar approach is used for the symmetric copepod with two pairs of legs.

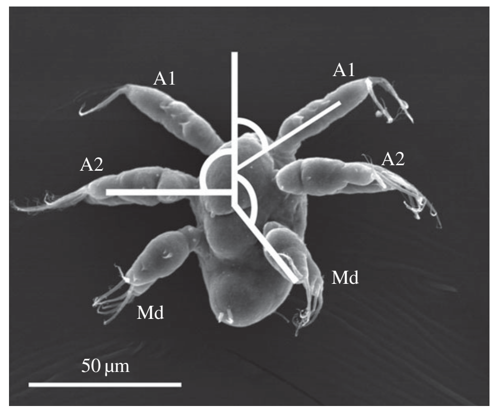


Fig. 1. Scanning electron microscopy image of a larval copepod, courtesy of Jenn Kong and reproduced from [1]. Copyright retained by the originator.

Here we present a general model swimmer consisting of slender legs protruding radially outward in a two-dimensional plane. In general the swimmer translates and rotates in the plane, but with reflective symmetry the swimmer translates along the line of symmetry. We explore the dynamics of symmetric swimmers with an arbitrary number of pairs of legs, focusing in particular on three pairs of legs, and analyze the the abnormal strokes for that specific case.

## II. MATHEMATICAL MODEL

### A. General Model

We consider a simple body consisting of a point from which $m$ slender legs extend radially in the $x-y$ plane (Figure 2). The position of the point is denoted by $\mathbf{x}_0 = [x(t)\,,\, y(t)]^T$ and the orientation angle with respect to the $x$ axis is denoted by $\phi(t)$. Below we derive a model that predicts the position and orientation of the swimmer in terms of the controllable angle $\theta_i(t)$ between the $i^{th}$ leg and the swimmer's orientation.

The model is based on slender body theory for Stokes flow, a suitable approximation for slender legs generating slow viscous flow at low Reynolds number [7]. Suppose the

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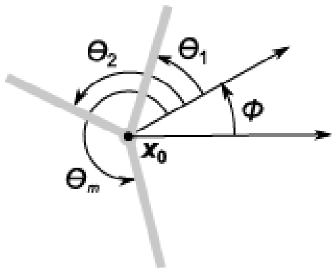



Fig. 2. Sketch of a general swimmer possessing $m$ legs. The center point of the swimmer is denoted by position $\mathbf{x}_0$ and the swimmer orientation angle is denoted by $\phi$.

$i^{th}$ leg is parametrized by

$$\mathbf{x}_i(s) = \mathbf{x}_0 + s\,\mathbf{n}_i, \tag{1}$$

where $s \in [0,1]$ is the parameter along the direction vector $\mathbf{n}_i = [\cos(\alpha_i)\,,\,\sin(\alpha_i)]^T$ with angle $\alpha_i(t) = \phi(t) + \theta_i(t)$. We assume all legs have a common length of 1 for simplicity; the model could be readily generalized by parametrizing each leg differently to account for legs with distinct lengths. According to slender body theory, the local velocity $\dot{\mathbf{x}}$ and force density $\mathbf{f}$ have a linear relationship

$$\dot{\mathbf{x}}_i(s) = C(\mathbf{I} + \mathbf{n}_i\mathbf{n}_i^T)\cdot \mathbf{f}_i(s) \tag{2}$$

where $C = \frac{\log\frac{2}{\epsilon}}{4\pi\mu}$ depends on the fluid viscosity $\mu$ and the small diameter-to-length ratio $\epsilon$ of the swimmer's legs. Combining (1) and (2) and solving for $\mathbf{f}_i$ gives

$$\mathbf{f}_i(s) = \frac{1}{C}\Big(\mathbf{I} - \frac{1}{2}\mathbf{n}_i\mathbf{n}_i^T\Big)\Big(\dot{\mathbf{x}}_0\ + s\,\dot{\mathbf{n}}_i\Big) \tag{3}$$

with $\dot{\mathbf{n}}_i = \dot{\alpha}_i\mathbf{t}_i$ and $\mathbf{t}_i = [-\sin(\alpha_i), \cos(\alpha_i)]^T$. In Stokes flow there is no net force or torque on the swimmer:

$$\sum_i \int_0^1 \mathbf{f}_i(s)ds = 0 \tag{4}$$

and $\hat{\boldsymbol{k}}\cdot\sum_i\int_0^1 s\mathbf{n}_i \times \mathbf{f}_i(s)ds = 0$ implies

