Chapter 12

Invertebrate ‘LocOlympics’: Investigation and Inquiry into Invertebrate Locomotion and Biomechanics

***Charlie Drewes*[1] *and Maria Oehler*[2]**

[1]Ecology, Evolution and Organismal Biology
339 Science II Building
Iowa State University
Ames, IA 5001
cdrewes@iastate.edu
http://www.eeob.iastate.edu/faculty/DrewesC/htdocs/

[2]Math and Science Department
247A Linn Hall
Kirkwood Community College
Cedar Rapids, IA 52404
moehler@kirkwood.cc.ia.us

Charlie Drewes received a BA from Augustana College (SD) and MS/PhD in zoology at Michigan State University. Currently a professor in Ecology, Evolution and Organismal Biology at Iowa State University, Charlie teaches courses in invertebrate biology, neurobiology and bioethics. During summers, he leads hands-on, residential workshops for high school biology teachers at Iowa Lakeside Lab. In 1998, he received the Distinguished Science Teaching Award from the Iowa Academy of Science and, in 2002 he received the Four-year College Biology Teaching Award from the National Association of Biology Teachers.

Maria Oehler received her BA from the University of Iowa and her MS in biology/physics from Iowa State University under the supervision of Dr. Charlie Drewes. Maria is currently a full-time instructor at Kirkwood Community College (IA) where she teaches several courses, including Anatomy and Physiology (I and II) and Introduction to Pathophysiology.

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Introduction

'Invertebrate LocOlympics' is an interdisciplinary laboratory investigation of animal locomotion. It provides excellent opportunities for achieving the following objectives: (a) integration of the concept of animal movement, a cornerstone feature of animal biology, with basic principles of physics; (b) incorporation of quantitative approaches, involving both distance and time, into a context of organismal biology; and (c) comparison and contrast of animal form, function, and behavior across a broad spectrum of animal phyla. The entire investigation (or selected portions of it) could be utilized at any level, from basic introductory biology to advanced biology, comparative physiology, or animal behavior.

The 'LocOlympics' videotape and PowerPoint files (on CD or WWW) show frame-by-frame documentation of locomotion in ten different invertebrates. Complete extraction and analysis of biomechanics-related data for all ten organisms may require several laboratory periods. So, the investigation is modular in design, making it relatively easy for a group of students to focus on one or two specific parameters (*e.g.*, an organism's forward velocity or wave frequency) for a few selected organisms. If desired, opportunities then exist to assign different groups of students with different parameters and organisms. Thus, collectively, the groups can cross-compare computational results from numerous species, as well as discuss the overall significance and implications.

Notes for the Instructor

This inquiry uses videotape or electronic images (PowerPoint files on CD or WWW) for frame-by-frame analysis of the biomechanics of locomotion in a variety of invertebrates. Types of locomotion include: undulatory swimming, swimming with appendages, walking, running, jumping, ciliary gliding, and others. One measure that students easily obtain for every organism is forward velocity. Other measures and calculations they might readily obtain include Reynolds number, wave velocity, and wave frequency (see Table 1).

The section entitled “Terminology and technical information” contains key information related to procedure, video technology, and physics principles. Typical results of computations, given in Appendix A, are mainly for reference by the instructor.

Table 1. List of organisms on the ‘LocOlympics’ videotape (or CD) and the calculations that students may obtain for each organism.

	Forward Velocity	Reynolds Number	Wave Velocity	Wave Frequency
Dero	X	X	X	X
Lumbriculus	X	X	X	X
Vinegar Eel	X	X	X	X
Leech	X	X	X	X
Daphnia	X	X		
Ostracod	X	X		
Copepod	X	X		
Centipede	X			
Millipede	X		X	X
Springtail	X			

Students use freeze-frame images on the “LocOlympics” video or PowerPoint files on CD (or WWW) to:

- Plot the path of an animal’s locomotor progress on a frame-by-frame basis
- Compute forward velocity of each moving animal
- Compute Reynolds number for swimming animals (this number relates to the types of drag forces that affect an animal’s movement in its aquatic or aerial environment)
- Determine the direction of a moving wave of appendages or body motion
- Compute the velocity of the locomotor waves that move along the body
- Compute the frequency of rhythmic locomotor movements
- Identify the power stroke and recovery stroke phases for rhythmic locomotor movements (*e.g.*, walking)
- Understand and appreciate how the medium of videotape (especially freeze-frame images) can be used to analyze the dynamics of animal movement

To help visualize certain animals’ motion and biomechanics in three dimensions, students should be encouraged to make and manipulate simple models, especially for *Lumbriculus*, *Dero*, vinegar eel, leech. Models of vermiform organisms can be made from electrical wire, pipe cleaners, or even twist ties. The temporal and spatial dynamics of undulatory and helical swimming movements can be easily simulated with such models.

To begin data collection, students make “datagrams” that plot an animal’s trajectory or shape during locomotion (see Figs. 1, 4, and 5 in “Terminology and technical information”). To do this, a transparency sheet is temporarily taped to the monitor screen and positions of the organism are recorded in successive frames. Once completed, these datagrams will contain most of the raw data necessary for making calculations and addressing questions, assuming that students have thoroughly and accurately recorded plots, scales, and labels on the transparency.

The activity could be assigned as homework by providing students with copies of the videotape or PowerPoint files, assuming that they have access to adequate video or computer display equipment at home. For video display, any medium-sized, hard-screen TV monitor linked to a VCR works well. If the monitor screen is much larger than an 8.5 X 11-inch transparency sheet, then several transparencies can be taped together to cover the screen. Some images may take up three-quarters of the screen.

