The Hydrodynamics of Water-walking Insects and Spiders

by

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Abstract

We present a combined experimental and theoretical investigation of the numerous hydrodynamic propulsion mechanisms employed by water-walking arthropods (insects and spiders). In our experimental study, high speed cinematography and flow visualization techniques are used to determine the form of the flows generated by water-walkers. In our supporting theoretical study we provide a formal fluid mechanical description of their locomotion. We focus on the most common means of walking on water such as the alternating tripod gait, rowing, galloping and leaping. We also examine quasi-static modes of propulsion in which the insect’s legs are kept stationary: specifically, Marangoni propulsion and meniscus-climbing. Special attention is given to rationalizing the propulsion mechanisms of water-walking insects through consideration of the transfer of forces, momentum and energy between the creature and its environment.

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In 1871, the entomologist Robert McLachlan said of the seafaring water strider, “if [one] can throw any light upon...this most wonderful insect,...he will confer the utmost benefit upon the natural sciences.” A century later, the elucidation of their propulsion mechanism remains an outstanding problem in the biological sciences.

The ability to walk on water has evolved numerous times throughout evolutionary history. Today, the skill is exhibited by insects, spiders, birds, reptiles and mammals, ranging from 1 mm to 1 m in size (see Figure 1-1). Among these creatures, there is a natural distinction between those small and large. Small creatures can rely on surface tension for support and so rest statically at the free surface. Larger creatures such as the basilisk lizard (Glasheen & McMahon 1996a) can only remain atop the water by slapping the surface with sufficient vigor to generate hydrodynamic forces that can bear their weight. This thesis will be devoted principally to an examination of small water-walkers, especially insects and spiders; however, a discussion of large water-walkers is included for the sake of completeness.

The study of biolocomotion has been mostly directly towards elucidating the propulsion mechanisms of terrestrial creatures, flying birds and swimming fish. The methods presented in this literature provide valuable context for our study, and so are briefly summarized here (for further detail, see Dickinson et al. (2000), Denny (1993), Vogel (2003), Alexander (1985), Biewener (2003)). A creature’s propulsion may be rationalized in terms of the transfer of
Figure 1-1: Water-walkers of the world. Like the ability to fly and swim, walking on water is a skill that has evolved numerous times in the animal kingdom during the course of evolutionary history. It is used by modern insects, spiders, birds, lizards and mammals. Water-walkers range in size from 1 mm to 3 m, and include the following: a Microvelia, b Mesovelia, c Anurida, d the fisher spider, e the basilisk lizard (photo courtesy of Joe McDonald), f Clark’s Grebe (photo from the feature film “Winged Migration”), g man (with the aid of flotation devices), and h the tail-walking dolphin.
force, momentum or energy between the creature and its environment. In order for any creature to move, it must apply a force to its environment; the reaction force then serves to propel it forward.

The reaction force used by terrestrial creatures consists of frictional forces between their bodies and land (Radhakrishnan 1998). An important consideration is that the creature must coordinate its legs to keep its body stable (Ting et al. 1994). Since the timescale of falling for a creature of size $L$ is $\sqrt{L/g}$ where $g$ is the acceleration of gravity, meter-scale walkers have seconds to make their next step and can keep their bodies dynamically stable by applying lateral forces. Conversely milimeter-scale walkers, with only milliseconds between steps, must maintain static stability by keeping at least a tripod of feet on the ground at all times. Indeed, this requirement is thought to be the reason that insects have six legs (Hughes 1952). Insects also rely on dynamic stability to travel over rough terrain in which footholds are scarce. There has been recent interest in understanding the stability of a creature’s propulsion on yielding surfaces such as sand (Lejeune et al. 1998, Kerdok et al. 2002), but little has been done towards characterizing the stability of water-walking creatures.

In the absence of aerodynamic resistance on a terrestrial creature, one may consider the energy as being transformed between the muscular strain, gravitational potential and kinetic energies of the creature. When a creature moves through a fluid medium, the kinetic energy of the fluid must also be considered in the energy balance. For some hovering insects, previously shed vortices may be used to generate lift, and so may be considered as an additional energy storage device external to the insect (Dickinson et al. 1999).

In order to move, swimmers and fliers rely on the hydrodynamic force generated by their driving stroke. The instantaneous hydrodynamic force on a body is simply expressed as the integral of the normal projection of the stress tensor over the body surface. Direct calculation of the hydrodynamic force acting on most creatures is generally impractical, as it requires a precise knowledge of the fluid velocity and pressure fields, and the integration of the resulting stresses over the surface of the body over the duration of the driving stroke. It is only for certain forms of geometrically simple propulsion that such a calculation is feasible; for example, for the undulatory motion of long, thin swimmers (Taylor 1961, Lighthill 1970, McHenry et al. 2003). For most creatures, the driving stroke is characterized by a complex time-dependent geometry, and a direct computation of the hydrodynamic force is best done
numerically. Such has been the approach most commonly taken in recent investigations of fish (Triantafyllou et al. 2000) and insects (Wang 2005); however, simplified two-dimensional geometries are often adopted. An alternative approach to rationalizing the propulsion mechanism of swimmers and fliers involves consideration of the fluid momentum.

The change of momentum of a swimmer or flier generated by its driving stroke is given by the time integral of the hydrodynamic force acting on the body. Provided losses due to viscous dissipation are negligible, conservation of linear momentum requires that the change in momentum of the body be equal to that of the suspending fluid. Consequently, instead of rationalizing the propulsion of a creature by evaluating the hydrodynamic forces acting on it, one may alternatively do so by measuring the net momentum in its fluid wake. Such an approach is most simply applied to creatures whose wakes are characterized by coherent vortical structures, such as the reverse Karman vortex street generated by the carangiform mode of fish swimming (Triantafyllou et al. 2000, Drucker & Lauder 1999) or the vortex rings generated by hovering birds (Rayner 1979b,a, Kokshaysky 1979), octupi, squid or salps (Linden & Turner 2004). For example, the vertical momentum transfer required for weight support in hovering birds has been considered by Spedding et al. (2003).

The dynamics of propulsion at the air-water surface requires additional consideration of the dynamics of the free surface and the forces generated by its distortion (Baudoin 1955), to be defined in §2. The characterization of the dynamics of water-walking creatures thus becomes a complex free-boundary problem, in which aerodynamic, hydrodynamic and surface forces may act. The energetics are similarly complicated by the presence of the interface, as the gravitational potential and surface energies associated with its distortion must be considered. It is presumably this added degree of dynamical complexity that has discouraged more vigorous work in this area. To date, fluid mechanical studies of water-walking creatures have been largely confined to elucidating the propulsion mechanisms of individual creatures, with particular attention having been paid to spiders (Suter et al. 1997), water striders (Andersen 1976) and basilisk lizards (Glasheen & McMahon 1996a). By examining the most common modes of walking on water in this investigation, we seek here to provide an integrative view of water-walking creatures.

The purpose of this thesis is to present the results of a fluid mechanical investigation of water-walking creatures that rationalizes their propulsion mechanism. We begin by reviewing literature on general biolocomotion and the biology and dynamics of water-walking
creatures. We describe the dynamics of water-walking insects in §1.1 and that of large water-walking creatures in §1.2. In §1.3 we present an outline of the research presented in this thesis.

1.1 Small water-walkers

100 million years ago, terrestrial insects and spiders began to colonize the water surface (Andersen 1976). Today, 1200 species of insects and 300 species of spiders, ranging in length from 0.1 to thirty centimeters, inhabit the surfaces of rivers, lakes and oceans around the world. Insects and spiders, distinguished by the number of their legs (6 and 8 respectively), are two classes of the arthropods, a phylum of creatures with jointed legs and no backbone. Water-walking arthropods are referred to as semiaquatic, meaning that they live on water but breathe oxygen from the air. Extensive reviews of the biology of water-walking arthropods are provided by Andersen (1976) and Hungerford (1919).

Water-walking insects are thought to have evolved from terrestrial ancestors (Andersen 1976), but many have since grown so specialized that they can walk faster on water than land. Many of today’s water-walking arthropods live exclusively on the water surface, others may temporarily reside on floating vegetation or upon shoreside rocks. The life cycle of these creatures (Figure 1-2) begins with an underwater birth followed by an arduous swim to the free surface. Upon penetrating the free surface, the water-walkers live atop it the remainder of their lives, only returning to the underlying fluid to lay their eggs.

Water-walking insects were first described during early efforts to classify all animals, the earliest of which is a description of “water lice,” Pediculus marinus, in History of Animals by the Renaissance naturalist Aldrovandi (1618). Later workers expressed interest in the versatility of water-walkers: Ray (1710) observes that cimices aquatici has “feet that are effective...on both land and water.” Geoffroy (1800) observed that water striders can support twice their weight on the water surface, as required during mating (Figure 5-3). Latreille (1802-1805) classified water-walking insects as water lice, “punaises d’eau.” He is the first to describe the water treader Mesovelia (Figure 1-1b), which runs on water using an alternating tripod gait (§3.2.1). Dufour (1833) categorized water-walking insects as the second of three families within the order Hemiptera: Hydrocorises (aquatic), Amphibicorises (semiaquatic) and Geocoresis (terrestrial). There were several reviews of the biology of
Figure 1-2: The life cycle of the most common water-walker, the water strider. Other insects have a similar cycle involving underwater birth and several stages of growth. Gestating female water striders penetrate the free surface to lay their eggs underwater. The infant water striders that emerge from these eggs are denser than water and sink to the bottom of the pond. Breathing through their plastron, they swim up to the water surface. They rise belly up towards the surface, allowing their natural hydrophobic coating to strip the water from their bodies. Once atop the water surface, they molt several times before becoming adults. During mating the larger female water striders support the weight of the males.

Understanding the locomotion of semiaquatic insects was delayed as it was necessarily predicated on the elucidation of surface tension in the late 19th century. The spreading of surfactant monolayers was reported by 18th century BC Babylonians (Edidin 2003), Pliny the Elder (AD 23-79) and Benjamin Franklin (1770). The spreading mechanism remained unknown until the development of the concepts of atoms and molecules. Plateau (1873) wrote a text on calculating the shapes of static surfaces formed by the action of surface tension that is cited extensively in subsequent studies of water-walking insects. A. Pockel, a German housewife, performed kitchen experiments that allowed her to measure the surface tension of water, a term she introduces in her letter to Nature (Pockels 1891). Her sponsor, Lord Rayleigh (1899), demonstrated that the surface layer was a single molecule thick.

According to Baudoin (1955), Brocher (1910), Plateau (1873) and Portier (1911) were the first to recognize the role of capillarity in the propulsion of aquatic insects. Brocher (1910) made extensive observations of the manner by which aquatic and semiaquatic creatures deform the free surface. He describes many types of locomotion, including the motion of insects walking atop the surface, the means by which insects cross the surface and the motion of snails inverted beneath the surface.
Baudoin (1955) used a specially constructed microscope to observe menisci around the legs of water-walking insects. By calculating the weight and supporting surface tension force of several water-walkers, he demonstrates that for each species of water-walker the margin of safety decreases as the insect grows in size. He is the first to report capillary propulsion, a novel technique to be detailed in §6.1. Baudoin also rationalizes a minimum size for water-walking insects. If a water-walker’s leg becomes trapped beneath the free surface, to free it, the insect must oppose the surface tension force acting on its leg, $F_s \sim L$. The greatest force $F$ an insect of characteristic length $L$ can produce is proportional to its cross-sectional area: $F \sim L^2$ (Alexander 1985). Insect of small sizes such that $F/F_s \sim L \ll 1$ are too weak to free their legs from the free surface.

The first paper dedicated entirely to the locomotion of water striders appeared following the invention of the high-speed video camera (e.g. Baxter 1942). This technology made possible for the first time cinematographic studies of limb coordination and gait changes of water-walking spiders and striders, which move too quickly to be observed by the human eye (Darnhofer-Demar 1969, Schultz 1987, Bowdan 1978). Darnhofer-Demar (1969) examined the dynamics of the water strider and concludes with a consistent physical mechanism for the strider’s movement: “when a water strider rows, it deforms the free surface, generating pivots from which it pushes off.” Darhofer-Demar’s physical picture of strider propulsion was built upon by Andersen (1976), who studied the motion of several species of water walking insects using high-speed video, and described in detail their leg coordination. After observing the wave train generated by water striders, Andersen (1976) stated that “the generation of surface waves is used by Velia and Gerris (and probably by all medium-sized and big surface bugs) as a means of increasing the resistance necessary for propulsion upon the water surface.” Andersen’s acknowledgement of the importance of wave drag was extended by Denny (1993), who assumed that they were a necessary prerequisite for motion. Classical hydrodynamic theory states that waves can only be generated by bodies moving steadily at the free surface when the body speed exceeds the minimum speed of capillary waves, $c_m = 23 \text{ cm/s}$ (Batchelor 2000). Infant water striders however were presumed to move their legs too slowly to generate waves; the conclusion that infant water striders cannot moved was named Denny’s Paradox (Suter et al. 1997). The formulation of Denny’s Paradox invigorated the study of semiaquatic insects by drawing the attention of both biologists and physicists to this method of thrust via wave generation. Experiments (Suter et al. 1997)
and calculations (Sun & Keller 2001) were performed to deduce the drag associated with the production of surface waves by a water-walking creature. We examine this paradox in closer detail in Chapter 5.

Suter and coworkers have published eight studies between 1997 and 2004 on the locomotion of the semiaquatic fisher spider *Dolomedes triton*. Many of Suter’s early results on the locomotion of spiders are presented in his review (Suter 1999). Suter’s experiments are the first to clearly visualize the surface deformation beneath spider legs. Suter et al. (1997) conducted experiments quantifying the leg speeds of live spiders and the forces on severed spider legs. On the grounds that spider legs move at constant angular velocity for the majority of the stroke duration, the authors examined a steady model of spider motion. Suter proposed that the hydrodynamic force acting on a steadily moving spider leg may be decomposed into three components: the surface tension force, wave drag and pressure drag. A rotating flume apparatus was constructed to measure the horizontal force acting on a severed spider leg held fixed at the surface above a steady stream. The authors verified experimentally that the leg generated no waves when moving under the minimum phase speed. When the surface tension was reduced by 10 % through the addition of surfactant to the free surface, the force on the leg did not change appreciably. A “flow disturbance index” was devised by measuring the intensity of light refracted by the flow downstream of the severed leg. The authors showed that their index was non-zero for all leg speeds, suggesting that momentum was transferred to the fluid. It was also shown that the force on the isolated leg was proportional to $U^{1.6}$, where $U$ is the leg speed, closely approximating the expected scaling ($\sim U^2$) from hydrodynamic theory. These observations led the authors to conclude that pressure drag is the primary propulsive force used by spiders. The dominant component of the hydrodynamic force acting on the driving legs of all water-walking creatures will be elucidated in Chapter 4.

Suter & Wildman (1999) examined the gait change of *Dolomedes*. High-speed cinematography was used to show that *Dolomedes* rows at speeds less than 0.2 m/s and gallops at speeds above 0.3 m/s. The anatomy of the spider leg forces the spider to stroke vertically during its galloping gait. Their rotating flume apparatus was used here to quantify the leg velocities and leg tip depths at which meniscus disintegration occurs. It was observed that leg forces induced by galloping cause disintegration of the meniscus around each leg. These anatomical and hydrodynamic constraints were found to be responsible for the discontinuity
in the speeds between rowing and galloping. Suter & Gruenwald (2000b) found that the surface rowing speed $V$ of *Dolomedes* scales with its mass $m$ as $V \sim m^{-0.31}$ where $V$ is in units of body lengths per second. The faster small spiders were found to use higher stride frequencies and leg angular velocities than their more massive counterparts.