$$\sum_i \int_0^1 s\mathbf{t}_i\cdot\mathbf{f}_i(s)ds = 0 \tag{5}$$

where the sum is over all legs with distinct angles $\theta_i$. Any bundle of legs oriented at the same angle is treated as one leg. This is because the bundle is approximated by an effective leg with a different aspect ratio $\epsilon$, but this ratio has only a weak logarithmic effect on $C$ and $\mathbf{f}_i$ appearing in the model. Applying (4) to (3), integrating over $s \in [0,1]$ and then combining the result with (5) gives

$$\mathbf{M}\dot{\mathbf{x}} = K \tag{6}$$

where $\dot{\mathbf{x}}(t) = [\dot{x}(t), \dot{y}(t), \dot{\phi}(t)]^T$ captures the respective time derivatives of the body's position and orientation. $\mathbf{M}$ is specified by

$$\begin{pmatrix} \sum(1+\sin^2(\boldsymbol{\alpha})) & -\sum\sin(\boldsymbol{\alpha})\cos(\boldsymbol{\alpha}) & -\sum\sin(\boldsymbol{\alpha}) \\ -\sum\sin(\boldsymbol{\alpha})\cos(\boldsymbol{\alpha}) & \sum(1+\cos^2(\boldsymbol{\alpha})) & \sum\cos(\boldsymbol{\alpha}) \\ -\sum\sin(\boldsymbol{\alpha}) & \sum\cos(\boldsymbol{\alpha}) & 2 \end{pmatrix}$$

and $\mathbf{K}$ is specified by

$$\begin{pmatrix} \sum\dot{\boldsymbol{\theta}}\sin(\boldsymbol{\alpha}) \\ -\sum\dot{\boldsymbol{\theta}}\cos(\boldsymbol{\alpha}) \\ -\frac{2}{3}\sum\dot{\boldsymbol{\theta}} \end{pmatrix}$$

The matrix $\mathbf{M}$ is often referred to as the *resistance matrix* of the body while its inverse $\mathbf{M}^{-1}$ is called the *mobility matrix*;

The instantaneous rate of work done by the swimmer is computed by

$$\dot{W} = \sum_i \int_0^1 \dot{\mathbf{x}}_i(s)\cdot\mathbf{f}_i(s)\,ds \tag{7}$$

We can substitute (3) into (7) to find $\dot{W} = \dot{q}^T\cdot E\cdot\dot{q}$, where $q = (x, y, \phi, \theta_1\cdots,\theta_m)^T$ for a swimmer with $m$ legs oriented at distinct angles and

$$E = \begin{pmatrix} U & V \\ V^T & S \end{pmatrix}. \tag{8}$$

Here $U$ is the 3×3 matrix

$$\begin{pmatrix} m & \frac{1}{2}(\sum\cos^2\alpha_i) & \frac{1}{2}SC & \frac{1}{2}(\sum\sin\alpha_i) \\ \frac{1}{2}SC & m & \frac{1}{2}(\sum\sin^2\alpha_i) & \frac{1}{2}(\sum\cos\alpha_i) \\ \frac{1}{2}(\sum\sin\alpha_i) & \frac{1}{2}(\sum\cos\alpha_i) & & \frac{m}{3} \end{pmatrix}$$

where $SC = \sum\sin\alpha_i\cos\alpha_i$ and $V$ is the $3{\times}m$ matrix

$$\begin{pmatrix} \frac{1}{2}\sin\alpha_1 & \frac{1}{2}\sin\alpha_2 & \dots & \frac{1}{2}\sin\alpha_m \\ \frac{1}{2}\cos\alpha_1 & \frac{1}{2}\cos\alpha_2 & \dots & \frac{1}{2}\cos\alpha_m \\ \frac{1}{3} & \frac{1}{3} & \dots & \frac{1}{3} \end{pmatrix}$$

and $S = \frac{1}{3}I$ where $I$ is the $m\times m$ identity matrix. Here we focus on swimming along a 1 dimensional line, but the model could be generalized in the future to account for swimming in 3 dimensions by allowing each leg to orient in 3 dimensions and introducing additional position and orientation coordinates to represent the state of the swimmer.