Each videotape episode of locomotion begins with a brief title followed by two repeated episodes of movement, displayed in "real time." A length scale is superimposed on each locomotor episode. At the end of the tape (and on the CD), frame-by-frame replays of various animals' locomotion are given. Each video frame is paused for 2-3 seconds. This allows time for students to plot an organism's forward progress and make tracings of the organism's shape as it is moving.

Organisms are grouped on the tape by locomotor mechanism in the following order:

- Undulatory swimming: helical swimmers - *Dero* and *Lumbriculus* (oligochaetes); and sinusoidal swimmers - vinegar eel (nematode) and leech (hirudinid)
- Swimming with appendages: daphnia, ostracod and copepod (all crustaceans)
- Running / walking: centipede and millipede (myriapods)
- Jumping: springtail (insect)

Materials

- Transparency sheets or clear acetate sheets (at least 10 sheets/group).
- Non-permanent markers in several colors.
- VHS videocassette recorder [A recorder with frame-by-frame replay capability, or jog and shuttle, is preferred so that the videotape can be precisely advanced.]
- Television monitor (13" recommended, preferably with hard, flat screen).
- Paper tape to secure transparency to the monitor screen.
- Computer (Mac or PC) with PowerPoint presentation capability and hard screen.
- White paper for backing the completed transparency sheets (datagrams)
- *"Invertebrate LocOlympics"* videotape* and/or PowerPoint files on CD (or WWW). For free web access to freeze-frame files, see <http://www.eeob.iastate.edu/faculty/DrewesC/htdocs/>
- Straight-edge for drawing lines.
- Calculator

***** Copies of the videotape, and color photos, are available for purchase for $10, which is less than actual cost. This cost includes: the "*Invertebrate LocOlympics*" videotape, shipping, plus four accompanying color copies that show selected freeze-frame images from the tape. For purchase of tape or questions, contact author (Charles Drewes).

Student Outline

Introduction for students

How fast can invertebrates swim, crawl, or run? How high can they jump? As they move, how frequently do their movements occur? How can an animal's locomotion be studied and measured? How do the forces of resistance encountered by an invertebrate during its locomotion differ from those that you encounter when you swim, crawl, or run?

The objective of this inquiry is to quantitatively study locomotion in a wide variety of invertebrates. To fully understand the movements of these animals, you must use a few principles from basic physics and mathematics. Some of the concepts that are relevant include: gravity, inertia, friction, viscosity, pressure drag, viscous drag, forward velocity, wave velocity and wave frequency. If you are not familiar with these terms, look them up in a dictionary and read the section entitled, "Terminology and technical information." Review them with others in your group or class.

Preliminary questions to consider and discuss

How many different methods of animal locomotion can you think of? Make a list. Compare your list to Table 2, which gives most methods of locomotion that are known in invertebrates (Barnes et al., 2001; Pechenik, 1999; Ruppert and Barnes, 1994; Vogel, 1994). Many of these methods of locomotion are used by vertebrate animals, as well. Which specific ones do you think are also used by vertebrates? Which are not?

General points about the forces that govern all animal movements:

- In some cases (such as, planaria and snail), propulsive forces are generated mainly by movement of cellular organelles (cilia). In most other cases, the forces are generated by contraction forces (that is, shortening) of specific muscles, or muscle layers.
- Muscle contractions are powered by ATP.
- Muscle forces usually act on some type of skeleton. In the vertebrates, muscles attach to, and work in conjunction with, a *bony internal skeleton*. In most hard-bodied invertebrates, muscles are attached to a rigid *exoskeleton*. In soft-bodied invertebrates, muscle layers act on a *hydrostatic skeleton* (fluid-filled body compartment).
- Inertial forces must be overcome to start moving. To keep moving, animals must contend with the forces of friction, drag, and gravity, which all tend to slow or stop motion.

General points about locomotor behavior:

- A given species may be capable of using more than one form of locomotion. For example, a cricket may use walking to find food, but it will jump to avoid becoming another organism's meal. Some leech species may use three different types of locomotion.
- A given species may change its form of locomotion as it progresses through different developmental stages. For example, certain insect larvae may use inch-worm movements to crawl, but the adult stage may use legs to walk or wings to fly.

- Some animals may use the same structure to simultaneously accomplish multiple functions. For example, a crustacean may use rhythmic movements of its thoracic appendages for both walking and gas exchange.
- The same locomotor function may be accomplished using different structures. For example, jumping can be accomplished either by using legs, as in some insects (grasshopper and cricket), or by using a special tail structure (furcula) that catapults the organism off the ground, as in other insects (springtails).
- As a result of convergent evolution, species in diverse taxonomic groups may use the same pattern of locomotion. Fore example, undulatory (sinusoidal) swimming is seen in certain nematode worms (unsegmented) as well as some marine polychaete worms (segmented).

Table 2. Major forms of invertebrate locomotion. Arrows at right indicate organisms with locomotion sequences shown on 'LocOlympics' videotape.