Suter & Gruenwald (1999) investigated the means by which spiders raise their legs to “sail” using the wind. He measured the speed of desiccated spiders floating in a pan of water in a wind tunnel. Under wind tunnel speeds approximating outdoor conditions, he found that the spiders with raised front legs sailed faster than those in a prone posture (Figure 1-3). Suter *et al.* (2003) conduct a cinematographic study of the gaits of water-walking spiders. Unlike *Dolomedes*, most water spiders can only walk on water and do not have specialized gaits such as the row and gallop. Suter & Gruenwald (2000a) use high-speed cinematography to examine the effectiveness of jumping by spiders as a means to evade predation. He determines experimentally a range of angles of attack $\alpha$ and attack velocities $V$ for which spider jumping is an effective means of escape. It was concluded that spider jumping is ineffective in avoiding trout that attack from below, but effective for eluding horizontal attacks.

Stratton *et al.* (2004a) found that the the water-walking capabilities of spiders are extremely variable. Some have hydrophilic surfaces and so cannot even reside at rest on the water surface. Others have adapted water-walking capabilities for a number of reasons, including: foraging on the water surface, the pursuit of mates, evasion of terrestrial predators, and the survival of heavy rains, floods and falls from trees and ballooning events (Humphrey 1987, Suter 1991, 1992) onto bodies of water. Suter *et al.* (2003) and Stratton *et al.* (2004a) classified the wettability and water-walking capabilities of 249 species of spider through a comprehensive cinematographic survey. The hydrophobicity of spiders was measured by observing the formation of droplets on spiders placed in a fine mist. Hydrophobicity, at least
over part of the body, was a necessary prerequisite for water-walking. Of the water-walkers, the majority propel themselves adequately using their terrestrial gait; however, others have developed a specialized rowing gait (Schultz 1987, Suter et al. 2003). Evaluation of the capabilities of the entire Arachnid population lead Stratton et al. (2004a) to conclude that the ability to walk on water has evolved several times among spiders and also been lost on occasion. In §2.1, we consider the influence of the hydrophobicity of spiders on their dynamics; in what follows we examine in greater generality the role of hydrophobicity in the life of water-walking arthropods.

The wetting properties of water-walking insects play a critical role in their life at the interface. Rationale for the waterproofing of water-walking insects was first suggested by Dufour (1833), who noted their important surface structure, “their legs are covered with a very fine velvet that is impermeable and gives these insects the ability to stand or run on water without getting wet” (Figure 1-4). Hairy surfaces and the wetting properties thereof have been well-studied in the context of synthetic textiles (Bartell et al. 1948) and the fur coats of animal and plant leaves (Cassie & Baxter 1945). Generally, all insects and spiders are hairy, but the water-walking species have an especially dense mat of hair (Figure 1-4) that repels water by increasing the energetic cost of wetting (Dufour 1833, Baudoin 1955). In §2.1 we describe relevant models of the arthropod hair layer. Water-walking creatures have two distinct hair layers (Figure 1-5), one with longer hairs for repelling water, the other with shorter hairs for maintaining an air layer, called the plastron, if the creature is submerged. The water-repellent hair layer is a key adaptation: if water-walkers were wetting, they would adhere to the water surface at each step (e.g. as occurs when the the striders are dunked, Figure 1-7). The hair covers of a number of water-walking insects

Figure 1-4: The non-wetting hair layer of the water treader Mesovelia. a, Front view of Mesovelia, whose body is covered with a dense hair layer which varies in density across the body. b, The front foot of Mesovelia resting upon the water surface. Leg width, 100 µm. c, Side view of Mesovelia. Long hairs project from the insect’s back and sides, giving its coat a reflective sheen.
Figure 1-5: The two hair layers coating the bodies of water-walking insects. The longer hair layer repels water; the shorter hooked hair layer maintains the plastron air layer around the insect should it become submerged.

Figure 1-6: Water-walking insects spend a great deal of time grooming their dense hair cover. *Hydrometra* grooming its antennae (a) and its hind legs (b). Note that *Hydrometra* stands on its front antenna in (b). c, *Microvelia* grooms its leg hairs.

has been well-characterized in microscope work by Andersen (1976) and are summarized in Table 1.1. The water strider’s middle tarsal segment have hairs that are tapering and covered with fine flutes and grooves. The geometry of the hair layer is similar in nearly all water-walkers, but the density varies among species, with the faster species having a higher hair density, a trend we shall rationalize in §2.1. The hair density also varies between the tarsi: for the water strider, the density is 4-6,000 hairs per mm$^2$ on the front tarsus, 12-16,000 per mm$^2$ on the middle tarsus and 8-10,000 per mm$^2$ on the hind tarsus. We note that the middle tarsus is used for rowing and must therefore sustain higher pressures than the front and hind tarsus. Andersen (1976) also noted the presence of thickened flexible “grooming” hairs located at joints of the leg tibia that the insect uses to neatly arrange the hairs on its body and legs (Figure 1-6).

The backsides of water-walking arthropods are also covered with a mat of hair (Figure 1-4c). This adaptation repels water should the insect be flipped over or doused in a rainstorm. Body hairs are groomed regularly with the same grooming devices used to organize the leg hairs. In our experimental study reported in Chapter 3, we observed water-walking arthropods cleaning themselves by rolling on their backs on the water surface. This behavior may exploit a self-cleaning property of hydrophobic surfaces (Blossey 2003) in which dust
Figure 1-7: A water strider that has wet its lower body (lost its plastron) after being submerged. Only with great exertion does it free itself from the free surface.

<table>
<thead>
<tr>
<th>Species</th>
<th>Density (hairs/mm²)</th>
<th>Length (µm)</th>
<th>Width (µm)</th>
<th>angle</th>
<th>Layer depth (µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Strider</td>
<td>12-16,000</td>
<td>20-40</td>
<td>1.5-2</td>
<td>30-50</td>
<td>20</td>
</tr>
<tr>
<td><em>Velia</em></td>
<td>10,000</td>
<td>30-40</td>
<td>1-2</td>
<td>50-60</td>
<td>6-10</td>
</tr>
<tr>
<td><em>Halobates</em></td>
<td>8-12,000</td>
<td>20-30</td>
<td>1</td>
<td>20-40</td>
<td>6-10</td>
</tr>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td><em>Mesovelia</em></td>
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<td>30-60</td>
<td>2-3</td>
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<td>NA</td>
</tr>
<tr>
<td><em>Hydrometra</em></td>
<td>2,000-3,000</td>
<td>15</td>
<td>5</td>
<td>NA</td>
<td>8</td>
</tr>
</tbody>
</table>

Table 1.1: Tarsal hair properties of water-walking insects and spiders. Insect data is compiled from Andersen (1976) and Andersen (1995); spider data is collected from Stratton et al. (2004b). The angle of inclination is measured between the hair and leg surface. Each hair is tapering so the width refers to that at the hair’s base.
Figure 1-8: A submerged fisher spider breathing through the plastron air layer (of characteristic thickness 0.5 mm) that appears as a silvery film coating its entire body.

and contaminants are removed by contact with water.

If the insect is submerged, the plastron hair layer (Figure 1-5) traps air that the insect uses for both respiration and buoyancy (Cheng 1973). The insect’s inhalation of the oxygen within the plastron is balanced by the inward diffusion of oxygen from the surrounding fluid. The process is so effective that the submerged Fisher spider (Figure 1-8) can survive for several minutes and the marine *Anurida* for five days if doused by a crashing wave. Scanning electron microscope images show that the plastron hairs of water striders are slightly bent, 4-10 µm long, 0.6 µm wide, are perpendicular to the cuticular surface and are spaced 1-7 µm apart. Unlike the water-repellent hair layer, the ends of the plastron hairs are randomly oriented and their density is much higher, 5-8 · 10^5 hairs/mm^2. The plastron layer of the seafaring *Halobates* consists of an array of short club-shaped hooked hairs 1.5 µm in height, 0.4 µm wide and spaced 1.5 µm apart and at a density of 6-7 · 10^5 hairs/mm^2 (Cheng 1973, Andersen 1995). Thorpe & Crisp (1947) show that an array of hooked hairs retains a plastron more effectively than an array of straight hairs. The plastron will be penetrated by water if the insect dives to a depth of which the hydrostatic pressure exceeds the curvature pressure on the hairs (Thorpe & Crisp 1947)

\[ \Delta p = \frac{2 \pi r \sigma \cos \theta}{\ell^2 - \pi r^2} \]  

where \( r \) is the hair radius, \( \ell \) the mean distance between hairs and \( \theta \) the contact angle of a single hair with the water surface. Crisp (1950) considers the elasticity of the plastron hairs and examines their stability under the combined influence of interfacial and buoyancy forces.

It is noteworthy that, while generally designed to be water-repellent, certain water-walking insects possess and exploit hydrophilic body parts. To deflect the water surface
upwards as is required for capillary propulsion up menisci (Chapter 6), certain insects utilize retractable hydrophilic claws or ungues (Andersen 1976). Certain springtails also possess a wetting tube on their undersides which they use in their specialized leaping mechanism (Noble-Nesbitt 1963, Baudoin 1955, Nutman 1941), to be described in Chapter 3. Anurida maritima possess tarsi in the shape of three-sided prisms, two sides of which are hydrophobic, one of which is hydrophilic. The hydrophilic side has been hypothesized to maintain stability when walking on water or climbing the slick walls of seaside caves (Janssens 2005).

1.2 Large water-walkers

Small anolis lizards and green iguanas run short distances over water (Hsieh 2004); however, only the basilisk lizard (Figure 1-1e) is capable of walking on water from infancy to adulthood. The basilisk lizard’s weight ranges from 2 g as hatchlings to over 500 g as adults. Throughout this size range, they are able to sprint across the water surface at speeds of approximately 1.6 m/s. Although comfortable walking on land or swimming beneath the water surface, they have developed the ability to walk on water to avoid aquatic predators (Rand & Marx 1967). Glasheen & McMahon (1996a) examined the surface locomotion of the basilisk lizard and elucidated their subtle water-walking technique. The authors characterized the driving stroke in terms of three distinct phases: slap, stroke, and recovery (Figure 7-1). The slapping phase is marked by the vertical impact of their driving foot on the water surface and an associated vertical reaction force. In the stroke phase, their feet generate a deep cavity, against the rear wall of which they push. The associated propulsive force thus results from combined form drag, added mass, and hydrostatic forces. The authors also demonstrate that a critical requirement for their successful surface propulsion is that the lizard be able to retract its foot before the collapse of the air cavity; if not, the resulting downward force on the driving leg will drag it under. While smaller lizards can initiate their water walking from within the water, older, larger, more sluggish lizards must get a running start from land (Rand & Marx 1967). Glasheen & McMahon (1996b) rationalized this dependence by considering the lizards’ anatomical and kinematic allometry. They predicted that 2-g lizards can generate more than twice the force required for weight support, whereas 200-g lizards can barely support their weight.

The model of Glasheen & McMahon (1996a,b) was based on an accompanying series of
experiments of vertical impacts of discs on a free surface (Glasheen & McMahon 1996c). Hsieh (2003) notes that the topology of the driving stroke is significantly more complex and provides a detailed kinematic description thereof. This study was built upon by Hsieh (2004), who elucidated the form of the flows generated by the driving stroke through three-dimensional digital particle image velocimetry. Their study demonstrates that substantial weight support is generated during the slap and stroke phases, whereas the principal forward thrust is generated during the stroke phase. Their flow visualization demonstrates that the lizard transfers momentum to the underlying fluid in the form of vortex rings that translate backward and downward.

The dynamics of other large water walkers have received very little attention. The ability of paddling ducklings to avoid wave drag by hydroplaning along the surface has been demonstrated by Aigeldinger & Fish (1995). Various waterfowl can sprint across the surface by vigorous slapping of the surface; some shorebirds do so to prepare for takeoff, using their wings to generate lift as needed. The Western Grebe (Figure 1-1f) sprints across water without using its wings as part of its elaborate mating ritual (Nuechterlein & Storer 1982). Steamer ducks propel themselves along the surface by slapping with both their feet and wings (Livezey & Humphrey 1983). If one defines walking on water as propelling oneself at the surface with the bulk of one’s body above the water, then the largest water walkers are mammals, specifically dolphins. By vigorously flapping their tails back and forth, dolphins can propel themselves along the free surface with only their tails submerged (Lang 1966; Figure 1-1h).

It is impossible for man to walk on water without the aid of flotation devices, such as those devised by 15th century ninjas (Figure 1-9a) or envisaged by Leonardo da Vinci (1475-1480) (Figure 1-1g). As we shall see in Chapter 2, the vertical force balance on water walkers requires that their weight be supported by buoyancy, surface tension or inertial forces associated with their feet slapping the surface. A man of mass $M = 70$ kg would require feet of perimeter $P = Mg/\sigma \sim 10$ km to be supported by surface tension. If he relies alternatively on the inertial forces generated by slapping his feet at a mean speed $U$, he would require feet with area $A = Mg/(\rho U^2)$. Even generous estimates for $U \sim 10$ m/s suggest that the area of a human’s feet must be of order $1 \text{ m}^2$ in order for him to walk on water. However, as for all creatures that generate weight support by slapping the surface, thrust generation is not everything: power generation and stability are primary concerns.
Figure 1-9: Man-made devices used for walking on water. a, 15th century ninjas developed flotation shoes called “Mizugo,” or water spiders, to be used for walking stealthily on the water surface. Mizugo consisted of four annular pieces of wood fastened with twine (b) and were attached to wooden clogs with hinged plates (c). Printed with permission of Ninja Yashiki museum (2003). d, Polyester ski-floats and a double-headed paddle were used by Remy Bricka to cross the Atlantic Ocean in 40 days, setting a world record for distance in 1998. In 1989, he also set a speed record of 7 minutes 7.41 seconds for 1 km.

Glasheen & McMahon (1996a) estimate that a human would be able to run on water only if he were able to achieve speeds of order 30 m/s, and to produce 15 times the muscle power available to him.

1.3 Thesis outline

In this thesis, we investigate several fluid mechanical aspects of the locomotion of water-walking arthropods. Much of this thesis is drawn from recent papers and preprints (Hu et al. 2003, Hu & Bush 2005, Hu et al. 2005, 2006, Bush & Hu 2006, Hu & Bush 2006). We begin in Chapter 2 with a theoretical treatment of the locomotion of water-walking creatures. The propulsion of water-walkers is rationalized through consideration of the transfer of forces, momentum and energy between the water-walker and its environment. We give particular attention to identifying and evaluating the dimensionless groups characterizing the dynamics of water-walkers and so identifying the dominant propulsive forces.

In Chapter 3 we present the results of an experimental study of the dynamics of water-walking arthropods. Using high-speed video and flow visualization, we characterize the dynamics associated with the most common means of propulsion on the water surface. In particular, we observe flows that allow us to quantify the momentum and energy transfers described theoretically in Chapter 2. In Chapter 4 we present the first dynamic classification of water-walking creatures. Specifically, we classify all water-walkers according to the
relative magnitudes of the hydrodynamic force components used for propulsion.

In Chapter 5 we examine in depth the propulsion mechanism of the most common water-walking insect, the water strider. We resolve Denny’s Paradox by rationalizing the propulsion of the water strider in terms of their momentum transfer as is revealed by flow visualization. In Chapter 6 we examine two means of quasi-static propulsion by water-walking insects. In the first, insects propel themselves up menisci in a fixed posture by deforming the free surface and so generating lateral capillary forces. In the second, insects propel themselves along the free surface by ejecting surfactant. In Chapter 7, we conclude by discussing the implications of our work and suggesting directions for future research.
Chapter 2

Fundamentals

“And when the disciples saw him walking on the sea, they were troubled, saying, It is a spirit; and they cried out for fear.”