### *B. Symmetric Copepod*

Hereafter we focus on a swimmer with a total of $m = 2N$ legs, where $N$ is the number of pairs of legs actuated symmetrically such that $\theta_{2N-i+1} = 2\pi - \theta i$ and $\dot{\theta}_{2N-i+1} = -\dot{\theta} i$. The upper half of the symmetric body is sketched in Figure 3. Note that due to the symmetry, motion in one direction only can be realized: $y = \phi \equiv 0$. Combining this with (6) reduces the model to:

$$\dot{x} = \frac{\sum_{j=1}^n \dot{\theta}_j\sin\theta_j}{\sum_{j=1}^n(1+\sin^2\theta_j)}. \tag{9}$$

As before, $n$ is the *effective* number of pairs of legs, where any bundle of legs oriented at the same angle is treated as a single leg.

## III. OPTIMAL STROKES

Introducing $q = (x, \theta_1\cdots,\theta_n)^t$, the symmetric copepod can be written as a driftless control system

$$\dot{q}(t) = \sum_{i=1}^n F_i(q(t))u_i(t) \tag{10}$$

where $F_i(q) = f(\theta_i)\frac{\partial}{\partial x} + \frac{\partial}{\partial\theta_i}$, $f(\theta) = \frac{\sin\theta}{\sum_{j=1}^n(1+\sin^2\theta_j)}$ and $u_i = \dot{\theta}_i$. As it is swimming, the copepod is minimizing

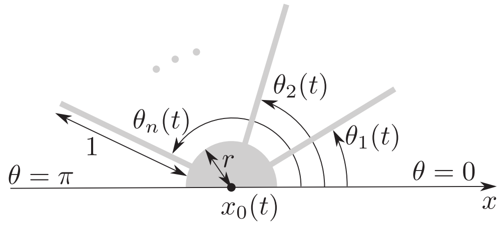



Fig. 3. Sketch of a symmetric swimmer possessing $n$ pairs of legs. Figure reproduced from [4].

what we refer to as the mechanical energy. The energy is a quadratic form given by $\dot{q}^T E \dot{q}$ where $E$ is a symmetric matrix:

$$E = \begin{pmatrix} n - \frac{1}{2}(\sum \cos^2 \theta_i) & -\frac{1}{2}\sin\theta_1 & \cdots & -\frac{1}{2}\sin\theta_n \\ -\frac{1}{2}\sin\theta_1 & \frac{1}{3} & \cdots & 0 \\ \vdots & \vdots & \cdots & \vdots \\ -\frac{1}{2}\sin\theta_n & 0 & 0 & \frac{1}{3} \end{pmatrix} \tag{11}$$

and the copepod is minimizing

$$\min \int_0^T \dot{q}^t(t) E(q(t)) \dot{q}(t) dt \tag{12}$$

Using the differential equation for $x$ it can be written as a quadratic function in the controls:

$$\int_0^T \sum_{i \le j; i,j=1}^{n} a_{ij}(\theta(t)) u_i(t) u_j(t) dt \tag{13}$$

where

$$a_{ii}(\theta) = \frac{1}{3} - \frac{\sin\theta_i^2}{2\sum_{j=1}^n (1+\sin^2\theta_j}), \tag{14}$$

$$a_{ij}(\theta) = -\frac{\sin\theta_i \sin\theta_j}{\sum_{j=1}^n (1+\sin^2\theta_j}),\ i \neq j. \tag{15}$$

$$\tag{16}$$

### A. Maximum Principle

The Prontyagin Maximum Principle [8] implies that if $q(.)$ is a time optimal trajectory there exists an absolutely continuous vector $p(.)$ and a constant $p_0$, $(p(t), p_0) \neq 0$ for all $t \in [0, T]$, called an adjoint vector, such that the following conditions hold almost everywhere:

$$\dot{q} = \frac{\partial H}{\partial p}(p, q, u),\ \ \dot{p} = -\frac{\partial H}{\partial q}(p, q, u) \tag{17}$$

where $H(p, q, u) = \sum_{i=1}^n p^t F_i(q) u_i + p_0 \sum_{i \le j; i,j=1}^n a_{ij}(\theta) u_i u_j$ is the Hamiltonian function, and the maximum condition holds:

$$H(p(t), q(t), u(t)) = \max_{v \in \mathcal{U}} H(p(t), q(t), v) \tag{18}$$

with the domain $\mathcal{U}$ given by $|\dot{\theta}_i| = |u_i| \le \alpha$ where $\alpha$ is a constant related to the angular velocity the copepod can produce through its strokes. We assume for simplicity in the sequel that $\alpha = 1$ since this normalization does not modify the structure of the optimal solutions. A triple $(p, q, u)$ which satisfies the maximum principle, in the sense just stated, is called an extremal. Let us introduce $H_i$ as the Hamiltonian lift: $H_i(p, q) = \langle p, F_i(q) \rangle$. The maximum principle provides only necessary conditions, hence to complete the analysis one must classify the behaviors of extremals of order zero near the switching surface to analyze the possible connections between singular arcs of order zero. Complicated phenomenon can occur such as the Fuller phenomenon, see [9]. A future objective, but out of the scope of this paper, is to do this classification.