FORM	BY USE OF:	EXAMPLES
Amoeboid	Pseudopodia	free-living protozoans
Swimming	Flagella	free-living and some parasitic protozoans
		sponge larvae
Swimming	Cilia	free-living protozoans
		small flatworms
		ctenophores
		rotifers
		bryozoan larvae
		planula larvae
		cestode larvae
		trochophore larvae
		veliger larvae
Swimming	Wave-like body undulations (mostly sinusoidal waves; a few with helical waves)	some flatworms
		some aquatic oligochaetes ←
		leeches ←
		some polychaetes
		some nematodes ←
		some anemones
		some marine gastropods
		some nemerteans
		urochordates and tunicate larvae
		some aquatic insect larvae
		nematomorphs
Swimming	Fluid Propulsion	jellyfish ←
		squid, cuttle fish and scallops
		a few aquatic insect larvae
Swimming	Movement of paddle-like or oar-like appendages (e.g., legs or parapodia)	some polychaetes
		aquatic arthropods ←←
		many crustaceans ←←
Creeping/gliding	Ciliary Waves	large flatworms ←
		gastrotrichs
		nemerteans
		many gastropods ←
Body peristalsis	Body muscle and a hydrostatic or hydraulic skeleton	nemerteans
		annelids
		sipunculids
		echiurids
Inch-worm movements (looping)	Body muscle and hydrostatic skeleton (also suckers or legs in some)	leeches
		some insect larvae
		some rotifers
Walking/running	Legs (prolegs in some insect larvae)	most arthropods arthropod larvae ←
		some tardigrades
Walking	Parapodia	some polychaetes
Mobile suction cups	Tube feet	echinoderms
Jumping	Legs in most (furcula in springtails)	many insects (orthopterans)
		some spiders
		some insects (springtails) ←
Flying	Wings	many insects
Pedal thrusting	Foot or pedal disk	bivalve mollusks and some anthozoans
Pedal gliding	Muscle waves / ripples	Gastropods and Chitons
Side-to-side wriggling	Lateral bending, but no waves	Nematodes
Floating and sailing	Buoyancy	some cnidarians and some cephalopods
Ballooning in air	Silk threads	some spiders

Table 3. Start times for locomotor episodes on videotape.

Organism	Start time for real time locomotion episodes	Start time for freeze-frame playbacks
Dero	0:30	4:31
Lumbriculus	0:46	5:17
Vinegar eel	1:02	5:57
Leech	1:18	6:46
Daphnia	1:33	7:32
Ostracod	1:52	8:03
Copepod	2:04	8:40
Centipede	2:18	9:08
Millipede	2:32	9:30
Springtail	3:00	10.25
Planaria	3:14	--
Pond snail	3:36	--
Jellyfish	3:56	--
Crayfish	4:12	--

In the beginning of the ‘LocOlympics’ videotape, brief episodes of locomotion are shown in “real time” for 14 different organisms (see Table 3, first column). During the last part of the tape, a series of successive freeze-frame images are presented for each of ten organisms (Table 3, second column). Each freeze-frame image shows a “snapshot” of the animal’s position at one brief instant in time. Each frame is displayed for about 2-3 seconds and then advanced to the next frame. Remember that each frame advance represents a jump forward in time of 1/30 of a second. Thus, the organism’s position in space and time can be directly determined.

Use transparency sheets taped to the monitor and marking pens to make “datagrams” that show the exact position and shape of the animal’s body during successive freeze-frames (see Section A in “Terminology and technical information” for details). Make sure that correct frame numbers are labeled (in a different color) for all tracking points or images. Also, be sure that the distance scale is traced onto each datagram. Use your datagrams to investigate and answer the following questions:

Questions and data collection

Tracking and velocity:

1) Does the datagram indicate that the animal’s head travels in a straight line during its forward locomotion? If not, describe the pattern and try to explain why the pattern is not linear.
2) Carefully compare the organism’s *net forward progression, along a linear path,* during a series of several successive video frames. Is the progress nearly the same, or uniform, for each frame advance? Suggest possible reasons why forward progress is, or is not, uniform.
3) Calculate and compare *forward velocity* for each of the ten organisms in Table 3 (see sections A and B in “Terminology and technical information.”) Express velocities in units of mm/sec.
4) Does the animal’s pattern of locomotion appear to involve a *repeated or rhythmic series* of movements, such as repeated formation of an S-shaped body wave that moves along the animal? If so, describe the frame-by-frame sequence of body shapes during one complete cycle of movement.

Reynolds numbers:

5) Calculate and compare the *Reynolds number* for the following seven swimming organisms: *Dero, Lumbriculus,* vinegar eel, leech, daphnia, ostracod, copepod (see section C in "Terminology and technical information" for discussion of Reynolds number calculation and its significance):

6) Based on these values of Reynolds number, what do you conclude about the main sources of drag that act on each of these organisms as they move?

7) Streamlining an animal's body helps to reduce pressure drag. How could reduced pressure drag be a benefit to an animal?

8) If an organism with a low Reynolds number suddenly stops its swim movements, would it coast? If an animal with a very high Reynolds number, such as a whale, stopped its swim movements, would it coast? Explain why one animal may be capable of coasting but another may not?

Direction, velocity and frequency of waves:

9) In what *direction* do waves of undulation move along the body in worm-shaped swimming invertebrates, such as *Dero, Lumbriculus*, vinegar eel, and leech?

10) At what *velocity* do the waves move along the body in these same four swimmers? Note in section D of "Terminology and technical information" that the tip of the head is always used as the reference point when calculating wave velocity.

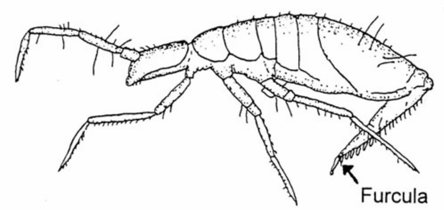
11) What is the *frequency* of waves in each of these four organisms? [See section F in "Terminology and technical information."]

12) Estimate and compare the *efficiency* of swimming in each. To obtain efficiency, divide forward velocity by wave velocity (See section E in "Terminology and technical information"). What does a higher efficiency number mean? What is the maximal and minimal efficiency that is possible?