- Matthew 14:26, King James Version

In this section we describe the motion of water-walkers through a formal fluid mechanical treatment. We begin in §2.1 with a discussion of the wetting properties of water-walking arthropods that play a critical role in their life at the interface. In §2.2 we enumerate the components of the hydrodynamic force that act on a creature propelling itself at the interface. Particular attention is given to consideration of weight support and lateral propulsion. We proceed by extending the analysis of Childress (1981) in order to examine the momentum transfer by a water-walking creature in §2.3 and the associated energy transfer in §2.4. In §2.5, we apply our theoretical developments to a number of special cases of biolocomotion including swimming, flying, propulsion on a thin film in vacua, walking on water, meniscus-climbing and Marangoni propulsion.

2.1 Wetting properties

The energetic cost of wetting can be increased by roughening a surface sufficiently to generate ridges and valleys on a scale much smaller than the capillary length (de Gennes et al. 2003). The surface cover of the water-walking arthropod has a complex microscopic topol-
Figure 2-1: Model of the insect leg. **a**, A schematic illustration of the complex surface presented by the hairy insect leg. Note that some hairs are long enough to penetrate the surface; others present a corrugated surface area that resists wetting. **b**, The contact angle $\theta$ made by water on a flat solid. **c**, The Wenzel model describes the effective contact angle $\theta^*$ on a surface with grooves that have imbibed the water. **d**, The Cassie model describes the effective contact angle $\theta^*$ on a surface with grooves that retain air pockets. $\delta$ refers to the distance between two adjacent peaks of the solid.

The Wenzel model describes the case where the entire surface is wetted and no air pockets are trapped (Figure 2-1c). The apparent wetting angle on such a surface is given by Wenzel’s law (Bico et al. 2001, Lafuma & Quéré 2003),

$$\cos \theta^* = r \cos \theta$$

where $r \geq 1$ is the roughness of the solid, defined as the ratio of the roughened to the smooth arclength, and $\theta$ is the contact angle on a planar solid (Figure 2-1b). A hydrophobic surface ($\theta < 90^\circ$) becomes more hydrophobic ($\theta^* < \theta$) upon roughening; and a hydrophilic surface becomes less so.

The Cassie model is appropriate for describing a surface that traps air pockets, such as an insect leg with a plastron. Consider a planar surface tiled with two materials characterized
by respective contact angles $\theta_1$ and $\theta_2$ and area fractions, $f_1$ and $f_2$ (Figure 2-1d). The Cassie-Baxter relation gives the apparent contact angle on such a surface as the mean of the contact angles in each region weighted by their area fraction,

$$
\cos \theta^* = f_1 \cos \theta_1 + f_2 \cos \theta_2
$$

(2.2)

If the tiled material designated as 1 is air (defined to have a contact angle $\theta_1 = 180$), then the Cassie-Baxter relation may be written

$$
\cos \theta^* = -1 + f_S + f_S \cos \theta
$$

(2.3)

where $f_S$ is the exposed area fraction of the solid substrate and $\theta$ is the contact angle of water on a plane of the solid substrate. The Cassie model has been applied to rationalize the observed $\theta^*$ on the legs of water striders (Gao & Jiang 2004). The effective contact angle was measured to be 168°, and the contact angle $\theta \approx 105°$. Gao & Jiang (2004) then used Cassie’s law, Equation (2.3), to infer that the air fraction, $1 - f_S$, between the legs and the water surface is 97%. Such a high effective contact angle means that a single strider leg can support 15 times the water strider’s weight. The effective contact angle $\theta^*$ on Fisher spiders may be as large as 152° (Stratton et al. 2004b).

The hydrophobicity of hair mats is dependent on the water not exceeding a critical pressure. For surface roughness characterized by a distance $\delta$ between two adjacent peaks (Figure 2-1d), the pressure required for the fluid to penetrate the tips of the peaks is given by the intrusion pressure $P_{int} \sim 2 \sigma \cos \theta / \delta$, with corrections associated with the finite height of the roughness (Journet et al. 2005). Water-walking insects therefore cannot apply a pressure with the driving leg greater than the intrusion pressure lest the insects wet and lose their plastrons. Using the data in Table 1.1, we can determine the surface Weber number based on the hair separation $\delta$: $We_s = \frac{\rho U^2}{\sigma/\delta}$. Figure 2-2 shows the trend between the leg speed $U$ and the $We_s$; the line of best fit was computed for insects only and excludes spiders. We find that the Weber number ranges between 0.005 and 0.2, indicating that the fluid is not expected to penetrate the spaces between the hairs at the typical insect leg speeds. Moreover, since the best fit $We_s \sim U$, we surmise that faster insects have a relatively dense hair layer (smaller $\delta$).
Figure 2-2: Leg speed versus the surface Weber number $W_{e,s} = \frac{\rho U^2 \delta}{\sigma}$ for a number of water-walkers. Dynamic data is taken from Chapter 3 and Table 1.1 and indicates that faster creatures have relatively fine hair covers.

2.2 Force balance on the creature

Consider a creature (Figure 2-3) with a rigid boundary defined by the position $r(x, t)$ in motion at a free surface. The creature has a contact line $C(t)$ and a contact area $S(t)$ with the underlying water. The water has a density $\rho$ and is characterized by a stress tensor $T = -pI + 2\mu E$ where $E$ is the rate of strain tensor, $p$ the fluid pressure and $\mu$ the viscosity (Batchelor 2000). The surface tension along $I$, the air-water interface, is $\sigma$. We consider
the upper fluid to be dynamically insignificant. The force balance on the creature is given by Newton’s Law

\[ M \dot{U}(t) = \sum_{\text{body, surface forces}} F = F_h(t) + F_S(t) + Mg \]  

(2.4)

where \( M \) is the object’s mass and \( \dot{U} \) the acceleration of its centroid. The hydrodynamic force and curvature force acting on the creature are, respectively

\[ F_h(t) = \int_{S(t)} T \cdot n \, dS \quad \text{and} \quad F_s(t) = \int_{C(t)} \sigma t \, d\ell. \]  

(2.5)

We proceed by decomposing the hydrodynamic force into its various components. As we shall see in Chapter 4, the Reynolds number characterizing virtually all water-walkers is large and therefore we may deduce the pressure from the time-dependent Bernoulli equation

\[ \frac{\partial \phi}{\partial t} + \frac{1}{2} |u|^2 + \frac{p}{\rho} - g \cdot x = c \]  

where \( \phi \) is the velocity potential, \( x \) the body position and \( c \) a constant. Substituting \( p \) into \( T \) and \( T \) into (2.4) we obtain

\[ M \dot{U} = Mg + \int_{S} \frac{\partial \phi}{\partial t} n \, dS + \int_{S} \frac{1}{2} \rho u^2 n \, dS + \int_{S} \rho g z n \, dS + 2 \mu \int_{S} E \cdot n \, dS + \int_{C} \sigma t \, d\ell. \]  

(2.6)

The viscous flow term (second to last) is negligible when the Reynolds number is large but is included here for the sake of completeness. The above equation shows that the hydrodynamic force may be decomposed into components associated with added mass, form drag, hydrostatic pressure, viscous stress and the surface tension force. We non-dimensionalize (2.6) by introducing dimensionless variables

\[ u' \sim \frac{u}{U}, \quad a' = \frac{a}{a_s}, \quad x' = \frac{x}{w}, \quad z' = \frac{z}{h}, \quad \phi' = \frac{\phi}{wU} \]  

(2.7)

where \( U \) is the characteristic leg speed, \( a_s \) the leg acceleration, \( w \) the leg width and \( h \) the mean leg depth. Dividing both sides by \( \sigma w \) and dropping primes for the non-dimensional
<table>
<thead>
<tr>
<th>Symbol</th>
<th>Dimensionless Number</th>
<th>Definition</th>
<th>Meaning</th>
</tr>
</thead>
<tbody>
<tr>
<td>We</td>
<td>Weber</td>
<td>$\frac{\rho U^2 w}{\sigma}$</td>
<td>inertia curvature</td>
</tr>
<tr>
<td>Ba</td>
<td>Baudoin</td>
<td>$\frac{Mg}{\sigma w}$</td>
<td>weight curvature</td>
</tr>
<tr>
<td>Ad</td>
<td>Added mass</td>
<td>$\frac{V_d a_s}{U^2 w^2}$</td>
<td>added mass inertia</td>
</tr>
<tr>
<td>Re</td>
<td>Reynolds</td>
<td>$\frac{wU}{\nu}$</td>
<td>inertia viscous</td>
</tr>
<tr>
<td>Bo</td>
<td>Bond</td>
<td>$\frac{\rho gh}{\sigma w}$</td>
<td>buoyancy curvature</td>
</tr>
</tbody>
</table>

Table 2.1: Dimensionless groups characterizing walking on water. $V_d$ refers to the volume of water displaced by the driving leg.

terms we obtain a dimensionless expression for the total force on the object

$$M \ddot{U}/\sigma w = -Ba \ddot{z} + We \left( Ad \int_S \frac{\partial \phi}{\partial t} ndS + \int_S n dS + \frac{1}{Re} \int_S n \cdot E dS \right) + Bo \int_S z n dS + \int_C t d\ell$$

(2.8)

where the dimensionless groups are the Baudoin number $Ba = \frac{M g}{\sigma w}$, Weber number $We = \frac{\rho U^2 w}{\sigma}$, Reynolds number $Re = \frac{wU}{\nu}$, Bond number $Bo = \frac{\rho ghw}{\sigma}$ and added mass number $Ad = \frac{V_d a_s}{U^2 w^2}$ where $V_d$ is the volume of fluid displaced by the driving leg, $V_d$, specifically the volume of the meniscus depression for small water-walkers and the volume of the air cavity for large water-walkers. The term $\int_S \rho g z n dS$ is the integral of the hydrostatic pressure over the body’s contact area, corresponding to the weight of the displaced fluid. The physical meaning of each of these groups is listed in Table 2.2.

Equation (2.8) gives the various components of the hydrodynamic force acting on a water-walker’s leg. In the limit of large $We$, surface tension forces become negligible relative to inertial terms. Equation (2.8) then provides the force on the driving leg of large water-walkers such as the basilisk lizard or western grebe. For instance, Glasheen & McMahon (1996a) showed that the dominant forces acting on the driving leg of the basilisk, for which $Re = 10^5, Bo = 100, We = 10^4$, were added mass, form drag and buoyancy. Of course, when the body is completely submerged in a fluid, interfacial forces vanish, $S$ becomes the entire body surface and Equation (2.8) represents the hydrodynamic force on a swimmer or flier.
2.2.1 Weight support

We proceed by examining the vertical force balance on a water-walker. The vertical component of the force balance is given by \( \ddot{z} \cdot (2.8) \); we divide by the Baudoin number to obtain

\[
M \dot{U} \cdot \ddot{z} / (Mg) + 1 = Mc \left( \frac{Ad}{s} \int \frac{\partial \phi}{\partial t} n \cdot \ddot{z} dS + \int \frac{n \cdot \ddot{z} dS}{s} + \frac{1}{Re} \int_{S} n \cdot E \cdot \ddot{z} dS \right) + \frac{Bo}{Ba} \int_{s} z n \cdot \ddot{z} dS + \frac{1}{Ba} \int_{C} t \cdot \ddot{z} d\ell. \tag{2.9}
\]

where \( V_b \) is the volume of fluid displaced above the leg and within the contact line \( C \) (see Figure 2-4) and we have introduced the McMahon number \( Mc = \frac{\rho U^2 w^2}{Mg} \). An object can be supported at the interface if the time average of \( \dot{U} \cdot \ddot{z} \) is zero. We note that the term \( \frac{Bo}{Ba} = \frac{\rho V_b}{Mg} \approx \frac{\rho}{\rho_b} \) where \( V_b \) is the volume displaced within the contact line of the creature and \( \rho_b \) is the density of the creature. First (2.9) indicates that small creatures (\( Ba = \frac{Mg}{\sigma w} < 1 \)) may reside at rest at the free surface (\( Mc = 0 \)), a statement we shall refine in the next section. For creatures too massive to rely on surface tension for weight support (\( Ba \gg 1 \)), (2.9) indicates two means of walking on water. If the creature has a density less than that of water (\( \rho_b / \rho < 1 \)), it may support its weight by flotation; however most creatures are composed of mostly water and have a density comparable to it (\( \rho_b / \rho \approx 1 \)). Such creatures can support their weight using inertial forces if \( Mc > 1 \).

Static weight support

In a static situation, (2.9) yields a generalized form of Archimedes principle: the force on a static floating body is equal to the weight of the fluid displaced. Mansfield et al. (1997) and Keller (1998) showed that the magnitudes of the buoyancy and curvature forces on a floating body are equal to the weights of the fluid displaced by the meniscus, respectively, in- and outside the line of tangency \( C \) (respectively \( V_b \) and \( V_m \) in Figure 2-4d). The force balance on a static floating body is thus

\[
Mg \cdot \ddot{z} = F_b \cdot \ddot{z} + F_c \cdot \ddot{z} = \int_{S} \rho g z n \cdot \ddot{z} dS + \sigma \int_{C} t \cdot \ddot{z} d\ell = \rho g V_b + \rho g V_m. \tag{2.10}
\]

This result is simply demonstrated for a 2D body such as an insect leg. We consider the force balance on a two-dimensional leg as shown in Figure 2-4a. Under the application of
Figure 2-4: a, Water-walking arthropods such as this water strider deform the free surface; the resulting curvature forces bear its weight. The strider has leg width $w$ and contact line $C$. The angle of tangency between the strider leg and the fluid is $\theta$ and the meniscus decays over the capillary length, $\ell_c$. b, Schematic of the forces on a floating non-wetting body of weight $M$ in contact with area $S$ of the free surface. The lightly shaded region denotes the volume $V_b$, the fluid bounded above $S$, below the unperturbed fluid line and between the lines of tangency. c, Schematic of the meniscus surrounding the floating body. $V_m$ is the volume of fluid displaced above the meniscus. d, The relative magnitudes of the volumes, $V_m/V_b$ indicate the relative magnitudes of the curvature and buoyancy force acting on the leg.
the insect’s weight, the surface is distorted into a curved meniscus that arcs away from leg on both sides. The buoyancy force is given by

\[ F_b = \int_S \rho g z n \, ds = \rho g V_b \hat{z}, \tag{2.11} \]

and thus equal to the weight of fluid \( V_b \) displaced above the body and inside the line of tangency \( C \) (Figure 2-4b). The curvature force may be deduced by applying Stoke’s Theorem (Levich & Krylov 1969) on the contact line,

\[ \sigma \int_C t \, d\ell = \int_S (\sigma (\nabla \cdot n) n - \nabla \sigma) ds. \tag{2.12} \]

We neglect Marangoni stresses and integrate the curvature pressure \( \sigma (\nabla \cdot n) \) over the same arclength to find

\[ F_c = \int_S \sigma (\nabla \cdot n) n \, ds = \int_S \sigma \frac{dt}{ds} \, ds = \sigma (t_1 - t_2) = 2\sigma \sin \theta \hat{z} \tag{2.13} \]

where \( \theta \) is the angle of tangency (Figure 2-4) and where we have applied the Frenet-Serret equation (e.g. do Carmo 1976),

\[ (\nabla \cdot n)n = \frac{dt}{ds}. \tag{2.14} \]

Therefore, the vertical force balance on the body may be written as \( Mg = \rho g V_b + 2\sigma \sin \theta \).