### B. Normal Curves

Normal extremals correspond to a nonzero constant $p_0$. We can normalize that constant to $p_0 = -\frac{1}{2}$ and the maximization condition gives us the following condition:

$$E(\theta) \begin{pmatrix} u_1 \\ \vdots \\ u_n \end{pmatrix} = \begin{pmatrix} H_1(p, q) \\ \vdots \\ H_n(p, q) \end{pmatrix} \tag{19}$$

which provide a closed form for the normal control in terms of $(p, q)$ since $E$ is invertible. Plugging the expressions for $u_i$ into $H$ produces the true Hamiltonian in the normal case. If we were to consider the flat metric as energy. i.e. $E$ is the identity matrix, we would obtain that: $H_n(p, q) = \frac{1}{2}\sum_{i=1}^n H_i^2(p, q)$. A normal stroke is a solution of $\overrightarrow{H_n}$ such that $\theta_i$ are periodic with period $T$. According to the transversality conditions of the maximum principle we also have that the dual variables $p_i$ to the angles $\theta_i$ are periodic of period $T$. In this paper, we focus on the abnormal extremals, but further numerical work will determine the normal optimal strokes by testing conjugate points along such extremals. In the normal case, the *first conjugate point* corresponds to the first point where a normal geodesic ceases to be minimizing with respect to the $C^1$-topology on the set of curves and they can be computed using the hampath software [10]. A normal stroke is called $C^1$-optimal on $[0, T]$ if there exists no conjugate point on the interval $]0, T]$.

### C. Abnormal Curves

Abnormal curves corresponds to $p_0 = 0$. In this case, we have

$$H(q, p, u) = \sum_{i=1}^n H_i(q, p) u_i \tag{20}$$

and the maximization conditions imposes that for all $i = 1, \cdots, n$):

$$H_i(q, p) = \langle p, F_i(q) \rangle = 0 \tag{21}$$

along an abnormal arc. Differentiating once more we obtain:

$$O(q(t), p(t)) u(t) = 0 \tag{22}$$

where the $n \times n$ skew-symmetric matrix $O$ whose entries are given by $O_{ij} = \langle p, [F_i, F_j](q) \rangle := H_{ij}(q, p)$. The rank of the matrix $O$ determines the existence of abnormal controls. We have here to distinguish cases depending on the parity of $n$. Indeed, for an odd number of legs $O$ is always singular. To understand the abnormal curves, let us first determine the

Lie algebra associated to the distribution $D$ generated by the vector fields $F_i(q)$. We have:

$$[F_i, F_j](q) = (f_j(\theta_i) - f_i(\theta_j))\frac{\partial}{\partial x} \quad (23)$$

where $f_j(\theta_i) = \frac{\partial f}{\partial \theta_j}(\theta_i) = \frac{2\sin\theta_i \sin\theta_j \cos\theta_j}{(\sum_{j=1}^n (1+\sin^2\theta_j))^2}$. Differentiating once more provides:

$$[[F_i, F_j], F_k](q) = (f_{kj}(\theta_i) - f_{ki}(\theta_j) - f_j(\theta_k))\frac{\partial}{\partial x} \quad (24)$$

where $f_{kj} = \frac{\partial^2 f}{\partial\theta_k \partial\theta_i}$. A quick calculation shows that

$$f_{kj}(\theta_i) = \frac{4\sin\theta_i \sin\theta_j \cos\theta_j \sin\theta_k \cos\theta_k}{(\sum_{j=1}^n (1+\sin^2\theta_j))^3} \quad (25)$$

We now consider both cases depending on the parity of the control.