Scaling and human comparisons:

13) Compare the running velocity of a centipede with the running velocity of the fastest human. [The top human sprinters can run about 10 m/s, or 100 meters in 10 seconds.]

14) Now compare the centipede and human in terms of *relative velocity*, expressed in units of body lengths (BL) per second? [Assume that the average human runner is 1.8 m tall (~6 feet).] Which organism, human or centipede, has the fastest relative velocity?



15) The springtail is a small insect that has a special tail-like appendage at the end of its abdomen called a furcula (diagram to the right after Christianson 1992). The furcula is held tucked up under the body by a latch-type mechanism that the springtail can release. When released, the furcula snaps backward with a high speed and force that propels the animal up into the air. Compare the *relative vaulting abilities* of the springtail with those of the world's top pole-vaulters. Express the abilities in terms of body lengths attained per jump. [NOTE: The top pole-vaulters can clear about 6 meters (~20 ft).]

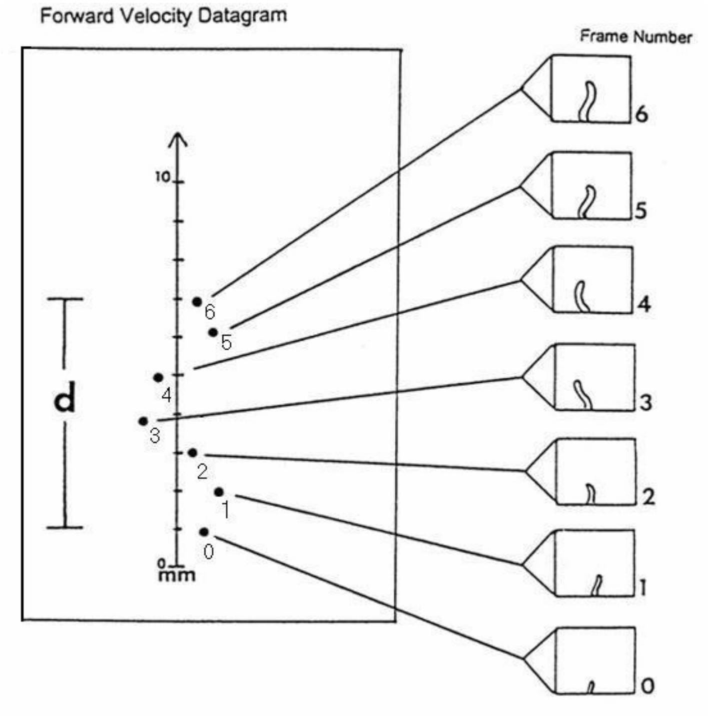
Terminology and technical information

Datagrams

A "datagram" may be created by taping a transparency sheet to the video monitor screen. Using a marking pen, the animal's entire body (or just its head position) is traced on the transparency during frame-by-frame playback of the videotape. The datagram is then used to calculate forward velocity or other parameters related to an animal's locomotion. As shown in Fig. 1, each dot represents the precise position of the animal's head on the video screen during a sequence of seven successive video frames, shown in the seven boxes at the right. The direction of movement is upward on the video monitor, as indicated by the arrow.

Note that the time it takes to move the distance "d" is equal to six elapsed frames, not seven, because the first frame is counted as "0" time. To convert the six elapsed video frames into seconds, multiply the number of elapsed frames by 1/30, since the time between successive frames for standard videotape is always 1/30th of a second.

Figure 1. Forward velocity datagram.



Forward velocity

The forward velocity of an animal is defined as the *linear distance* (d) traveled divided by the *elapsed time* (t) it takes for the animal to go that distance, or:

$$V = \frac{\text{change in distance}}{\text{change in time}} = \frac{\Delta d}{\Delta t}$$

Reynolds number and drag effects

The Reynolds number is a unit-less number that is used to predict (1) what types of drag effects are most influential when an animal is swimming or flying, and (2) what happens to the water or air molecules as the animal is moving (Vogel. 1994). As an animal moves through water or air, it encounters resistive forces (or drag) that slow its movement. These drag forces are not the same for microscopic organisms as compared to large animals. Also, the source of drag forces may change as the animal moves faster. Finally, the amount of drag depends on the viscosity of the medium. Calculation of the Reynolds number (*Re*) for a swimming or flying animal takes into account the length of an animal, how fast it is moving, and the viscosity of the medium in which it is moving.

$$Re = \frac{(\text{length of animal}) \times (\text{forward velocity})}{(\text{kinematic viscosity})}$$

To calculate Reynolds number, you will need to know the animal's forward velocity (in meters/sec) and its body length (in meters). The kinematic viscosity for freshwater is 1.0×10^{-6} m^2/s (at 20 ˚C). If you have done your calculations correctly, then units should cancel out, leaving you with a dimension-less number. It is important to always keep in mind that any Reynolds number is an approximation, or "ball park" estimate, in which variations or differences of 5-10% are probably meaningless.

So, what does the Reynolds number mean? As an animal moves through water (or air), molecules in the medium surrounding it are displaced and the animal leaves behind a "wake." This wake can be laminar or turbulent. If it is laminar, then the displaced molecules return to their original position as the animal continues moving past these molecules of medium (see Figure 2).