Each point on the meniscus outside the equivalent line of tangency satisfies the Young-Laplace equation, \( \rho g z = \sigma \nabla \cdot n \), which may be integrated to show that \( -2\sigma \sin \theta = \rho g V_m \), and therefore \( F_c \cdot \hat{z} = \rho g V_m \). For long thin bodies such as water-walking insect legs, the ratio of buoyancy to curvature forces is thus given by the square root of the Bond number, or equivalently the ratio of the leg radius \( w \) to the capillary length \( \ell_c \):

\[ \frac{F_b}{F_c} \sim \frac{V_b}{V_m} \sim \frac{w}{\ell_c} \sim \sqrt{Bo} \tag{2.15} \]

where \( \ell_c = \left(\frac{\sigma}{\rho g}\right)^{1/2} \). Water striders (with weight 3-10 dynes and leg width 20-80 µm), have \( 10^{-4} < Bo < 10^{-2} \), and are thus supported almost exclusively by surface tension. The relatively stubby Fisher spider (with weight \( 10^2 - 10^3 \) dynes and leg width up to 0.17 cm) has \( 10^{-3} < Bo < 10^{-1} \) and so may have up to 1/3 of their weight supported by buoyancy.
Finally we note that an insect can augment its buoyancy by increasing its effective volume using a plastron air layer around its body (Thorpe & Crisp 1947). The characteristic Bond numbers of other water-walking insects considered in our study are listed in Table 4.

In light of the fact that water-walking insects are supported predominantly by surface tension forces, we see that their shape (specifically, their leg perimeter $P = 2(L_1 + L_2 + L_3)$ where $L_i$ is the length of the $i$th leg segment in contact with the water, as shown in Figure 2-5) determines their margin of safety at the free surface, defined previously as the Baudoin number

$$Ba = \frac{Mg}{\sigma P}.$$ (2.16)

Figure 2-5 plots the relation between the maximum possible surface tension force $F_s$ and the weight $F_g$ of water-walking insects. Creatures above the line $Ba = 1$ may be statically supported by surface tension; those below cannot. Baudoin (1955) predicted that the margin of safety, $Ba$, should increase as the square of the insect size $L$, $Ba \sim L^2$, as should be expected since $M \sim L^3$ and $P \sim L$ assuming the insects are isometric. The best fit for Figure 2-5 is $F_s \sim F_g^{0.46}$, and the margin of safety is $\frac{F_s}{F_g} \sim \frac{F_g^{0.5}}{F_g} \sim L^{1.5}$. This reflects a weaker dependence than Baudoin predicted because water-walker’s legs evidently grow proportionally longer with increasing body size. In Chapter 5, we shall see that a similar variance from isometry arises for the water striders.

### 2.2.2 Lateral propulsion

The horizontal component of the force balance on a water-walker is given by the $\hat{x}$ component of (2.8):

$$M \hat{U} \cdot \hat{x}/(\sigma w) = We \left( Ad \int_{S} \frac{\partial \phi}{\partial t} n \cdot \hat{x} dS + \int_{S} n \cdot \hat{x} dS \right)$$

$$+ Bo \int_{S} z n \cdot \hat{x} \, dS + \int_{C} \sigma t \cdot \hat{x} \, d\ell$$ (2.17)

For large creatures ($We \gg 1$ and $Bo \gg 1$), surface tension is negligible. Equation (2.17) shows that such water-walking creatures may propel themselves using inertial and hydrostatic pressures. For example, the basilisk lizard generates thrust using hydrostatic pressure by generating an air cavity with its feet and pressing against the cavity’s back wall (Glasheen...
Figure 2-5: Margin of safety for water-walkers. $F_g = Mg$ is the weight of the creature and $F_s = \sigma P$ is the maximum supporting surface tension force, where the contact perimeter $P = 4(L_1 + L_2 + L_3)$.

& McMahon 1996a). We note that the hydrostatic pressures can only produce a lateral force on a body with a meniscus or cavity that is not fore-aft symmetric. When $We \ll 1$, surface tension dominates inertial forces. As we shall see in Chapter 4, most water-walking insects propel themselves using some combination of inertia forces and surface tension. In what follows we examine the propulsion by surface tension forces alone.

Figure 2-6: a, A body with contact line $C$. b, A body moving quasi-statically by curvature forces in the presence of a meniscus ($\theta_1 \neq \theta_2$). c, A body moving under the influence of surface tension gradients ($\sigma_2 \neq \sigma_1$).
Quasi-static propulsion

In this section we examine quasi-static propulsion mechanisms that allow creatures to propel themselves without moving their legs. Rather than driving their legs against the free surface and using inertial forces, these creatures are able to move purely by using surface tension forces. This mode of propulsion, called “spontaneous motion” in the context of microfabrication by Darhuber & Troian (2005) and others, has been used to move small parcels of fluid in miniature devices. When the \( We \ll 1 \) and \( Bo \ll 1 \), Equation (2.17) yields

\[
M \dot{U} = \int_C \sigma t d\ell
\]

which in dimensionless form is

\[
\frac{M \dot{U}}{\sigma w} = \int_S (\nabla \cdot n) n \cdot \hat{x} dS - Ma \int_S \nabla \sigma \cdot \hat{x} dS
\]

where we have used Stoke’s identity (2.12) on the contact line (Figure 2-6a) and introduced a new dimensionless number, the Marangoni number, \( Ma = \frac{\nabla \sigma}{\sigma/L} \) which prescribes the relative magnitudes of the Marangoni to curvature forces. For most floating bodies, the lateral force in (2.18) is zero; however if a creature deforms the free surface in the presence of a fluid meniscus, it may generate a non-zero lateral force (Figure 2-6b). Alternatively, by releasing surfactant and thus changing \( \sigma(x, t) \), the creature may be propelled forward (Figure 2-6c). We note that the unbounded acceleration suggested by (2.18) will be checked by an appropriate drag as the body speed increases sufficiently.

As we shall see in §6, propulsion by surface deformation is exploited by a number of water-walking insects to climb mensici. In §6 we shall arrive at the lateral propulsive force \( F_h \) by considering the gradient of the potential energy \( U \) of the system,

\[
F = \frac{dU}{dx}
\]

as has been done by Kralchevsky & Denkov (2001). In the following section we examine the conservation of momentum for an organism-fluid system.
2.3 Momentum transfer

An alternative means of rationalizing the propulsion of creatures is through consideration of the momentum transferred in its wake. Childress (1981) provided a theoretical description of momentum and energy transfers by an organism submerged in a fluid. Here, we extend his treatment in order to consider a creature propelling itself at the free surface.

Figure 2-7: An organism with boundary S in a hemisphere Σ. A free interface I divides the water and air; the interfacial tension of the interface is σ. n is taken outward normal from S and upward from the interface.

In the previous section we considered the hydrodynamic force on an insect leg deforming the free surface. We proceed by extending our treatment to consider the hydrodynamic force on an entire water-walking creature. Consider the physical picture in Figure 2-7. An organism can be taken to be an impenetrable region having a boundary S(t) with the fluid. The centroid of the organism moves with time-averaged speed $-<U>$. There is a hemisphere Σ moving at the same speed $-<U>$ as the organism. Let V be the volume of the fluid between S and Σ. There is a free surface I adjoining the sphere at a contact line C.

If $S_0$ denotes the set of boundary points at $t = 0$, and if $r_S(t, r_0)$ is the position of a boundary point initially at $r_0$, then the fluid boundary condition is

$$u(r_S(t), t) = \dot{r}_S(t, r_0), r_0 \in S_0$$ (2.21)

where $r_S(t)$ is the position of a point on the boundary originally at position $r_0$ at $t = 0$. 
Using Reynold’s transport theorem\(^1\) (2.22), we can write the momentum contained in the region \(V\) as

\[
\frac{D}{Dt} \int_V \rho u dV = \int_V \left( \frac{\partial}{\partial t} (\rho u) \right) dV + \int_\Sigma \rho uu \cdot ndS + \int_I \rho uu \cdot ndS - \int_S \rho u \cdot \dot{r}_S \cdot ndS \quad (2.23)
\]

The flow satisfies the Navier-Stokes equations

\[
\rho \left( \frac{\partial u}{\partial t} + uu \cdot \nabla \right) = \nabla \cdot T + \rho g \quad (2.24)
\]

where we have used \( T = -pI + 2\mu E \) where \( p \) is the pressure. We substitute for \( \frac{\partial}{\partial t} (\rho u) \) from the Navier-Stokes into (2.23) to obtain

\[
\frac{D}{Dt} \int_V \rho u dV = \int_V (-\rho u \cdot \nabla u + \nabla \cdot T) dV - \int_S \rho u \cdot \dot{r}_S \cdot ndS + \int_\Sigma \rho uu \cdot ndS
\]

\[
+ \int_I \rho uu \cdot ndS + M_V g \quad (2.25)
\]

where \( M_V g = \int_V \rho gdV \) is the weight of the fluid in the control volume. Applying the divergence theorem to the volume integrals over \( V \), and using the identity

\[
\nabla \cdot (uu) = (u \cdot \nabla)u + (\nabla \cdot u)u, \quad (2.26)
\]

where \( (\nabla \cdot u) = 0 \), we obtain an expression describing the evolution of momentum within \( V \),

\[
\frac{D}{Dt} \int_V \rho u dV = \int_\Sigma T \cdot ndS + \int_S \rho u (u - \dot{r}_S) \cdot ndS
\]

\[
+ \int_I T \cdot ndS + \int_I T \cdot ndS + \int_I \rho gzn dS + \int_\Sigma \rho gzn dS + M_V g \quad (2.27)
\]

\(^1\)In the following sections we shall use the following Reynold’s transport theorem (Batchelor 2000): for any quantity \( Q \) defined in \( V(t) \),

\[
\frac{D}{Dt} \int_{V(t)} Q dV = \int_{V(t)} \frac{\partial}{\partial t} Q dV + \int_{\partial V(t)} Qu \cdot n dS \quad (2.22)
\]

where \( n \) is outward from the boundary of \( V \), \( \partial V(t) \).
The momentum within $V$ may change owing to the flux of momentum ($\rho u u \cdot n$) across, and the hydrodynamic stress ($T \cdot n$) acting on, the bounding surfaces. We proceed by simplifying (2.27). As $\Sigma$ expands to $\infty$, the flux of momentum across and the hydrodynamic force acting on $\Sigma$ vanish identically. The flow generated by an isolated disturbance such as an object striking the interface will decay at least as fast as a dipole,

$$u \sim \frac{1}{r^2}.$$  \hfill (2.28)

Therefore, the flux of momentum through the boundary $\Sigma$ vanishes as

$$\lim_{r \to \infty} -\rho u u \cdot n \sim \lim_{r \to \infty} \int_{\Sigma} u^2 dS \sim \frac{1}{r^4} \int_{r \to \infty} r^2 \sim \frac{1}{r^2} \lim_{r \to \infty} r = 0$$  \hfill (2.29)

and the hydrodynamic force at $\Sigma$ reduces to

$$\lim_{r \to \infty} \int_{\Sigma} T \cdot n dS \sim \lim_{r \to \infty} \frac{1}{r^4} r^2 \sim \lim_{r \to \infty} \frac{1}{r^2} = 0$$  \hfill (2.30)

where we have used $\lim_{r \to \infty} T \sim -p + 2 \mu E \sim \rho u^2 + \mu \nabla u$ as is appropriate for high Reynolds number motion. We note that in (2.27), the boundary condition of the free surface,

$$T \cdot n = \sigma(\nabla \cdot n) \cdot n - \nabla \sigma,$$  \hfill (2.31)

implies that

$$\int_{I} T \cdot n dS = \int_{I_{\infty}} \sigma t \ d\ell - \int_{C(t)} \sigma t \ d\ell = - \int_{C} \sigma t \ d\ell$$  \hfill (2.32)

where we have used Frenet-Seret (2.14) and Stoke’s equation (2.12) on the free surface $I_{\infty}$; $I_{\infty}$ refers to the contact line between the free surface $I$ and $\Sigma$. The total curvature force acting about $I_{\infty}$ vanishes identically for $r \to \infty$. Lastly we note that the hydrostatic pressure on the control volume balances its weight,

$$\int_{\Sigma} \rho gz dS + \int_{I} \rho g z dS = M_V g.$$  \hfill (2.33)
Combining these results yields a simplified form of (2.27):

\[
\frac{D}{Dt} \int_V \rho u dV = -\int_S T \cdot n dS - \int_C \sigma t \, dl
\]  

(2.34)

The total momentum of the fluid may be altered by the hydrodynamic forces applied by the creature and surface forces applied at the contact line. The result obtained by Childress (1981) for swimming and flying is the same as above when \( \sigma = 0 \). Substituting for \( F_h \) from (2.4) yields an equation describing the rate of change of momentum of the creature and fluid:

\[
M \dot{U} = -\frac{D}{Dt} \int_V \rho u dV + \Delta Mg
\]

(2.35)

where \( \Delta Mg = Mg - \int_S \rho g z n dS \) is the creature’s reduced weight. We shall use this equation in \( \S 2.5 \) to determine the equations of momentum transfer for various modes of locomotion. Note that surface tension does not arise in the final statement of conservation of momentum: while it contributes a force to the body and the control volume, these contributions are equal and opposite.

2.4 Energetics

We proceed by examining the transfer of energy between the water walker, the free surface and underlying fluid. We examine the energy balance for the creature and then the fluid.

2.4.1 Energy of the creature

The forces on the creature are prescribed by Newton’s equation (2.4). The creature converts internal metabolic energy into motion of its boundary \( S(t) \). We expect therefore that the rate of work performed by the creature to be given by the product of the force and velocity at its boundary. We begin by taking the dot product of (2.4) and the velocity \( U(t) \):

\[
M \dot{U}(t) \cdot U(t) = F_h(t) \cdot U(t) + F_s(t) \cdot U(t) + Mg \cdot U(t) + F_b \cdot U(t)
\]

(2.36)
where we have used the dynamic pressure in $F_h$ and thus pulling out the buoyancy force $F_b$. Writing (2.36) in terms of exact differentials yields

$$\frac{d}{dt} \left( \frac{1}{2}MU^2(t) + \Delta Mgz \right) = \int_{S(t)} u \cdot T \cdot ndS + \int_{C(t)} \sigma u \cdot t d\ell \quad (2.37)$$

where $\Delta Mgz$ is the sum of the gravitational and buoyancy forces on the creature where we have used $-\frac{d}{dt}(Mg \cdot X(t))$ (according to Figure 2-7) and the position of the body $X(t)$. (2.37) states that the rate of change of kinetic and gravitational potential energy of the creature is equal to the rate of work performed by the fluid and free surface on its boundary. We may write the rate of work performed by hydrodynamic forces on the creature as

$$W_h = \int_{S(t)} u \cdot T \cdot ndS \quad (2.38)$$

where we have used the fact the velocity $U$ of the centroid of a rigid body is equal to that at its boundary and so $U \cdot \int_{S(t)} T \cdot ndS = \int_{S(t)} u \cdot T \cdot ndS$. Similarly, the work performed by surface tension forces on the creature is given by

$$W_s = \int_{C} \sigma u \cdot td\ell \quad (2.39)$$

where $C$ is the contact line of the body. We return briefly to our statement earlier that the metabolic energy of the creature is converted into work done at its boundary:

$$\dot{E}_c + W_h + W_s = \Phi_c \quad (2.40)$$

where $\dot{E}_c$ is the rate of change of the internal energy stores of the creature (given by its metabolic energy supply such as ATP) and $\Phi_c$ is the creature’s internal dissipation due to inefficiency associated with converting metabolic energy into motion of its muscles. We proceed by writing the energy balance for the fluid surrounding the creature.
2.4.2 Energy of the fluid

Using Reynold’s Transport Theorem (2.22) with \( Q = \frac{1}{2} \rho u^2 \) we have

\[
\frac{D}{Dt} \int_V \frac{1}{2} \rho u^2 \, dV = \int_V \frac{\partial}{\partial t} \left( \frac{1}{2} \rho u^2 \right) \, dV - \int_S \frac{1}{2} \rho u^2 \mathbf{r}_S \cdot \mathbf{n} \, dS + \int_\Sigma \frac{1}{2} \rho u^2 \mathbf{u} \cdot \mathbf{n} \, dS + \int_I \frac{1}{2} \rho u^2 \mathbf{u} \cdot \mathbf{n} \, dS
\]