*1) $n$ is even:* In that case, we have that the rank of $O$ is even (the eigenvalues are pure imaginary and come in conjugate pairs). If the matrix $O$ is of full rank it is invertible and we obtain the control $u = 0$. This corresponds to a stationary copepod and therefore is of no interest. Assume the rank is even. In that case, there exists an orthogonal matrix $Q$ such that $O = Q\Sigma Q^T$ where $\Sigma$ is a block matrix of the form

$$\Sigma = \begin{bmatrix} 0 & \lambda_1 & 0 & 0 \\ -\lambda_1 & 0 & 0 & 0 \\ 0 & 0... & 0 & 0 \end{bmatrix} \quad (26)$$

with $2r$ the rank of $O$. It is equivalent to $O = (O_1, 0)$ where $O_1$ is block component of the matrix that includes the terms with the eigenvectors. The control is then computed as follows. We introduce $v = Qu = (v_1, v_2)$ with $v_1 \in R^{2r}$, and we have $Q\Sigma Q^t v = 0$ which can be rewritten as

$$O_1(q,p)v_1 = 0 \quad (27)$$

and implies $v_1 = 0$. The control is calculated using $u = Q^T(0, v_2)^T$ where $v_2$ is arbitrary. A special case corresponds to the situation when rank$O = 0$. This means that $[F_i, F_j](q) = 0$ for all $i, j$. The case of two pairs of legs can be found in [5], in this paper we explicit the situation for three pairs of legs below.

*2) $n$ is odd:* An odd skew-symmetric matrix is always singular since the rank must be even. The matrix $O$ can be put in a block-form similarly than in the even case with at least one row and one colum of zeroes. The rest of the procedure to compute the control is similar. Let us look at the specific case $n = 3$. By definition, we have:

$$O = \begin{bmatrix} 0 & H_{12} & H_{13} \\ -H_{12} & 0 & H_{23} \\ -H_{13} & -H_{23} & 0 \end{bmatrix} \quad (28)$$

If the rank is 0, then $H_{ij} = 0$ for all $i, j$. Since we are in four dimension and that $H_{ij} = \langle p, [F_i, F_j](q)\rangle$ it implies that $[F_i, F_j](q) = 0$. Indeed, otherwise we would have a contradiction with the fact that $p \neq 0$ along an abnormal curve since $H_j(p,q) = 0$ and rank$\{F_i, [F_i, F_j]\}_{i,j}$ is four. Along such abnormal curve we have:

$$\frac{2\sin\theta_i \sin\theta_j(\cos\theta_j - \cos\theta_i)}{(\sum_{j=1}^n (1+\sin^2\theta_j))^2} \quad (29)$$

for all $i, j$, and the curve belongs to the vertex and edges of the set defined by:

$$\{\theta;\ \theta_1 \leq \theta_2 \leq \theta_3,\ \ \theta_i \in [0,\pi]\}. \quad (30)$$

More precisely, the following equalities must be satisfied:

$$\sin\theta_1 \sin\theta_2(\cos\theta_1 - \cos\theta_2) = 0, \quad (31)$$

$$\sin\theta_1 \sin\theta_3(\cos\theta_1 - \cos\theta_3) = 0, \quad (32)$$

$$\sin\theta_2 \sin\theta_3(\cos\theta_2 - \cos\theta_3) = 0. \quad (33)$$

We can consider 4 cases.

1) There exists $i \neq j$ such that $\sin\theta_i = \sin\theta_j = 0$. Together with constraint (30) it implies that the possible solutions are $(0, 0, \theta(t))$, $(0, \theta(t), \pi)$ and $(\theta(t), \pi, \pi)$ where $\theta(t) \in [0, \pi]$. This corresponds to the case when two legs are fixed at one of the boundary value and the third one moves.
2) We have $\cos\theta_i = \cos\theta_j$ and $\sin\theta_k = 0$ for a triplet $i \neq j \neq k$. That implies that the possible solutions are given by $(0, \theta(t), \theta(t))$ and $(\theta(t), \theta(t), \pi)$ where $\theta(t) \in [0, \pi]$. In this case one leg is static at one of the boundary value and the two others move together.
3) We have $\cos\theta_i = \cos\theta_j$ and $\sin\theta_i = 0$, where $i \neq j$. Thus, $\theta_i = \theta_j$ and $\sin\theta_i = \sin\theta_j = 0$ which reduces to case 1.
4) We have $\cos\theta_1 = \cos\theta_2 = \cos\theta_3$ for . Thus $\theta_1 = \theta_2 = \theta_3$, so the solution is $(\theta(t), \theta(t), \theta(t))$ where $\theta \in [0, \pi]$. This is the case when the three legs are identified a single one.