Organisms whose movements are described by low Reynolds numbers (<10) create laminar flows in their wakes. Their movements are mainly affected by *viscous drag* that retards forward progress. Viscous drag will also tend to keep the organism suspended or "stuck to" its location in the medium. Under these conditions it is difficult for the organism to establish any momentum for "coasting." To get an idea of what it must be like to be an animal with a low Reynolds number swimming in water, imagine yourself trying to swim in thick molasses or liquid asphalt. A low Reynolds number organism must continually work (expend energy) to keep moving, or it will abruptly come to a stop as a result of viscous drag.

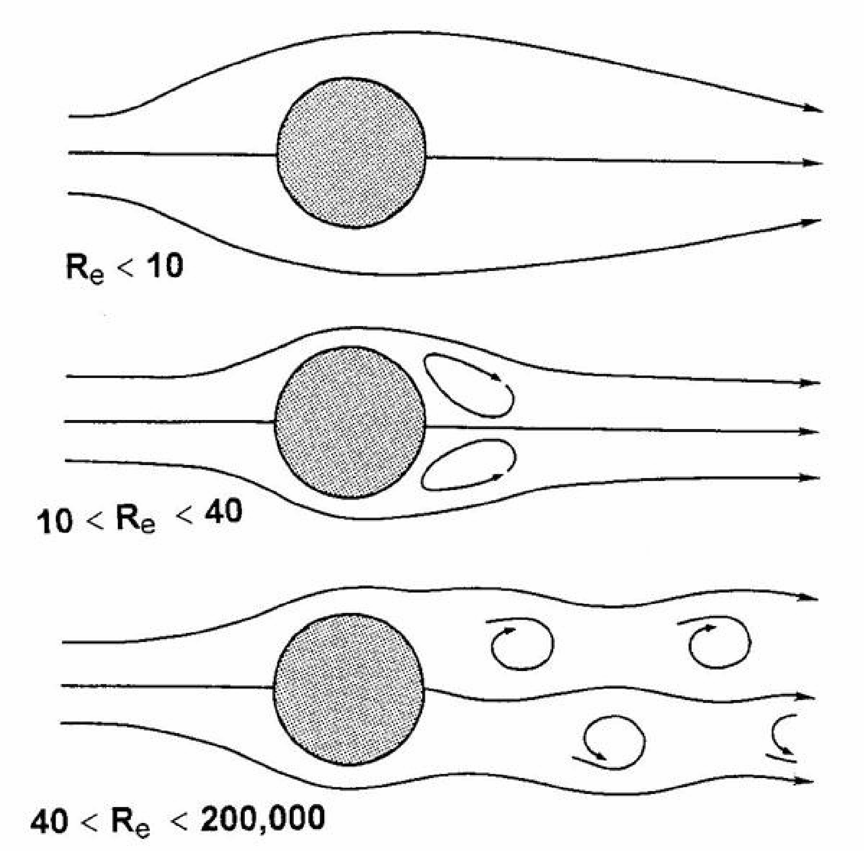


Figure 2. Adapted from Vogel (1994)

Organisms with high Reynolds numbers (>200,000) tend to be larger and faster moving organisms. They tend to create somewhat turbulent flows in their wakes. Turbulent wakes occur when molecules in the medium become so displaced that they cannot return to their original position. As this happens there is also a drop in pressure behind the animal compared to the pressure in front of the organism. This pressure difference retards the movement of the organism, so it is said to experience the effects of *pressure drag*. By comparison, animals with low Reynolds number don't experience much pressure drag effects; rather, they experience viscous drag forces that tend to act over the animal's entire surface area.

Pressure drag is reduced by "streamlining." Streamlining tends to reduce the formation of vortices and return the wake to laminar flow. This decreases the energy the animal must expend to keep moving. It also allows the animal to swim faster. Figure 3, below, summarizes the drag forces that affect various organisms in relation to its Reynolds number and velocity.

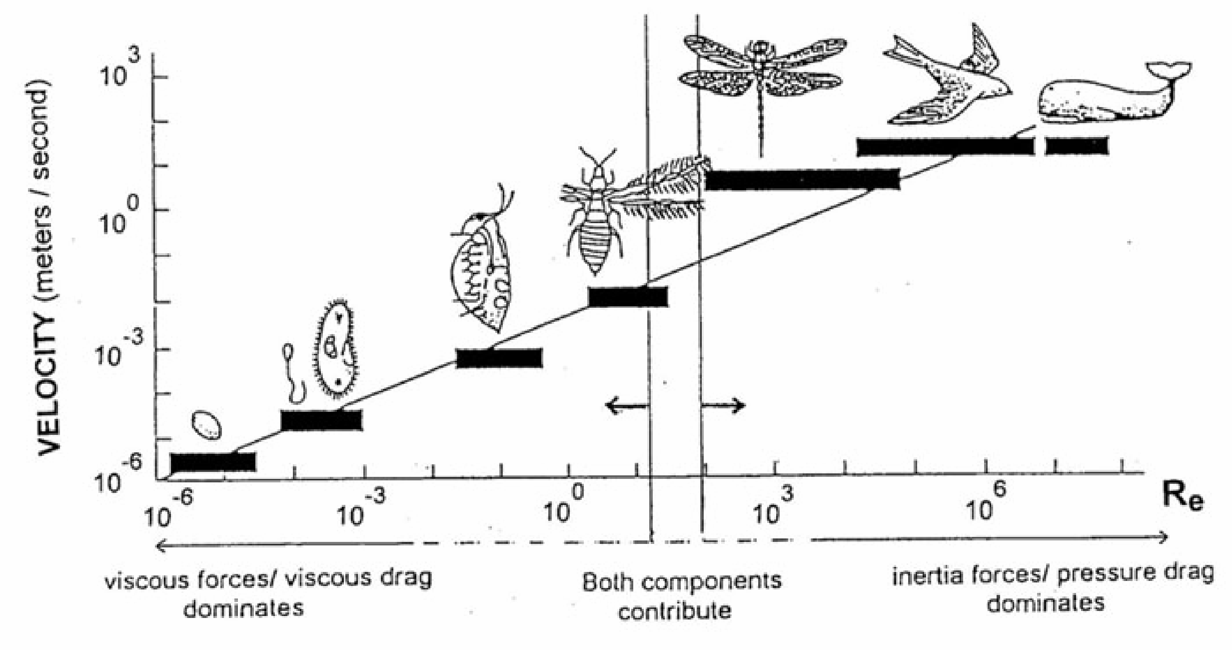


Figure 3. Adapted from Nachtigall (1983)