(2.41)

We now multiply equations (2.24) by \( \mathbf{u} \) to obtain the energy equation in a fluid (Batchelor 2000)

\[
\frac{D}{Dt} \left( \frac{1}{2} \rho u^2 \right) = \mathbf{u} \cdot \nabla \cdot \mathbf{T} + \rho \mathbf{u} \cdot \mathbf{g}.
\]

(2.42)

We use the identities \( \mathbf{u} \cdot (\mathbf{u} \cdot \nabla \mathbf{u}) = (\mathbf{u} \cdot \nabla) \frac{1}{2} u^2 \) and

\[
\nabla \cdot (\mathbf{T} \cdot \mathbf{u}) = (\nabla \cdot \mathbf{T}) \cdot \mathbf{u} + \mathbf{T} : \nabla \mathbf{u}
\]

(2.43)

to write (2.42) as

\[
\rho \left( \frac{\partial}{\partial t} \left( \frac{1}{2} u^2 \right) + (\mathbf{u} \cdot \nabla) \frac{1}{2} u^2 \right) = \nabla \cdot (\mathbf{T} \cdot \mathbf{u}) - \nabla u + \rho \mathbf{u} \cdot \mathbf{g}.
\]

(2.44)

Substituting \( \frac{1}{2} \rho u^2 \) from (2.44) into (2.41) and applying the divergence theorem to the volume integrals yields

\[
\frac{D}{Dt} \int_V \frac{1}{2} \rho u^2 \, dV = \int_S \mathbf{u} \cdot \mathbf{T} \cdot \mathbf{n} \, dS + \int_I \mathbf{u} \cdot \mathbf{T} \cdot \mathbf{n} \, dS
\]

\[
+ \mu \int_V \mathbf{E} \cdot \mathbf{E} \, dV - \int_S \mathbf{u} \cdot \mathbf{T} \cdot \mathbf{n} \, dS + \int_V \rho \mathbf{g} \cdot \mathbf{u} \, dV
\]

(2.45)

Equation (2.45) represents the rate of change of energy of the control volume and consists of terms associated with the rate of work done against hydrodynamic forces \( \mathbf{u} \cdot \mathbf{T} \cdot \mathbf{n} \) at the various boundaries. We proceed by simplifying (2.45).

The term \( \int_I \mathbf{u} \cdot \mathbf{T} \cdot \mathbf{n} \, dS \) represents the rate of work against surface forces, which can be
reexpressed via the boundary condition at the free surface (2.31) as

$$\int_{\Gamma} \mathbf{u} \cdot \mathbf{T} \cdot \mathbf{n} \, dS = \int_{\Gamma} \mathbf{u} \cdot \left( \sigma \left( \nabla \cdot \mathbf{n} \right) \mathbf{n} - \nabla \sigma \right) dS = \sigma \frac{dA}{dt} - \int_{\Gamma} \mathbf{u} \cdot \nabla \sigma dS, \quad (2.46)$$

where $A$ denotes the total area of the free surface $\Gamma$. To obtain relation (2.46), we have applied Stokes Theorem (2.12), the Frenet-Seret equation (2.14) and the identity

$$\int_{\Gamma} \mathbf{u} \cdot \left( \nabla \cdot \mathbf{n} \right) \mathbf{u} \cdot \mathbf{n} \, dS = \frac{dA}{dt}, \quad (2.47)$$

where $A = \int_{\Gamma} \sqrt{1 + \eta_x^2 + \eta_y^2} \, dS$ is the total surface area of the interface $I : z = \eta(x, y)$, which can be proven using differential geometry (pers. comm. Nikos Savva). (2.46) states that the rate of work done against surface stresses is given by the change in the surface area and work performed against Marangoni stresses.

We further simplify Equation (2.45) by extending the boundary $\Sigma$ to $\infty$. Using methods from §2.3, it can be shown that the flux of kinetic energy, the rate of work performed against hydrodynamic force vanish identically. We thus obtain a simplified form of (2.45),

$$\frac{D}{Dt} \int_{V} \frac{1}{2} \rho \mathbf{u}^2 dV + \int_{V} \rho g \cdot \mathbf{u} dV + \int_{S} \mathbf{u} \cdot \mathbf{T} \cdot \mathbf{n} dS + \sigma \frac{dA}{dt} - \int_{\Gamma} \mathbf{u} \cdot \nabla \sigma dS = \mu \int_{V} \mathbf{E} : \mathbf{E} dV, \quad (2.48)$$

which states that the rate of change of kinetic, gravitational and surface energy of the fluid is equal to the rate of work performed by the creature minus the viscous dissipation into heat. Equation (2.48) states that the total kinetic energy of the fluid may be altered by the work performed by the creature or heating $\Phi$ due to viscous dissipation. Ignoring the terms involving the energy of the interface, (2.48) provides the relation found previously by Childress (1981) for a swimming creature.

Combining (2.48) and (2.37) we can eliminate $W_h = \int_{S} \mathbf{u} \cdot \mathbf{T} \cdot \mathbf{n} dS$ to write the energy conservation for the creature-fluid system,

$$\frac{d}{dt} \left[ \frac{1}{2} M U^2(t) + \Delta M g z + \int_{V} \frac{1}{2} \rho \mathbf{u}^2 dV + \int_{V} \frac{1}{2} \rho g z dV + \sigma A \right] - \int_{\Gamma} \mathbf{u} \cdot \nabla \sigma dS - \int_{C} \sigma \mathbf{u} \cdot \mathbf{t} \, d\ell = \Phi \quad (2.49)$$

where the dissipation $\Phi = \mu \int_{V} \mathbf{E} : \mathbf{E} dV$. Equation (2.49) relates the rates of change of the kinetic energy and gravitational potential energy of the creature and fluid; the rates of
change of the surface energy; and the viscous dissipation into heat.

We non-dimensionalize (2.49) by defining the dimensionless primed variables

$$u' \sim \frac{u}{U}, \quad x' = \frac{x}{w}, \quad z' = \frac{z}{w}, \quad A' = \frac{A}{w^2}, \quad t' = \frac{t}{w/U} \quad (2.50)$$

where $w$ is the characteristic length scale of the creature, $U$ the insect speed, and $M$ the insect mass. Dividing both sides by $\rho U^2 w^3$ we obtain

$$\frac{d}{dt'} \left[ \lambda \left( U' \rho^2 + \frac{Bo}{We} M' z' \right) + \frac{Bo}{We} \int_V u'^2 dV' + \frac{1}{We} \int_V \left( A' - \int_C u' \cdot t dl' - Ma \int_I u' \cdot \nabla \sigma' dS' \right) \right] = \frac{1}{Re} \int_V E' : E'dV' \quad (2.51)$$

where we have introduced the dimensionless group $\lambda = \frac{\Delta M}{Mw}$ which prescribes the ratio of (the weight of the creature minus the weight of the fluid displaced over the control volume) to the weight of the fluid in the control volume; the Weber and Bond numbers of the flow and the Marangoni number $Ma$ (defined in (2.19)). Note that the dissipation term becomes important over long time scales ($t > U/w$).

### 2.5 Limiting cases of interest

In §2.3-2.5 we derived relations for the transfer of momentum (2.35) and energy (2.49) for a creature at a free surface. In this section we consider the limits of these equations as they pertain to different modes of locomotion. We examine the momentum and energy transfers for swimming fish, hovering birds, a creature on a thin film, and water-walking insects. In the regime of water-walking insects we consider further an insect leaping and an insect moving using quasi-static means such as capillary and Marangoni propulsion.

#### 2.5.1 Swimming fish ($\Delta M = 0, \sigma = 0$)

Consider the limit in which no interface exists ($\sigma = 0$) and the creature is neutrally buoyant ($\Delta M = 0$). In this limit, we obtain equations for the motion of a fish. The transfer of horizontal momentum is given by (2.35), which can be integrated with respect to time to yield

$$M \dot{U} \cdot \dot{x} = -\int_V \rho u \cdot \dot{x} dV + C \quad (2.52)$$
where \( C \) is a constant based on the initial momentum of the fish and the fluid. This equation states that the momentum of the fish is equal and opposite to that of the fluid. Steady motion may be produced by the steady transfer of momentum to the surrounding fluid. The momentum in the wake of a fish often appears in the form of coherent vortices, for example the reversed Karman vortex street (Wilga & Lauder 2002).

### 2.5.2 Hovering birds (\( \Delta M = M \))

We again consider the limit of a single fluid with no interface in order to describe a hovering bird; the density of the bird is much higher than that of the fluid so \( \Delta M = M \). Here the bird holds a static position so \( \dot{U} = 0 \) and the \( z \)-component of our momentum equation (2.35) is

\[
Mg = -\frac{\partial}{\partial t} \int_V \rho u \cdot \hat{z} dV. \tag{2.53}
\]

The time-rate of change of momentum in the fluid is equal to the bird’s weight. Spedding et al. (2003) rationalized the weight support in pigeons by measuring the momentum flux in their wakes.

### 2.5.3 Motion on a thin film (\( We \rightarrow 0, Bo \rightarrow 0, Re = 0 \))

We here consider the hypothetical case of a creature jumping on a free surface such as a soap film in a vacuum. This limit may be obtained by considering small Weber number \( We \), small Bond number \( Bo \), and zero Reynolds number. In this limit, the momentum of the fluid \( \int_V \rho u dV \) is zero because the fluid has zero density. The force balance on the creature, (2.4), assumes the form

\[
M \dot{U} \cdot \hat{z} = \int_C \sigma t \cdot \hat{z} d\ell + Mg. \tag{2.54}
\]

in which the only forces acting on the creature are those due to surface tension and gravity. (2.54) states that the creature is static (\( \dot{U} = 0 \)) when its weight is balanced by the curvature force associated with a deformation of the free surface. The corresponding energy transfer equation, from (2.49) yields

\[
\frac{d}{dt} \left( \frac{1}{2} MU^2 + Mgz + \sigma A \right) = 0 \tag{2.55}
\]
which states that the sum of the kinetic and potential energies of the creature and the surface energy remains constant.

### 2.5.4 Water-walking insects ($We \leq 1, Bo \ll 1, Re \gg 1$)

Water-walking insects generally propel themselves by driving their legs impulsively against the free surface. As we shall see in Chapter 3, these insects are characterized by $Bo \ll 1, Re \gg 1$ and depending on their size, have small to moderate Weber number. For $We \ll 1$ and $Bo \ll 1$, (2.17) yields

$$MU = F_s - Mg$$

which states that the motion on the leg is resisted by surface tension forces only and there is negligible motion of the fluid. For moderate $We$, we can integrate (2.35) to obtain

$$MU \cdot \hat{x} = - \int_V \rho u \cdot \hat{x} dV + C.$$  

(2.57)

where $C$ is a constant of integration. The horizontal momentum of the creature and a water-walking insect are equal up to a constant, as was found for fish (2.52). We shall apply (2.57) in Chapter 4 to determine the momentum transfer of water striders.

The conservation of energy, (2.51) may then be expressed as

$$\frac{d}{dt} \left[ \lambda \left( \frac{1}{We} \frac{Bo}{M} \Delta M' Z' + \int_V u^2 dV' + \frac{1}{We} \left( A' - \int_C u' \cdot t d\ell' - Ma \int_I u' \cdot \nabla' \sigma' dS' \right) \right) \right] = \Phi$$

(2.58)

When $We \ll 1$, the creature propels itself by driving its leg to deform the surface, generating surface energy that dominates over the fluid kinetic energy. Over the surface relaxation time ($t = (\rho \ell_s^2 / \sigma)^{1/2} \approx 0.01$ s), the surface will relax and the surface energy will be transferred into kinetic energy of the fluid and heat. In this next section we consider the motion of creatures in which the leg is not driven, but instead the creature moves quasi-statically.

### 2.5.5 Quasi-static motion

Some water-walking insects are capable of propelling themselves without moving their legs. This limit may be obtained by considering zero Weber number (as there is no fluid motion)
Figure 2-8: A small massless particle that deforms the surface by applying a vertical force $Tz$ at a horizontal distance $x_0$ from the wall.

and low Bond number. There are two modes of quasi-static motion and we consider each in turn.

**Meniscus-climbing** ($u = 0; Re \gg 1, \lambda \ll 1, We \gg 1$)

We first examine the energetics on the basis of (2.51) and (2.49). For meniscus-climbing insects, we have $Re \gg 1, Ms \ll 1, We \gg 1$ and $Bo \ll 1$ and the fluid motion $u = 0$. Moreover, the mass of the insect greatly exceeds the mass of fluid that has been perturbed (so $\lambda \gg 1$).

The shape of the fluid meniscus, $z = \eta(x, y)$, is prescribed by the Young-Laplace equation that expresses the balance between hydrostatic and curvature pressures at the interface

$$\rho g \eta = \sigma \nabla \cdot n$$

where $n$ is the unit outward normal. We consider an effectively two-dimensional meniscus generated by the contact line on a log. For meniscus contact angles $\theta$ between $55^\circ$ and $125^\circ$, the interfacial slope is sufficiently small, $\eta_x \ll 1$, for the Young-Laplace equation to be linearized (Gryzbowski et al. 2001). Using the boundary conditions

$$\eta_x(0) = -\cot \theta, \quad \eta(\infty) = 0,$$

the linearized equation may be solved to yield a meniscus shape

$$\eta(x) = \ell_c \cot \theta e^{-x/\ell_c}.$$
Consider a small massless particle that deforms the surface by applying a vertical force \( Tz \) at a horizontal distance \( x_0 \) from the wall (Figure 2.67. Substituting \( u = 0 \) into (2.58) and integrating with respect to time, we have as the energy of the system the sum of the kinetic and potential energies

\[
V = \frac{1}{2} MU^2; \quad U = \Delta Mg z + \sigma (A + \Delta A)
\]  (2.62)

where \( A \) is the surface area of the unperturbed meniscus and \( \Delta A \) is the anomalous surface area deformation made by the particle. Gryzbowski et al. (2001) have shown computationally that the potential energy decreases as the particle approaches the background meniscus, which provides the physical basis for the capillary lateral forces. Nondimensionalizing the equation for \( U \) using the length scale \( L \) of the deformation by the particle and the capillary length \( \ell_c \), we use the dimensionless variables,

\[
A' = \frac{A}{\ell_c^2}, \quad \Delta A' = \frac{\Delta A}{L^2}, \quad z' = \frac{z}{\ell_c}, \quad \Delta M' = \frac{Mg}{T}
\]  (2.63)

and obtain the equation

\[
U/(\sigma \ell_c^2) = \frac{T}{\sigma \ell_c} \Delta M' z' + (A' + Bo \Delta A')
\]  (2.64)

where the Bond number prescribes the ratio of the size of the deformation to the capillary length (or the length scale of the meniscus). Thus when \( Bo \ll 1 \), the surface area \( A \) does not change appreciably with motion of the deformation of the particle. The anomalous surface energy can be neglected and the system’s potential energy can then be considered to consist of the energy driven by buoyancy, \( \Delta Mg z = Tz \) (Chan et al. 1981). The Lagrangian \( \mathcal{L} \) of the system is the difference between the system’s kinetic and potential energies (Crandall et al. 1968),

\[
\mathcal{L} = \frac{1}{2} M \dot{x}_0^2 - T \eta + \sigma (A + \Delta A).
\]  (2.65)

where we have used \( x_0 \) for the position of the particle and \( \eta(x_0) \) for \( z \). At small Bond number the Lagrangian simplifies to \( \mathcal{L} = \frac{1}{2} M \dot{x}_0^2 - T \eta \) and may be substituted into the Lagrange equation,

\[
\frac{d}{dt} \left( \frac{\mathcal{L}}{\partial \dot{x}_0} \right) - \frac{\partial \mathcal{L}}{\partial x_0} = 0
\]  (2.66)
to provide the lateral force on the particle,

\[ F = -\frac{dU}{dx_0} = -\frac{d}{dx_0}(-T\eta(x_0)) = -T\cot\theta e^{-x_0/\ell_c}. \quad (2.67) \]

A small buoyant object \((T > 0)\) floating in the presence of a larger meniscus decreases in potential energy as it approaches the meniscus and is attracted to the meniscus; conversely, a negatively buoyant body \((T < 0)\) is repelled by the meniscus.