On Fig. 4 we display the set (30) which is formed by the interior and boundary of the domain, and the abnormal arcs are the edges of this domain. An abnormal stroke is a $2\pi$-periodic motion formed by a concatenation of motions along the edges of the domain. Let us look at these specific strokes. Based on our analysis motions along the edges corresponds to fixing one or more angle to the extremity of the interval $[0, \pi]$ and move the other angles simultaneously.

Assume the initial configuration of the legs to be $(\theta_1(0), \theta_2(0), \theta_3(0)) = (0, 0, 0)$, see Fig 5 (a). To create an abnormal stroke we must first bring all the legs to the opposite extremity of the interval: $\theta_i = \pi$. This can be done in three ways moving one leg at a time; moving two legs together and then one leg; or moving the three legs simultaneously. Consider the copepod's displacement in the variable $x$ in each of these cases.

- Case 1a. Only one leg $\theta_i$ moves from time $t_1$ to $t_2$, and by construction the other legs stay both at 0 or $\pi$ . Thus $\theta_i(t_1) = 0, \theta_i(t_2) = \pi$ and $\dot{x}(t) = \frac{\sin\theta_i(t)\dot{\theta}_i(t)}{2+\sin^2\theta_i(t)}$. Integrating we obtain $x(t_2) - x(t_1) = \int_{t_1}^{t_2} \frac{\sin\theta_i(t)\dot{\theta}_i(t)}{2+\sin^2\theta_i(t)}\,\mathrm{d}t = \int_{t_1}^{t_2} \frac{\sin\theta_i(t)\dot{\theta}_i(t)}{3-\cos^2\theta_i(t)}\,\mathrm{d}t$. Introduce $u = \cos\theta_i(t)$, then we have that

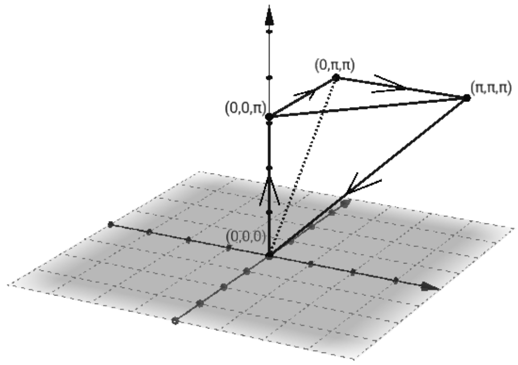
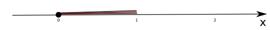
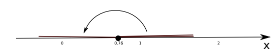


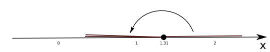

Fig. 4. This figure represents the domain $0 \leq \theta_1 \leq \theta_2 \leq \theta_3 \leq \pi$. The abnormal arcs corresponding to rank$O = 0$ are on the vertices and the edges. The arrows indicates the periodic stroke seen in Figure 5.



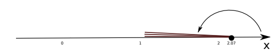
(a) Initial position



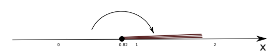
(b) Leg $\theta_1$ moves



(c) Leg $\theta_2$ moves



(d) Leg $\theta_3$ moves



(e) All three legs move back

Fig. 5. Concatenation of abnormal strokes.

$x(t_2) - x(t_1) = \int_{-1}^{1} \frac{\mathrm{d}u}{3-u^2} = \frac{1}{\sqrt{3}} \ln(\frac{\sqrt{3}+1}{\sqrt{3}-1})$.

- Case 1b. Only one leg $\theta_i$ moves from time $t_1$ to $t_2$, and by construction the other legs stay one at 0 and another at $\pi$. Thus $\theta_i(t_1) = 0, \theta_i(t_2) = \pi$ and $\dot{x}(t) = \frac{\sin\theta_i(t)\dot{\theta}_i(t)}{3+\sin^2\theta_i(t)}$. Integrating we obtain $x(t_2) - x(t_1) = \int_{t_1}^{t_2} \frac{\sin\theta_i(t)\dot{\theta}_i(t)}{3+\sin^2\theta_i(t)}\,\mathrm{d}t = \int_{t_1}^{t_2} \frac{\sin\theta_i(t)\dot{\theta}_i(t)}{4-\cos^2\theta_i(t)}\,\mathrm{d}t$. Introduce $u = \cos\theta_i(t)$, then we have that $x(t_2) - x(t_1) = \int_{-1}^{1} \frac{\mathrm{d}u}{4-u^2} = \frac{1}{2}\ln(3)$.