Wave Velocity

Wave velocity is the distance that a specific wave travels in a certain amount of time.

$$W_v = \frac{\text{Distance wave travels}}{\text{Change in time}} = \frac{\Delta d}{\Delta t}$$

There are numerous worm-like invertebrates that move through water by swimming without the use of appendages. To do this, muscles along the body contract, producing wave-like bending or undulations of the body (Gray, 1939; Gray, 1953; Gray and Lissmann, 1964; Drewes, 1999; Drewes and Fourtner, 1993). As these waves of contraction move backward along the body, the animal is propelled in a forward direction. Knowing the velocity of this moving wave is important because it is a direct reflection (and indirect measure) of the velocity with which electrical excitation moves along the animal's central nervous system, in turn causing sequential and coordinated excitation of muscle.

There are two types of undulatory waves that invertebrates may use to create forward propulsion: sinusoidal waves and helical waves. Sinusoidal, or "S" waves, are two-dimensional, meaning that all the motion takes place in a single plane, either a left-to-right plane or a dorsal-to-ventral plane. Table 2 shows a wide variety of invertebrates that use sinusoidal swimming movements. There are a few invertebrates that use helical swimming movement – specifically, some freshwater oligochaetes. Such waves consist of three-dimensional, spiral-like movements of the body. Usually only one wave travels along the body at any given time. Looking head-on at a worm that is producing a helical wave, you would see a circle. Curiously, the waves of helical movement alternate successively between clockwise and counter-clockwise orientations. It is believed that this alternation increases propulsive thrust and improves the overall efficiency of locomotion.

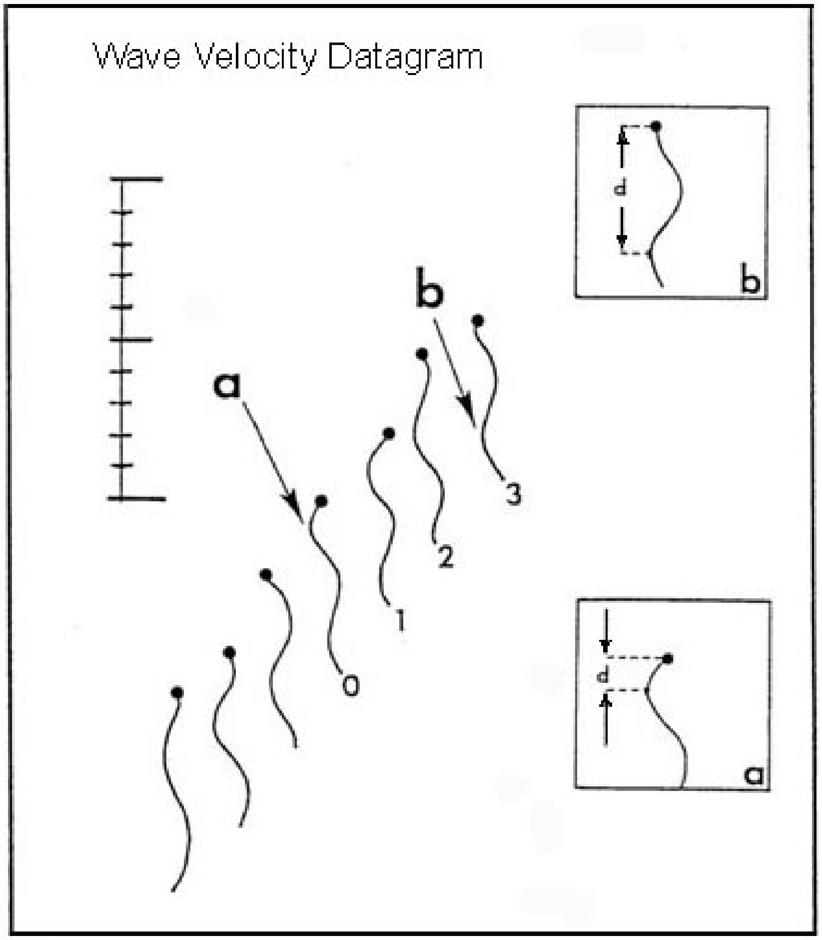


Figure 4. Wave velocity datagram.

Both sinusoidal and helical waves travel down the body at a specific and measurable velocity, termed the "wave velocity." The result is that the animal is propelled forward with a specific "forward velocity." The datagram in Figure 4 shows one way to calculate wave velocity. Note in frame "0" that the arrow at "a" shows bending of the body toward the left. In the next two frames, this zone of bending shifts progressively toward the tail and, as seen in frame "3", the same bending zone is near the tail (see arrow "b"). Thus, in three video frames (= 3/30 sec), the wave has moved posteriorly along the body over a linear distance equal to "Δd." [Note in the datagram that the image for each frame is slightly shifted to the right of the previous one. This is the result of deliberately repositioning the transparency on the screen. Repositioning the transparency in this way makes it easier to visualize body shape and compute rearward progress of the wave, but it does not affect results because the reference point that is used in computing wave velocity is the animal's head.]