**Marangoni propulsion \((Ma \gg 1, Re \gg 1, We \gg 1)\)**

In Marangoni propulsion, the Marangoni number \(Ma\) is high because the insect ejects a surfactant that generates surface tension gradients. The force balance equation (2.4) is

\[ M\dot{U} = \int_S -\nabla\sigma dS. \quad (2.68) \]

The change in kinetic energy of the creature may be written from (2.58) as

\[ \frac{d}{dt} \left( \frac{1}{2} MU^2(t) + \int_V \frac{1}{2} \rho u^2 dV \right) - \int_S u \cdot \nabla\sigma dS = \Phi, \quad (2.69) \]

which can be rearranged and integrated with respect to time to yield

\[ \frac{1}{2} MU^2 + \int_V \frac{1}{2} \rho u^2 dV + CPE = C + \int \Phi \, dt, \quad (2.70) \]

where \(C\) is a constant and we have introduced the term \(CPE\) which denotes the chemical potential energy of the surfactant equal to the work performed against Marangoni stresses. (2.70) states that the kinetic energy of the creature and fluid may be increased at the expense of chemical potential energy.
Chapter 3

Experiments

Imagine a vast sheet of paper on which...figures, instead of remaining fixed in their places, move freely about, on or in the surface, but without the power of rising above or sinking below it, very much like shadows.

- from Flatland: A Romance of Many Dimensions by Edwin A. Abbott (1884)

3.1 Techniques

In this section we report the results of an experimental investigation of the dynamics of insects and spiders (Figure 3-1). These arthropods were selected to represent the entire spectrum of water-walking techniques. For comparison, the limited water-walking abilities of thirty species of terrestrial insects were also examined. The water-walking arthropods were collected using aquarium nets from Fresh Pond, Massachusetts and from Halibut Point, Rockport, Massachusetts; terrestrial insects were collected from the grounds of MIT. A list of equipment used in these experiments may be found in the Appendix. Water striders could be bred in 40 gallon aquaria for several months. Insects were filmed using a digital still camera (Sony DSC-F707), a digital video camera (Sony DCR-TRV950), and a high-speed digital video camera (Redlake Motionscope PCI 8000) and the films digitized using Midas motion analysis software. Specimens were filmed at 1/1000 s exposure time at 30 to 500 frames per second. Plan views were filmed in a tank 15 cm x 15 cm x 4 cm; side views were filmed in a tank 3 cm x 20 cm x 20 cm. The insects’ leg widths were measured using a light microscope (Edmund Scientific). The subsurface flows generated by the insects
Figure 3-1: Water-walking arthropods examined in our experimental study. (a) Water striders/Pond skaters *Gerridae*, (b) Springtail *Anurida maritima*, (c) *Microvelia*, (d) Water treader *Mesovelia*, (e) Water measurer *Hydrometra stagnorum*, (f) Fisher spider *Dolomedes triton*, Scale bars, 1 mm.

were characterized by standard flow visualization techniques and recorded using high speed video. Particle tracking was performed by seeding water with either Kalliroscope *AQ-1000* (Kalliroscope) or Pliolite particles (*S-6B*, Goodyear Chemicals) ground with mortar and pestle to reduce its grain size to 50-100 µm. The subject was lit from above, and a dark background was placed beneath the tank.

Subsurface flows were also visualized using a thymol blue technique adapted from Voropayev & Afanasyev (1994). The wake was visualized using a 15 cm x 15 cm x 4 cm tank filled to a depth of 0.5-1 cm with a dilute concentration of sodium hydroxide (pH 9.2); the tank was lit from below and thymol blue sprinkled on the surface. The dye gradients can be smoothed by mixing the dye into the fluid rather than sprinkling or simply waiting for sharp dye gradients to diffuse. The thymol blue prompted Marangoni convection (Scriven & Sterling 1970) with rolls of width equal to the depth of the dye layer; the resulting surface color texture was wrapped up by the vortices generated by the driving legs of the arthropods. Vortices remain visible for several seconds after they are generated. Surface tension gradients were measured by examining the motion of either thymol blue or Lycopodium spores on the water surface.

The insects were induced to move using a variety of prodding techniques. We found that prodding with a thin wire and blowing the insect using puffs of air were effective in
encouraging it to move in a preferred direction. If the room was darkened, a beam of light would also attract the insect. Prodding using a stick or wire was effective in encouraging Microvelia to secrete surfactant and so use the Marangoni propulsion technique detailed in §6.2.

Generally, we found that high-speed filming of the insects’ dynamics required a high degree of precision. The water-walking insects are of such minute size that the focal length of the camera only allowed a narrow plane of the field of view to be in focus. The insect therefore had to be chased into the plane of focus and encouraged to move in that plane. The small size of the insects also demanded a great deal of light for illumination; their capricious nature patience. A specialized low-heat light fixture was used to reduce the insects’ discomfort.

Qualitative experiments on the arthropod’s sensitivity to surfactant were performed. We confirmed that the addition of detergent caused water striders to sink (Brinkurst 1960). We note that the addition of surfactant does not lower the surface tension sufficiently to sink an arthropod since most water-walking arthropod have a high margin of safety on the surface (see Chapter 4). Rather, the surfactant destroys the hydrophobicity of the water strider’s legs, causing the legs to wet and the strider to sink.

3.2 Observations

In this section we describe the most common gaits of water-walking arthropods. Speeds and other variables that characterize the gaits are listed in Table 3.2; these are later used to compute the relative magnitudes of the hydrodynamic force components, as presented in Table 4. We have summarized the work of previous investigators on the gaits of a number of water-walking arthropods in Table 3.2.

3.2.1 Alternating tripod and other walking techniques

The alternating tripod gait is the most common gait among insects on the water surface and is similar to that exhibited by the most terrestrial insects. It is used by water-walking insects that divide their time between land and water (e.g. Mesovelia, Microvelia, Hydrometra) and use the same gait on both surfaces. In this gait, the insect stands on alternating tripods of leg support and moves forward by driving these three legs backwards in unison (Figure 3-2).
Table 3.1: Dynamics of water-walking arthropods. $w$ and $L$ refer to the width and length of the driving leg, $P$ the total contact perimeter of the arthropod’s legs, $W$ the arthropod’s weight, $U$ and $\omega$ the peak speed and frequency of the driving stroke. These dynamical variables were used in calculations of dimensionless groups in Chapter 4.

<table>
<thead>
<tr>
<th>Mode</th>
<th>Species</th>
<th>Investigators</th>
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<tbody>
<tr>
<td>Alternating</td>
<td>Microvelia</td>
<td>Andersen (1976)</td>
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<tr>
<td>Tripod</td>
<td>Mesovelia</td>
<td>Andersen (1976)</td>
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<td></td>
<td>Hydrometra</td>
<td>Andersen (1976)</td>
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<tr>
<td></td>
<td>Anurida</td>
<td>§3.2.1</td>
</tr>
<tr>
<td>Rowing</td>
<td>Striders (Gerridae)</td>
<td>Andersen (1976), §5</td>
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<tr>
<td></td>
<td>Spiders</td>
<td>Suter et al. (1997)</td>
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<tr>
<td>Galloping</td>
<td>Spiders</td>
<td>Suter &amp; Wildman (1999)</td>
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<tr>
<td>Jumping</td>
<td>Striders</td>
<td>§3.2.4</td>
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<td></td>
<td>Spiders</td>
<td>Suter &amp; Gruenwald (2000a)</td>
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<td></td>
<td>Anurida</td>
<td>Hopkin (1997)</td>
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<tr>
<td>Marangoni propulsion</td>
<td>Microvelia</td>
<td>Andersen (1976), §6.2</td>
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<td></td>
<td>Velia</td>
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<td></td>
<td>Rove beetles (Stenus)</td>
<td>Linesenmair (1963)</td>
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<tr>
<td>Meniscus-climbing</td>
<td>Microvelia</td>
<td>Andersen (1976), Miyamoto (1955)</td>
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<tr>
<td></td>
<td>Mesovelia</td>
<td>Andersen (1976), §6.1</td>
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<td></td>
<td>Hydrometra</td>
<td>Andersen (1976), Miyamoto (1955)</td>
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<td>Anurida, Collembola</td>
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<td></td>
<td>Mites</td>
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<td></td>
<td>Stenus</td>
<td>Miyamoto (1955)</td>
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<tr>
<td></td>
<td>Pyrrhalta nymphaeae</td>
<td>§6.1</td>
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Table 3.2: Modes of walking on water. Representative insects for each mode are listed, along with the associated investigators.
Figure 3-2: The alternating tripod gait of (a) *Microvelia*, (b) *Mesovelia* and (c) *Hydrometra*. The creature is supported by three legs which it sweeps backward (direction given by arrows). Meanwhile the three remaining legs move into position to row. The result is a gait in which the creature rotates the angle of its body with every stroke. The time between photos in (a,b,c) is $\Delta t = 0.01$ s. Scale bar (a), 1 mm. Scale bar (b), 6 mm. Scale bar (c), 1 cm.
Figure 3-3: Flow visualization of the walking gait of *Hydrometra*. Each propulsive cycle leaves two rows of three vortices, as visualized using thymol blue. Scale bar, 3 mm.

When the water surface is lit from above, concave depressions in the water surface diffuse light outward, marking the shadow of the insect leg tips with dark spots. During this gait, the meniscus under each leg increases in size as the leg is driven backward. We note that the insects cannot balance torques as they walk; Figure 3-2a shows that the midline of their bodies may vary over an angle of ± 30 degrees to their mean direction of motion. Flow visualization shows that *Hydrometra* and *Mesovelia* generate two rows of dipolar vortices as they walk (Figure 3-3). We observe that *Microvelia* generates weak fluid motions but no discernible vortices.

While it is more adept at walking on rocks and cave walls, *Anurida maritima* must occasionally walk on water. Its short legs do not extend beyond its body perimeter and it walks on water on the pointed tips of its feet as it does on land. Unlike other water-walkers, its legs move backward in the same path that they move forward; as a result it is an inefficient water-walker. Only after stroking its legs hundreds of times does it move a
Figure 3-4: Flow visualization of the walking gait of Anurida. A large vortex dipole is generated in the underlying fluid. Scale bar, 3 mm.

few body lengths. Flow visualization shows that the leg motion eventually generates a flow that rolls up into a dipolar vortex beneath its body (Figure 3-4).

3.2.2 Rowing

Water striders and fisher spiders move by rowing their long legs, a gait considered by biologists (Andersen 1976) to be the most effective and highly evolved of the water-walking gaits. The water strider rows with its middle pair of legs while supporting its weight on its front and hind legs (Figure 3-5). During the driving stroke of duration 0.01 s, the middle legs are pressed downward on the surface to generate a meniscus and these menisci are then swept backward. The strider is generally sent airborne after which it lands and glides for several body lengths (Figure 3-5a). The strider can row so vigorously that it rockets into the air and lands more than ten body lengths away (Figure 3-5c). The water striders evidently generate additional thrust by rowing with its rear supporting legs (see hind legs in Figure 3-5b).
Figure 3-5: Rowing (a-b) and the escape stroke (c) of the adult water strider that launches the strider at a 45° angle from the free surface. Capillary waves are visible in its wake. The inset in the rightmost frame of c provides a close-up of the capillary waves in the water strider’s wake. Time between photos, \( \Delta t = 0.01 \) s.

Flow visualization of the strider wake reveals two salient flow structures, capillary waves and vortices. The rowing motion of the middle legs sends a train of waves rearward (Figure A-1). Landing after the stroke generates forward-moving waves that issue from the front legs (Figure A-1). Our measurements indicate that the leg stroke typically generates a wave train of three waves. From digitized frames from high speed video, we measured that the largest wave packet has amplitude \( a \approx 0.04 \pm 0.005 \) cm, wavelength \( \lambda \approx 1 \pm 0.1 \) cm, width \( d \approx 0.2 \pm 0.1 \) cm, speed \( c \approx 30 \pm 2 \) cm/s and wave number \( k = 2\pi/\lambda \approx 6 \pm 0.6 \) cm\(^{-1}\).

A video sequence of the strider’s stroke, visualized using thymol blue, shows that the water strider generates vortex dipoles with each leg stroke (Figure 3-6). Vortices entrain dyed fluid and translate backward following the strider’s driving stroke. Still photographs (Figure 3-7) using thymol blue and particle tracking (Figure 3-8) also illustrate the vortical wake of the strider. Finally we note that when the water strider lands after its rowing stroke, stopping vortices roll up next to its supporting legs (Figure 3-9).

Fisher spiders *Dolomedes* propel themselves by rowing with the first two or three pairs of their eight legs and support their weight using their remaining legs and sometimes also their underbelly (Figure 3-11a-b). Side views of the rowing stroke indicate that the leg
Figure 3-6: Frames from a video of vortex generation by a water strider, with time sequence [0 s, 0.03 s, 0.2 s, 0.8 s]. Dyed and clear fluid are separated by a nearly vertical front across which the strider strokes its driving legs. The result is a pair of dyed hemispherical dipolar vortices translating through clear fluid. Their radial and vertical extents were measured from plan and side views; their mass and velocity may be readily calculated. Scale bar, 1 cm.
Figure 3-7: Flow visualization of the rowing gait by the water strider. a, An infant water strider sends vortices backwards as it rows. Scale bar, 1 mm. b, Following a particularly vigorous driving stroke, a water strider is sent forward several body lengths. c, The water strider rows twice to generate two pairs of vortices. Scale bars (b-c), 1 cm.
Figure 3-8: Particle tracking of the wake of water striders constructed from superimposed photographs. The direction of the flows are indicated. a, Vortices in the wake of a one-day-old water strider. Fifteen photographs take 0.002 s apart are superimposed. Scale bar, 1 mm. b, Vortices in the wake of an adult water strider during a leisurely stroke. Scale bar, 1 cm.

Figure 3-9: Thymol blue flow visualization of stopping vortices rolling up around the strider’s legs following its landing. Scale bars, 1 cm.
Figure 3-10: Frames from a high speed film of an adolescent water strider. The strider generates waves with its driving legs during its propulsive stroke and subsequently with its front legs upon landing. Scale bars 2 mm.

Figure 3-11: The fisher spider propels itself with (a-b) a rowing gait at low speeds ($U < 20$ cm/s) and (c-d) a galloping gait at high speeds ($U > 30$ cm/s). When rowing, the legs are swept horizontally along the water surface. When galloping, the legs are bent at the joint and driven vertically against the fluid. The spider is lit from above in a and c; note that the surface deflection adjoining the driving leg generates shadows beneath the spider. In the side views, $\Delta t = 1/200$ s; In the top views, $\Delta t = 3/200$ s. Insets indicate the different forms of the dynamic menisci during the rowing and galloping gaits. Note that during galloping the leg tips penetrate the free surface. Scale bars, 7 mm.
Figure 3-12: The wake of the fisher spider visualized using thymol blue. The driving stroke of each leg generates a vortex. Scale bar, 6 mm.

is swept downward and backward, generating a meniscus approximately 2 mm in depth. The fisher spider rarely has an airborne phase during its rowing stroke. Flow visualization shows that the spider generates a dipolar vortex with each leg stroke (Figure 3-12). The characteristic wake of the rowing spider thus includes sets of dipolar vortices. We note that the vortices are often overlapping and hence obscured.