- Case 2. Two legs move simultaneously. Then $\theta_i(t) = \theta_j(t)$ and $\dot{x}(t) = \frac{\sin\theta_i(t)\dot{\theta}_i(t)}{2+\sin^2\theta_i(t)}$. Then as in case 1a, $x(t_2) - x(t_1) = \frac{1}{\sqrt{3}}\ln(\frac{\sqrt{3}+1}{\sqrt{3}-1})$.

- Case 3. Three legs move simultaneously. Then, $\dot{x}(t) = \frac{\sin\theta_i(t)\dot{\theta}_i}{1+\sin^2\theta_i(t)}$. Similar calculations shows that $x(t_2) - x(t_1) = \int_{-1}^{1} \frac{\mathrm{d}u}{2-u^2} = \frac{1}{\sqrt{2}}\ln(\frac{\sqrt{2}+1}{\sqrt{2}-1})$.

Therefore, in case 1 after all three legs move to $(\pi, \pi, \pi)$, the displacement of the copepod is $\frac{1}{2}\ln(3) + \frac{2}{\sqrt{3}}\ln(\frac{\sqrt{3}+1}{\sqrt{3}-1}) \approx 2.07$, in case 2 it is $\frac{2}{\sqrt{3}}\ln(\frac{\sqrt{3}+1}{\sqrt{3}-1}) \approx 1.52$ and in case 3 we have $\frac{1}{\sqrt{2}}\ln(\frac{\sqrt{2}+1}{\sqrt{2}-1}) \approx 1.25$. Note that our computations demonstrate that the $x$-displacement does not depend on time and that the most efficient way to go forward is to move one leg at a time. A periodic stroke involves bringing back the legs to the initial configuration, and to produce a final maximum net displacement we use the case 3. The total displacement is then $2.07 - 1.25 = 0.82$. This motion is illustrated in Figure 5 with the sequence of abnormal arcs, and in Figure 4 where the stroke discussed above is denoted using the arrows. In case of two pairs of legs, it was shown that the displacement is of the order of 0.3.

Let us look at the case when rank $O = 2$. We then must have $H_{ij} \neq 0$ for all $i, j$. Indeed, if for instance $H_{12} = 0$ either $\sin\theta_1 = 0$, $\sin\theta_2 = 0$ or $\cos\theta_1 = \cos\theta_2$. In the first and second scenario it would respectively mean that $H_{13=0}$ (resp. $H_{23} = 0$) which contradicts the rank of the matrix and in the third caser it would imply that $\theta_1 = \theta_2$ and $u_3 = 0$ which corresponds to having only one pair of legs and produces no motion. Assuming that $H_{ij} \neq 0$ we have to solve the following system of equations:

$$H_{12}u_2 + H_{13}u_3 = 0 \quad (34)$$
$$-H_{12}u_1 + H_{23}u_3 = 0 \quad (35)$$
$$-H_{13}u_1 - H_{23}u_2 = 0 \quad (36)$$

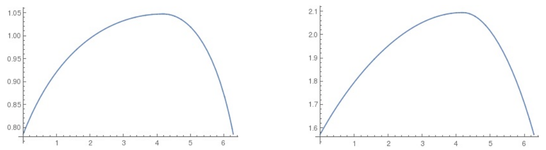
We obtain a one-parameter family of solutions. If we parametrize the solution using $u_3$ an abnormal control is given by:

$$u_1 = \frac{H_{23}}{H_{12}}u_3, \qquad u_2 = -\frac{H_{13}}{H_{12}}u_3 \quad (37)$$

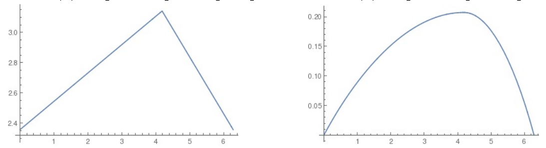
Computing, and using the following feedback transformation $\hat{u}_3 = \frac{\sin\theta_3}{\sin\theta_1\sin\theta_2(\cos\theta_2 - \cos\theta_1)}u_3$ we have:

$$u_1 = \sin\theta_2(\cos\theta_3 - \cos\theta_2)\hat{u}_3, \quad (38)$$
$$u_2 = \sin\theta_1(\cos\theta_3 - \cos\theta_1)\hat{u}_3. \quad (39)$$

It can be shown that since with three pairs of legs we obtain a one parameter family no displacement can be produced using these abnormal extremals. Indeed, see Figure 6 for an example. It clearly demonstrates that if the strokes is parametrized by $\theta_3$ then the horizontal displacement is zero. The conclusion is that for three pairs of legs these strokes can be neglected since they do not produce any net displacement. Note that for more pairs of legs the situation is different because we will have two angles parametrizing the abnormal strokes when rank $O$ is not zero and net displacement can be then produced.