Efficiency

Because swimming is never 100% efficient, forward velocity is always less than wave velocity. The "efficiency" with which rearward-directed wave motion is converted into forward motion of the animal can be estimated by dividing forward velocity by wave velocity:

$$\text{Efficiency} = V_f / V_w$$

Wave Frequency

You can easily determine wave frequency by watching a specific point on the body of the animal where there is a wave peak and noting how long it takes for the next wave peak to again form at that same location on the body. Figure 5 shows a sample datagram for computing wave frequency.

It is easy to see a bend to the right at arrow "a." This will be used as a reference image and is labeled with a "0". During the next wave, another bend to the right (similar to the first bend "a") eventually occurs, as seen in image 3. This second bend is labeled by arrow "b." [Note again that the images for each successive frame are shifted slightly to the right. This is done by moving the transparency to the left, thus enabling clearer comparisons of individual images.]

The elapsed time between the first bend (a) and the next bend (b) is the "*cycle time*." On the datagram in Fig. 5, the cycle time is estimated by counting the number of elapsed video frames (three frames, in this case) required for the body shape to precisely repeat itself in a later frame. This number of elapsed frames is multiplied by 1/30 to obtain the cycle time, expressed in seconds. In Fig. 5, the cycle time is thus 3/30th, or 1/10th of a second. The reciprocal of the cycle time is the wave frequency, expressed in cycles per second. Thus, wave frequency in Fig. 5 is the reciprocal of 1/10, or 10 cycles per second.

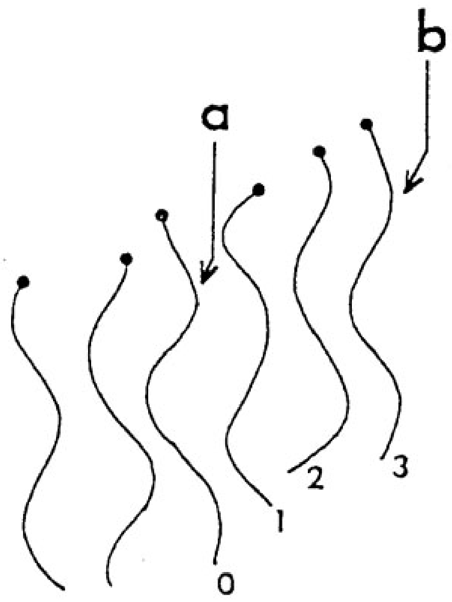


Figure 5. Wave frequency datagram.

Power stroke and recovery stroke for leg movements

At any instant during walking, a multi-legged invertebrate, such as a millipede, has some legs that are touching the ground and some that are not. A leg that is touching the ground moves to propel the animal forward in a phase of leg movement called the "power-stroke." The power stroke for a single leg in a hypothetical animal is shown in Fig. 6. Once a leg has completed the power-stroke it begins a "recovery-stroke." During the recovery stroke, the leg quickly lifts up and swings forward toward the head, thus re-positioning itself for the next power-stroke. During walking or running in invertebrates such as arthropods, there is a rhythmic, wave-like progression of alternating power-stroke movements and recovery stroke movements along the animal. Thus, leg movements in one segment are slightly out of phase with respect to leg movements in adjacent segments.

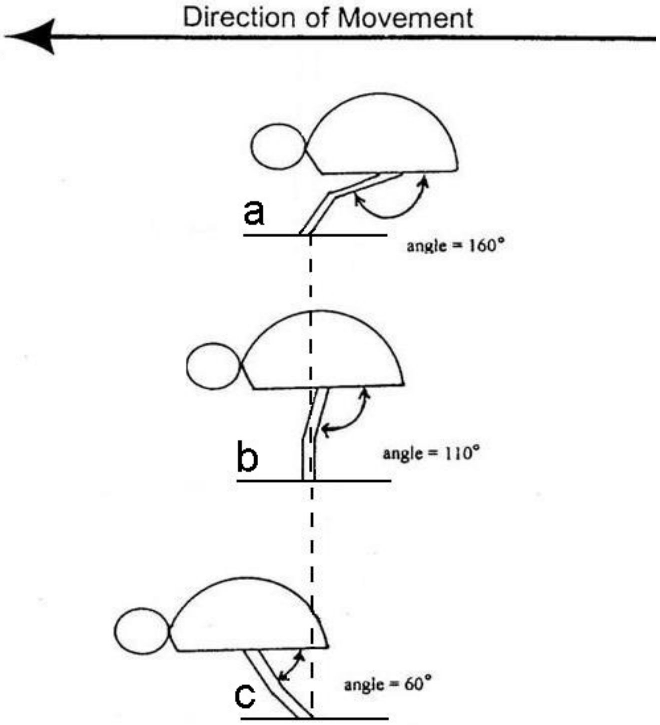


Figure 6. During the propulsive "power stroke" the leg is in continuous contact with the same point on the ground while the angle shown between the leg and body decreases (a, b, and c). This change in the angle is caused by muscle contractions. During the "recovery stroke" (not depicted), the leg lifts off the ground and swings back to a forward-directed position in order to begin another power stroke at a location one step ahead of its previous one. During the recovery stroke, the leg is moving but it is not in contact with the ground.