3.2.3 Galloping

Fisher spiders row to obtain body speeds up to 20 cm/s (Suter et al. 1997), but to attain speeds higher than 30 cm/s, they switch to a galloping gait. In rowing, the spider’s front-most three pairs of legs sequentially strike the water surface sending the spider springing forward (Figure 3-11c-d). While the legs are held out straight and swept horizontally during rowing, during galloping the legs are bent at the joints and driven vertically. Side views of the leg stroke (Figure 3-11c) indicate that the legs generate a meniscus nearly 4 mm in depth that remains intact through the first half of the driving stroke. Subsequently, as the spider increases the force applied to the meniscus, its leg tip begins to penetrate. Experiments by Suter & Wildman (1999) indicate that despite penetration, the leg tips remain covered by a plastron.

3.2.4 Leaping

A number of water-walking arthropods, including water striders, spiders and Collembola can leap off the free surface. Here we describe our observations of leaping on the water surface. We shall rationalize the peak heights of leaping by consideration of energetics.
Figure 3-13: Leaping by the water strider. a, Superimposed video frames of a water strider leaping. The downward motion of its driving legs launches the strider vertically. Upon landing, its front legs briefly penetrate the surface of the water, but contact is precluded by the persistence of a plastron around its legs. Background grid size, 0.25 cm. Time sequence of frames, \([0 \text{ s}, 0.02, 0.04, 0.06, 0.12, 0.18, 0.20, 0.22, 0.24]\). b, Schematic of a water strider leaping. The insect deforms the free surface, generating anomalous surface energy that is transformed into gravitational potential energy at the apex of the leap. c, Front view of a strider leaping. The maximum depth of the dynamic meniscus generated by the driving stroke is 3 mm. Time between video frames, \(\Delta t = 0.004 \text{ s}\). Scale bars, 1 cm.
Water striders can leap to achieve heights of ten body lengths (Figure 3-13a). To leap, the water striders simply modify their rowing stroke, driving their middle legs downward and deforming the free surface (Figure 3-13b-c). The striders land with splayed legs in order to distribute the force of impact over their bodies. We observed that upon landing, the striders may penetrate the free surface with their front legs (Figure 3-13a). Flow visualization using Kalliroscope (Figure 3-13c) indicates that the meniscus is deformed to a depth of 0.3 cm, comparable to the maximum static meniscus depth for a body supported by surface tension, \( \sqrt{\frac{2\sigma}{\rho g}} = 0.36 \) cm (Batchelor 2000), and greatly in excess of the meniscus depth beneath a stationary strider, 100 \( \mu \)m, as measured by Matsuda et al. (1985). We observed that striders leap during intense combat on the water surface. Striders will often clasp onto each others legs and leap together into the air, somersaulting and landing on their partners. We also note that the peak leap height on land is comparable to that on water.

Spiders can also leap to achieve heights of several body lengths. The spider leaps by driving its eight legs downward simultaneously (Figure 3-14a,b), deforming the free surface to depths of 0.3 cm (see inset, Figure 3-14a). Like the water strider, the spider lands on its body and splayed legs to distribute the force of impact over their bodies (Figure 3-14c).

Various semiaquatic Collembola, also known as springtails, leap using the same mechanism as their terrestrial counterparts. These Collembola have a forked tail or furcula that is folded under their abdomen and held in place by a clasp when they are at rest. When the clasp is released, the furcula swings downward and against the water surface, sending the Collembola to heights of 20 body lengths (Hopkin 1997). Wigglesworth (1950), Nutman (1941), Baudoin (1955) and Noble-Nesbitt (1963) report that certain surface-dwelling springtails have a wetting ventral tube vesical that allows them to locally raise the free surface. The springtail may sit atop the surface like a loaded spring (Figure 3-15): the vertical curvature forces acting on its head and tail balance its weight in addition to the capillary force generated by its ventral tube. The release of the free surface from the ventral tube results in an unbalanced force that propels it vertically to a height of 3 mm, a technique used to evade aquatic predators.

We can rationalize the peak jumping height of the water-walking insects using scaling arguments. In order to avoid penetrating the water surface and wetting, the arthropods cannot exceed a force per unit length \( 2\sigma \) along their legs. During lift-off, a water strider’s leg of tarsal length \( L \) applies a force \( F = 2\sigma L \) over a displacement \( L \), doing work \( 2\sigma L^2 \).
Figure 3-14: The fisher spider leaps by simultaneously driving its eight legs downward. a, Side view. The inset shows a close-up view of the deformation of the free surface by the driving leg. b-c, Top view. Four frames of a spider (b) jumping and (c) landing. Note that the spider lands primarily on both its legs and belly. Time between frames for (a-c), $\Delta t = 0.0125$ s. Scale bars, 7 mm.
Figure 3-15: The leaping mechanism of the water-walking springtail. Anurida pulls upward on the free surface with its ventral tube, and pushes downward with its nose and tail. Release of the free surface from its ventral tube results in an unbalanced force that launches it upward. a, A schematic of Anurida’s specialized leaping mechanism. b, Frames from a video of Anurida leaping. Δt = 0.03 s. c, Side view of Anurida in a resting position and in the surface-deforming position. Note the deformation underneath the ventral tube and its head and tail. d, A view from below of Anurida in a resting position and in the surface-deforming position. The inside of the collophore (wetting ventral tube) is orange when open; in the second frame, the collophore is pulling up on the free surface, as demonstrated by the light reflected off the surface deflection. Scale bars, 1 mm.

Assuming zero dissipation, this work is completely converted to gravitational potential energy $MgH$ at the apex of the leap. Therefore, the peak leap height may be written

$$H = \frac{nFL}{Mg} = \frac{n2\sigma L^2}{Mg},$$

(3.1)

where $n$ is the number of driving legs. The leap height of the strider (Figure 3-13) indicates that the strider can generate 50 dynes of force. Using similar means we can determine the force applied by a spider. In Figure 3-14, a spider of mass $M=0.1$ g leaping to a height $H = 1$ cm applies a force $F = \frac{MgH}{8L} \approx 40$ dynes. We note the force per unit length for both spiders and strider is comparable to the surface tension of water, suggesting that they are applying the maximum force possible without penetrating the surface.

The height achieved by Anurida can be determined using a similar argument. During lift-off, Anurida applies a known force $F = 2\pi R\sigma$ to the ventral tube of radius $R$, which is balanced by the force applied by the legs and head. When the ventral tube is released, the surface applies the force $F$ to the head and tail for a duration corresponding to the meniscus relaxation time, $\tau = (\rho l^2 / \sigma)^{1/2}$, imparting a momentum $MU = F\tau$ to the creature where $M$ and $U$ are the creature’s mass and take-off speed. A rough estimate for the height can
Figure 3-16: In order to escape predators, Microvelia ejects surfactant that propels it along the surface. a, A soapboat, whose wake is visualized using thymol blue dye. Scale bar, 1 cm. b, Microvelia propelling itself in a green dye field, generating a region of surfactant in its wake. Scale bar, 2 mm. c, Frames from a high-speed film of Microvelia using Marangoni propulsion. The white particles are Lycopodium spores placed on the surface; their motion indicates the surface divergence in the wake of the water-walker. $\Delta t = 1/100$ s. Scale bar, 2 mm.

be found using conservation of energy, $Mgh = \frac{1}{2}MU^2$:

$$h = \frac{2\pi^2 R^2 \sigma \rho \ell^3}{(gM^2)} \approx 2 \text{ mm.}$$

(3.2)

where $R = 0.1$ mm and $m = 10^{-3} \text{ g}$ for a 2 mm Anurida. This height is in accord with our observations.

### 3.2.5 Marangoni propulsion

While normally relying on the alternating tripod and rowing gait respectively, Microvelia (Figure 3-1c) and Velia can secrete surfactants and propel themselves by generating Marangoni stresses. The fluid mechanics of their propulsion will be considered in greater detail in Chapter 6.

Microvelia typically propels itself at 17 cm/s (approximately twice its walking speed) and leaves a surfactant trail 3 mm wide and 1 cm long as visualized with Lycopodium spores or thymol blue (Figure 3-16 and Figure 3-17). Microvelia has approximately 3 loads of surfactant available to it before it must rest to regenerate its supply. During the propulsive
Figure 3-17: Flow visualizations of Marangoni propulsion. The surface divergence caused by the ejected surfactant sweeps away the dye on the surface. As the fluid is lit from below, the surfactant-covered region appears as a light spot. There is great variation in the motion of the insect following surfactant release. a, The insect makes a $180^\circ$ turn. b, The insect follows a weakly curved trajectory. Scale bars, 2 mm.

phase, the insect braces its legs along its body, presumably to streamline it and maximize its speed (Andersen 1976). Upon releasing surfactant, the paths taken by the insect can vary greatly. Once ejected, the surfactant spreads out due to the associated Marangoni stresses: since the insect begins its propulsion from rest, it ejects a continuously decreasing flux of surfactant per unit length as it accelerates. One may thus rationalize its characteristic triangular trail of surfactant.

Linsenmair & Jander (1976) and later Andersen (1976) examined the Marangoni propulsion of *Microvelia*. Linsenmair & Jander (1976) show that an insect could not generate surfactants if its probosis was blocked, an observation suggesting that the insect’s saliva is surface-active. Certain terrestrial insects such as rove beetles *Stenus* also secrete surfactants from specialized glands on their abdomen to use as an emergency propulsion mechanism if they accidentally fall into water (Jenkins 1960, Linsenmair 1963). The chemical composition and the surface tension of *Stenus*’s surfactant was determined by Schildknecht (1976).
Figure 3-18: Frames from a video sequence of *Microvelia* escaping a surface covered with an irritant, thymol blue. To avoid contact with the irritant, *Microvelia* ejects surfactant that generates Marangoni stresses and sweeps away the dye. The insect moves forward only when the path ahead of it has been cleared of the dye. Other *Microvelia* trace the steps of their leader into the dye-free region. Scale bar, 2 mm.

Finally, we report a controlled use of surfactant by *Microvelia* to clear irritants on the free surface. Generally, *Microvelia* will not walk upon a surface covered with thymol dye unless coerced. If surrounded by a field of thymol blue, *Microvelia* progresses forward by ejecting an amount of surfactant sufficient to clear the dye, but insufficient to propel the insect. The insect thus advances through the dyed region, sweeping away the dye with surfactant before stepping forward (Figure 3-18). This leader is followed by other *Microvelia* similarly keen on avoiding the irritant.

### 3.2.6 Meniscus-climbing

Figure 3-19: The larva of *Pyrrhalta* approaching emergent vegetation using capillary propulsion. Side (a) and front (b) views illustrate the deformation of the free surface near the larva’s head and tail. Scale bars, 2 mm.

Certain water-walking and terrestrial insects are able to ascend the meniscus surrounding land or floating bodies by assuming static postures in which they deform the free surface. Capillarity was recognized as the physical basis of this lateral force by Baudoin (1955). In Chapter 6, we examine in detail the physics underlying this means of propulsion and develop a theoretical model thereof.
Figure 3-20: The larva of *Pyrrhalta* deforms the free surface in order to approach the meniscus adjoining a partially submerged wetted leaf. Scale bars, 2 mm.

Figure 3-21: Meniscus-climbing by the larva of the water lily leaf beetle *Pyrrhalta*. The beetle larva is a terrestrial insect unsuited to walking on water; nevertheless, it is able to ascend the meniscus, from left to right. It is partially wetting and so circumscribed by a contact line (a). It deforms the free surface by arching its back, thus generating the desired capillary thrust (b). (c), The beetle larva’s ascent is marked by peak speeds in excess of 10 cm/s. Scale bars, 3mm.
The water lily beetle larvae *Pyrrhalta*, a terrestrial creature, is highly wetting and a poor swimmer (Figure 3-19); however if it falls into water, it return to land using capillary propulsion. *Pyrrhalta* has a contact line around its perimeter; therefore, it may deform the surface by arching its back (Figure 3-21, Figure 3-20). If it is within several capillary lengths of the nearest emerging land, by locking into this static posture, *Pyrrhalta* is pulled landward. If *Pyrrhalta* is near a wall, it will naturally rotate by arching its back. By doing so, the larva is oriented perpendicular to the wall and pulled toward the wall so that it always abuts it tail or head first (Figure 3-22). This peculiar behavior will be rationalized in §6.2.

Figure 3-22: When the beetle deforms the free surface by arching its back near a wall, it is rotated and oriented such that it always abuts the wall tail first. Grid size, 0.625 cm.

Though generally covered in a water-repellent mat of hair, *Mesovelia*, *Microvelia* and *Hydrometra* have non-wetting leg tips that enable them to pull up on the surface. To climb...
Figure 3-24: Capillary propulsion by the water treader *Mesovelia*. a, *Mesovelia* approaches a meniscus, from right to left. The deformation of the free surface is evident near its front and hind tarsi. b, High speed video images of its ascent. Lighting from above reveals the surface deformation produced. In pulling up, the insect generates a meniscus that focuses the light into a bright spot; in pushing down, it generates a meniscus through which light is diffused, casting a dark spot. Characteristic speeds are 1-10 cm/s. Scale bars, 3 mm.

Figure 3-25: Body postures assumed during meniscus-climbing. a, *Mesovelia*. b, *Microvelia*. c, *Hydrometra*. d, *Pyrrhalta*. White and black circles indicate, respectively, upwards and downwards surface deflection.
the meniscus, these creatures will run towards it at full speed; as they slide back down they assume a characteristic posture (Figure 3-25) that draws them up the meniscus.

Previous investigators have described the characteristic postures assumed by meniscus-climbing insects (Baudoin 1955, Andersen 1976, Miyamoto 1955). The postures assumed by all such known insects are depicted in Figure 3-25 and we describe them in turn. To ascend the meniscus, *Mesovelia* (0.3-0.6 cm) extends and pulls up with its front and hind legs and pushes down with its middle legs, as shown in Figure 3-24 and Figure 3-25a. *Microvelia* (0.1-0.2 cm) assumes an asymmetric climbing posture in which it extends and pulls up with its front left leg and hind right leg, while pressing down with its remaining legs (Figure 3-25b). *Hydrometra*, described by Andersen (1976), also climbs using an asymmetric body posture in which it extends and pulls up with the front left leg and hind right leg while pushing down with the remaining legs (Figure 3-25c). As previously described, the wetting climber *Pyrrhalta* simply climbs by arching its back (Figure 3-25d).

Figure 3-26: An infant *Hydrometra* climbing the meniscus. It deforms the free surface by pushing down with its middle legs and pulling up in front and back. The adult *Hydrometra* climbs the meniscus using the posture depicted in Figure 3-25c. Scale bar, 2 mm.

Figure 3-27: *Anurida* deforms the free surface by pushing down with its head and tail and pulling up with its wetting ventral tube. Position is similar to that taken during leaping (Figure 3-15). **a**, Side view. **b**, Top view. The surface is lit from above and the surface deformations are indicated by the reflections. Scale bars in **(a-b)**, 1 mm. **c**, The self-assembly (Whitesides & Grzybowski 2002) of an *Anurida* colony on the water surface. These creatures are naturally drawn together when they assume the posture in **a** and **b**. Scale bar, 1 cm.
Figure 3-28: Two Anurida brought together by capillary attraction. In a-b, the two Anurida walk in parallel directions. In c the left Anurida assumes the arched posture. In d its partner follows suit and the two insects are brought together by capillary attraction. ∆t = 0.1 s. Scale bar, 3 mm. e, The direction of the capillary forces for several configurations of two Anurida. f, Side view of two Anurida brought together by capillary attraction. Scale bar, 1 mm.