(a) $\theta_1(.) : [0, 2\pi] \to [0\pi]$ (b) $\theta_2(.) : [0, 2\pi] \to [0\pi]$



(a) $\theta_3(.) : [0, 2\pi] \to [0\pi]$ (b) $x(.) : [0, 2\pi] \to [0\pi]$

Fig. 6. This example shows to an abnormal strokes parametrized by $\theta(.)$. It can be observed that there is zero horizontal displacement.

## IV. Discussion

In this last section, we compare our results to experimental observations of a larval copepod (stage 5 nauplius). Figure 7 shows how it swims using three pairs of legs, each leg pair performing a sequence of power strokes and then all legs returning together in unison.

From observations, the nauplius displays physical constraints on the positioning of his legs. More precisely, the two front legs (A1) on Figure 7 show a variation $\in [5°, 130°]$. The second pair of legs' constraint is that $\theta_2 \in [40°, 135°]$ (A2), and $\theta_3 \in [110°, 160°]$ (Md). On Figure 7, we see the appendage angles and timing of power and return strokes during 1.5 cycles of swim sequence. It can be observed that $\theta_3$ starts moving toward $180°$ at first while the other two pairs of legs position themselves to maximize the amplitude they will use (this is equivalent to Fig. 5 (b) for our model). Once $\theta_2, \theta_3$ reach their constraint (first for the second pair of legs) they start moving toward the back of the nauplius (Fig. 5 (c) and (d)). The three pairs of legs move with a phase shift to create the maximal displacement forward. Since the third pair of legs (Md) arrives to its physical constraint first it then await the other two legs to reach their physical constraints. The return stroke is done by coordinating the three legs (especially $\theta_1 = \theta_2$) for a good fraction of the stroke which is what we have in Fig 5 (e) for our computational model. The correlation with our work is that the larval copepod uses the same strategy than the one with the abnormal strokes on the edges of the angles domain, the main differences are that: first the physical domain has limitation in terms of the amplitude of the motion of each pair of legs; and second there is a breaking mechanism in the larva copepod.

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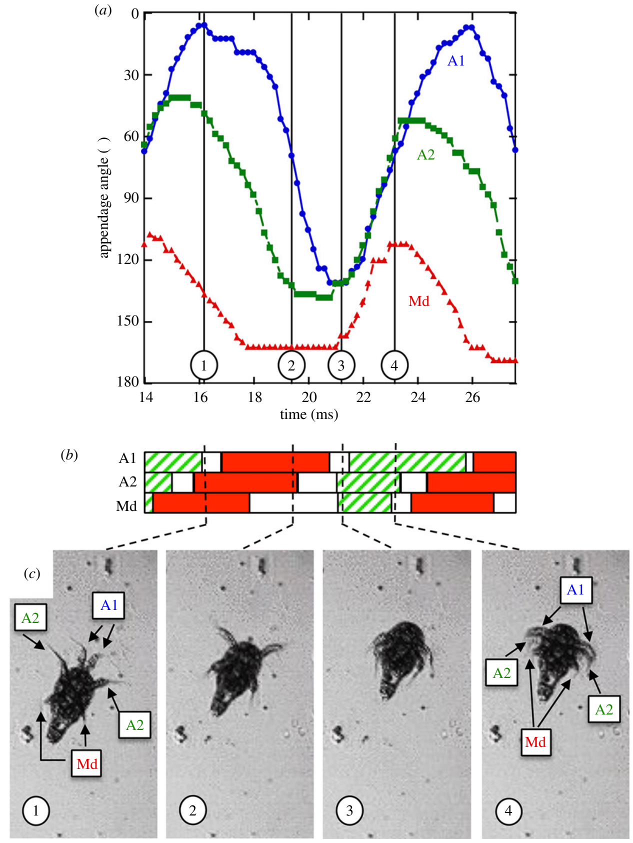


Fig. 7. Measured movements of a larval copepod. Panel (a) shows variations over time of the orientation angles of three leg pairs, labeled as A1, A2, Md. Panel (b) shows time intervals when each leg pair performs a power stroke (red), a return stroke (green stripes), or remains stationary (white). Panel (c) shows snapshots of the copepod at four representative times. Figure reproduced from [1].

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