When you walk, each of your legs goes through a power-stroke and recovery-stroke, too. The power-stroke for one leg is the phase that begins when your heel touches the ground in front of you and ends when your foot lifts off the ground behind you. The recovery-stroke begins when your leg is lifted off the ground behind you. To complete the recovery stroke, the leg is then bent and swung forward in front of you, thus preparing the leg for another power-stroke one step ahead.

When the millipede's legs are in the recovery stroke they are raised off the ground and appear to be closer together resulting in a crest-like appearance along the body, when viewed from the side. Since the legs move through the recovery stroke sequentially, the crest moves in a wave-like fashion.

Videotape Technology

By studying videotape recordings of moving invertebrates, we can begin to comprehend and appreciate the amazing array of locomotor design and function in nature. A basic understanding of how the video system works (Macauley, 1998), is important in appreciating, interpreting, and analyzing locomotor behavior.

Light reflected from the subject enters the camera lens and is focused on a charge-coupled device (CCD). A CCD is shaped like a computer chip and contains an array of photo-sensors.

When the light ray strikes the sensors, electrical signals are generated. These signals may be sent directly to a monitor, which uses the information in the signals to recreate an image of the subject on the monitor screen. Alternatively, the signals may be sent to a VCR (video cassette recorder) that creates a magnetic template on videotape. During playback of the videotape, the VCR heads detect the magnetic template and convert it back to an electrical signal that is sent to a monitor for video display.

An important feature of a video camera is that light is not allowed to continuously stimulate the light sensors. Instead an electronic "shutter" repeatedly and briefly interrupts light detection 30 times each second, thus creating a series of 30 different electromagnetic templates on the tape. When the tape is played back, these frames are sequentially displayed on the monitor screen, again at 30 frames/second, but our eyes and brain perceive this rapid sequence of video frames as a continuous image rather than a series of separate images.

If we pause the tape to look at a freeze-frame image of one video frame in more detail, the image may appear blurry if the subject, such as an animal, was moving too fast or the shutter was open too long during the frame. This problem is overcome by changing the shutter speed on the video camera. Many video cameras have several shutter speed setting, such as 1/60, 1/500, 1/1000 sec. These values refer to the fraction of a second that the shutter remains open during each frame. A decrease in the shutter setting, decreases the duration of time that light is detected by the sensors during each frame, thus resulting in a sharper image. Fast shutter speeds may create another problem, however, such as light intensity that is too weak for generating an adequate video image of the moving animal.

The sequences recorded on the "LocOlympics" videotape involved several camera set-ups to optimize the contrast and keep shutter speeds fast enough to obtain clear, freeze-frame images of the moving animal. White backgrounds were used to enhance contrast when taping *Lumbriculus*, leech, centipede, millipede and springtail. A black background and side lighting were used for taping the *Dero*, vinegar eel, daphnia, ostracod, and copepod. Shutter speed was set at 1/1000 for all fast-moving animals, except *Lumbriculus* and the leech, which were taped with a shutter speed of 1/500.

The leech and springtail were placed in a lucite container and viewed from the side. The centipede and millipede were also placed in a lucite container but were viewed from below. *Lumbriculus* and *Dero* were placed in a standard plastic petri dish and viewed from above. Other animals (vinegar eel, daphnia, ostracod, and copepod) were all placed in a deep well projection slide (Connecticut Valley Biological, Southhampton, MA., Cat. # AP 120) and viewed from above.

The following animals were videotaped using a JVC TK-1070U camera attached to an Olympus S2-CTV STB 2 microscope: *Dero*, *Lumbriculus*, vinegar eel, daphnia, ostracod, copepod. The leech and springtail were videotaped using a JVC TK-1070U camera attached to a tabletop tripod. In all cases above, the light source was a Fostex 8375 dual-light pipe, fiber optic illuminator. In both camera set-ups above, the camera was connected to a JVC HR-S7300U videocassette recorder. The centipede and millipede were videotaped using a Panasonic AG-187U video camera. S-VHS videotapes were used for video documentation.

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Appendix A: Typical values obtained from video and electronic images

[**NOTE**: Animals do not always maintain a constant forward velocity. Thus, values may vary depending on particular frames that are studied and subjectivity in measurements. Figures below were calculated over one cycle of locomotion.]

	Forward Velocity
Dero	10 mm/s
Lumbriculus	60 mm/s
vinegar eel	1.2 mm/s
leech	66 mm/s
daphnia	11 mm/s
ostracod	9 mm/s
copepod	51 mm/s
centipede	480 mm/s
Millipede (w/scale = 10 mm)	6.4 mm/s
springtail	u≈ 148 mm/s

	Reynolds number	**Body length**	**Forward velocity**
Dero	55	5.5 mm	10 mm/s
Lumbriculus	1500	35 mm	60 mm/s
vinegar eel	≈ 1	1.2 mm	1.2 mm/s
leech	1164	30 mm	66 mm/s
daphnia	1980	1.6 mm	11 mm/s
ostracod	≈ 3	0.6 mm	9 mm/s
copepod	82	1.6 mm	51 mm/s

	Wave velocity	**Efficiency**	**Wave frequency**
Dero	30 mm/s	0.33	9 waves/s
Lumbriculus	128 mm/s	0.47	10 waves/s
vinegar eel	9 mm/s	0.13	6 waves/s
leech	120 mm/s	0.55	5 waves/s
millipede	8.2 mm/s	0.78	2 waves/s

Scaled values:

Running: centipede = 20 BL/s; human = 5.4 BL/s (thus, centipede runs about 4 times faster)

Jumping: springtail = 32 BL; human = 3.3 BL (thus, springtail jumps about 10 times higher)