By pulling up on the water surface with its wetting ventral tube and pushing down with its nose and tail (Figure 3-27a,b), Anurida uses capillary attraction to attract partners and so ultimately form floating colonies of twenty to fifty individuals (Figure 3-27c). When in the body posture illustrated in Figure 3-27ab, normally slow-moving anurida are attracted to one another on the water surface. When two Anurida approach end-to-end, the attractive forces are so strong that they must exert extreme effort to separate (Figure 3-28).

In this chapter we have reported several distinct styles of propulsion that we will rationalize using the theoretical framework presented in Chapter 2. Water-walking insects have developed numerous adaptations for coping with the special constraints presented by the water surface. One adaptation is that the creatures use their wetting properties to their advantage, for either attracting or repelling the fluid. Our experimental study has demonstrated clearly that water-walkers have developed various gaits, some analogous to those of terrestrial creatures (such as leaping and galloping), others with no terrestrial counterpart. In the following chapter, we compare quantitatively the modes of locomotion by insects to those of large water walkers.
Chapter 4

Dynamic classification

*If one morning I walked on top of the water across the Potomac River, the headline that afternoon would read “President Can’t Swim.”*

–Lyndon B. Johnson (1908 - 1973)

Our experimental investigation in Chapter 3 illustrated the numerous gaits available to water-walking arthropods. In this chapter, we classify water-walkers according the relative magnitudes of the components of the hydrodynamic force that they generate. This approach has been used previously for aquatic animals (e.g. for shrimp by Daniel & Meyhöffer 1989), but has yet to be applied to locomotion at the free surface.

The total force on the leg of a water walker was given in (2.4) as the sum of the hydrodynamic and surface tension force,

\[ F = F_h + F_s = \int_{s} T \cdot n \, dS + \int_{s} \sigma(\nabla \cdot n) \, ndS - \int_{s} \nabla \sigma dS \]  \hspace{1cm} (4.1)

where we have again used Stoke’s theorem (2.12) to write the surface tension force as the sum of components due to curvature and Marangoni stresses. As we saw in (2.8) the
approximate magnitudes of these terms, in addition to the viscous force, may be evaluated in terms of the characteristic leg speed $U$, area $A$ and width $w$ of the body in contact with the fluid, the characteristic cavity volume $V_d$ and the mean leg depth $h$ below the unperturbed surface height:

$$|F| \sim \rho U^2 A + \rho gh A + \rho V_d \frac{dU}{dt} + \mu U A + \frac{1}{w} A - \nabla \sigma A$$ (4.2)

form drag buoyancy added mass viscosity curvature Marangoni

where we assume that the local curvature of the meniscus at the area of contact corresponds to the leg width $w$. As we’ve seen in §2.2.3, if the body strikes the surface asymmetrically, it may utilize the hydrostatic pressure for lateral propulsion. The added mass force arises from the requirement that fluid be accelerated around an accelerating body; the body’s apparent mass increases accordingly (Daniel 1984). The curvature forces are important for water-walking insects: the generation of fore-aft asymmetry in the meniscus of their driving legs plays a critical role in their propulsion (Brocher 1910). Finally, the generation of Marangoni stresses through the release of surface-active fluid is used as an emergency propulsion mechanism by a number of insects (§3.2.5, §6.2). A characteristic viscous force is included for the sake of completeness.

Consider the driving leg of a water-walking creature striking the free surface with frequency $f$ (Figure 2-3). As we saw in §2.3, the relative magnitudes of the six forces enumerated in Equation (4.2) are prescribed by five dimensionless groups, the Reynolds $Re$, Weber $We$, Bond $Bo$, Strouhal $St$ and Marangoni $Ma$ numbers, defined, respectively, by

$$Re = \frac{U w}{\nu} = \frac{\text{inertia}}{\text{viscous}} \quad We = \frac{\rho U^2 w}{\sigma} = \frac{\text{inertia}}{\text{curvature}} \quad Bo = \frac{\rho gh^2}{\sigma/w} = \frac{\text{buoyancy}}{\text{curvature}}$$

$$St = \frac{f w}{U} = \frac{\text{added mass}}{\text{inertia}} \quad Ma = \frac{\nabla \sigma}{\sigma/w} = \frac{\text{Marangoni}}{\text{curvature}}$$

We also introduce the group describing the aspect ratio of the leg of length $L$ and width $w$, $\lambda = w/L$. We determined the values of the numbers above using our experimental measurements and those from the literature and present them in Table 4.1. Assessment of the magnitudes of these dimensionless groups indicates that the great majority of water-walkers depend principally on some combination of curvature forces and form drag for their forward propulsion. For water-walkers, the treatment of added mass is complicated by the
Table 4.1: Values of dimensionless groups characterizing walking on water. The fisher spider data was kindly provided by Suter et al. 1997.

<table>
<thead>
<tr>
<th>Species</th>
<th>$\lambda$</th>
<th>$Re$</th>
<th>$Bo$</th>
<th>$We$</th>
<th>$St$</th>
<th>$Ba$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Strider</td>
<td>0.02</td>
<td>$8 \cdot 10^2$</td>
<td>$9 \cdot 10^{-3}$</td>
<td>$2 \cdot 10^{-3}$</td>
<td>$1 \cdot 10^{-2}$</td>
<td>$3 \cdot 10^{-2}$</td>
</tr>
<tr>
<td>Mesovelia</td>
<td>0.05</td>
<td>2.3</td>
<td>$1.6 \cdot 10^{-5}$</td>
<td>$2.2 \cdot 10^{-3}$</td>
<td>$2.7 \cdot 10^{-2}$</td>
<td>$1.1 \cdot 10^{-2}$</td>
</tr>
<tr>
<td>Microvelia</td>
<td>0.37</td>
<td>$2.5 \cdot 10^1$</td>
<td>$5.7 \cdot 10^{-6}$</td>
<td>$4.3 \cdot 10^{-1}$</td>
<td>$6.6 \cdot 10^{-2}$</td>
<td>$7.7 \cdot 10^{-4}$</td>
</tr>
<tr>
<td>Hydrometra</td>
<td>0.032</td>
<td>6.1</td>
<td>$1.2 \cdot 10^{-4}$</td>
<td>$2 \cdot 10^{-3}$</td>
<td>$2.9 \cdot 10^{-2}$</td>
<td>$3.7 \cdot 10^{-4}$</td>
</tr>
<tr>
<td>Anurida</td>
<td>0.17</td>
<td>1.7</td>
<td>$5.4 \cdot 10^{-6}$</td>
<td>$2.1 \cdot 10^{-3}$</td>
<td>$6.7 \cdot 10^{-2}$</td>
<td>$1.3 \cdot 10^{-1}$</td>
</tr>
<tr>
<td>Fisher spider</td>
<td>0.12</td>
<td>$2.6 \cdot 10^2$</td>
<td>$7.7 \cdot 10^{-3}$</td>
<td>1.3</td>
<td>$3.8 \cdot 10^{-2}$</td>
<td>$9.2 \cdot 10^{-2}$</td>
</tr>
<tr>
<td>Basilisk lizard (adult)</td>
<td>0.5</td>
<td>$1.5 \cdot 10^3$</td>
<td>$4.8 \cdot 10^2$</td>
<td>$8 \cdot 10^3$</td>
<td>$0.12$</td>
<td>$1 \cdot 10^2$</td>
</tr>
<tr>
<td>Clark's Grebe</td>
<td>0.3</td>
<td>$4 \cdot 10^4$</td>
<td>$3 \cdot 10^2$</td>
<td>$1 \cdot 10^3$</td>
<td>$0.23$</td>
<td>$1 \cdot 10^4$</td>
</tr>
</tbody>
</table>

The fact that the driving leg is often accompanied by a volume of air, either a meniscus for water-walking insects or an air cavity for larger creatures. While the resulting added mass may also provide a significant source of thrust for large water-walkers ($0.1 < St < 1$), it is negligible for water-walking insects ($0.01 < St < 0.1$).

Figure 4-1 illustrates the dependence of the Bond number on the Weber number for all water-walking creatures for which data was available. Note that there is a natural division at $Bo = 1$. Small creatures, specifically insects, for which $Bo \ll 1$ rely on surface tension for weight support (see §2.3.1, (2.9)). Their leg speeds are generally characterized by $We < 1$; consequently, their driving legs do not penetrate the free surface, as verified in our experiments in §3. The only insect for which $We > 1$ is the fisher spider in its high-speed galloping mode (Suter & Wildman 1999; see §3.2). Larger creatures, for which $Bo > 1$, rely on surface tension for neither weight support nor forward propulsion: their large Weber numbers indicate that their peak leg speeds are unconstrained by surface tension (2.9).

Figure 4-2 illustrates the dependence of the Reynolds number on the Weber number, and illustrates that $0.1 > Re > 10^5$ for all the water-walkers examined: the principal hydrodynamic force acting on the driving legs of water-walkers is inertial rather than viscous. Finally, we note the dependence of the dimensionless groups $Bo \sim We$, $Re \sim We^{3/4}$ evident in Figures 4 and 5, which may be rationalized if the leg speed depends on the leg width as $U \sim w^{1/2}$. Provided $w \sim L$, these relations are consistent with Froude’s Law of Equivalence of Velocities (Thompson 1961), that relates body speed to body length, $U \sim L^{1/2}$, and is known to be valid for birds and fish. We thus surmise that Froude’s Law is also valid for water-walking creatures, presumably as they evolved from terrestrials.
Figure 4-1: The Bond $Bo = \rho gw^2/\sigma$ and Weber $We = \rho U^2 w/\sigma$ numbers for water-walkers. Water-walking creatures small relative to the capillary length ($Bo < 1$) are supported by surface tension. Maintenance of the menisci on their driving legs requires that $We < 1$, a criterion satisfied by all water-walking insects apart from the galloping fisher spider (§3.2.3). Large water-walkers ($Bo \gg 1$) are unconcerned with the effects of surface tension. Note the dependence of the best fit line: $Bo \sim We$. A number of terrestrials capable of walking on water are included. Data for leg width $w$ and speed $U$ collected from: (1) §5.4, (2) Suter et al. (1997), (3) Suter & Wildman (1999), (4) Suter & Gruenwald (2000a), (5) Nuechterlein & Storer (1982), (6) Aigeldinger & Fish (1995), (7) Livezey & Humphrey (1983), Glasheen & McMahon (1996b), and F. Hacket (personal communication).
Figure 4-2: Reynolds $Re = Uw/\nu$ and Weber $We = \rho U^2 w/\sigma$ numbers for all water-walkers. Note the absence of low $Re$ water-walkers, and the observed dependence of the best fit line: $Re \sim We^{2/3}$. The sources for the data are listed in the caption for Figure 4-1.

We take a brief diversion to rationalize Froude’s Law for swimmers, fliers and water-walkers. Froude’s law has been rationalized for fish and birds (Schmidt-Nielsen 1984). While gliding, a bird can attain a lift $F_L \sim \rho U^2 L^2$, where $\rho U^2$ is the dynamic pressure and $L^2$ the wing area; the bird’s weight scales as $L^3$. The vertical force balance requires $U \sim L^{1/2}$, a fact validated by experimental measurements on flying birds (Greenwalt 1975, McMahon & Bonner 1985). Froude’s law is shown for fish by considering a horizontal force balance Bainbridge (1961). The metabolic power $P$ supplied by the fish scales as the weight of its muscles, $P \sim L^3$. For fish generating laminar flow, the metabolic power is dissipated by the rate of working $P_s$ by skin friction on the surface area of the body, $P_s \sim U^3 L^2 Re^{-1/2} \sim U^{5/2} L^{3/2}$. Equating, $P = P_s$ in the horizontal force balance yields $U \sim L^{3/5}$. For the case of a fish swimming sufficiently fast to generate turbulent flow, the power use $P_{sturb}$ by skin friction is given by $P_{sturb} \sim U^3 L^2 Re^{-1/5} \sim U^{14/5} L^{9/5}$; the horizontal force balance now gives $U \sim L^{3/7}$. Later investigations assumed the average of these two scalings, that is $U \sim L^{1/2}$.
Chapter 5

Locomotion of the water strider

“How precisely [infant water striders] manage to propel themselves across the water surface remains a mystery.”


Water striders Gerridae are common water-walking insects of characteristic length 1 cm and weight 10 dynes that reside on the surface of ponds, rivers, and the open ocean (Figure 5-1; Andersen 1976). As we saw in chapters 2 and 3, their weight is supported by the surface tension force generated by curvature of the free surface, and they propel themselves by driving their central pair of hydrophobic legs in a sculling motion. As detailed in §1.1, the body and legs of the water strider are covered by thousands of hairs that render it effectively non-wetting (Andersen 1976). During their rowing stroke, water striders drive their middle legs against the water without penetrating the surface and may achieve peak speeds of 150 cm/s (Andersen 1976). The striders may launch themselves with a vertical component, or glide along the surface (Figure 3-5).

Previous investigators have assumed that the hydrodynamic propulsion of the water strider relies on momentum transfer by surface waves (Andersen 1976, Denny 1993, Suter et al. 1997, Sun & Keller 2001). This assumption leads to Denny’s paradox, the statement that infant water striders cannot move (Denny 1993, Suter et al. 1997). In this chapter, this paradox is resolved through reporting the results of high-speed video and particle-tracking studies. In §5.1, we describe the assumptions leading to Denny’s Paradox. In §5.2 we examine the water strider’s static weight support via curvature forces (as examined for other water-walking insects in §2.2) In §5.3 we quantify the momentum transfer by the
water strider based on the flow visualization and particle tracking techniques described in Chapter 3. In §5.4, we report a self-contained mechanical water strider whose means of propulsion is analogous to that of its natural counterpart.

Figure 5-1: An adult water strider *Gerris remigis*. Note the deformation of the free surface; the associated surface tension force supports the weight of the strider.

### 5.1 Denny’s Paradox

Denny’s Paradox is the conclusion that infant water striders cannot move. The paradox was quite reasonably generalized by Suter *et al.* (1997) to the following form, “small or slow-moving surface dwelling arthropods should not be able to propel themselves horizontally.”

The three assumptions underlying the original Denny’s Paradox are

1) the hydrodynamic force acting on the water strider relies exclusively on capillary waves generated by its driving legs.

2) in order to generate capillary waves, the strider leg speed must exceed the minimum wave speed, \( c_m \sim 23 \text{ cm/s} \).

3) the infant water strider’s leg speed does not exceed \( c_m \).

As we shall demonstrate in what follows, each of these assumptions is incorrect. Assumption 1 is predicated on the assumption that the only force resisting the leg motion of the water strider is wave drag. When bodies move at a free surface, they may generate a field of waves that transport energy away from the body; the ratio of the associated power lost to body speed is defined as the wave drag. The presumed necessity of wave drag likely arose because the only visible manifestation of water strider motion is the field of capillary waves in their wake (e.g., Figure A-1). The shortcomings of Assumption 1 reveal that one may readily resolve Denny’s Paradox simply by identifying a hydrodynamic force.
other than wave drag that acts on the insect’s driving leg. In Chapter 4, we showed that the dominant force acting upon the driving leg of the water strider was curvature, resulting from distortion of the free surface.

Classical potential flow theory (Lighthill 1978) indicates that steady surface waves satisfy a dispersion relation between wave speed $c$ and wavelength $\lambda = 2\pi/k$:

$$c^2 = \frac{g}{k} + \frac{\sigma k}{\rho}$$

(5.1)

This dispersion relation shows that waves have a minimum speed, $c_m = \left(\frac{4\rho g}{\sigma \rho}\right)^{1/4} = 23$ cm/s (Lamb 1932, Kundu 1990); therefore, objects moving steadily at a free surface can only generate waves if their speed exceeds $c_m$. Assumption 2 is thus strictly true only for steady motions and so is not applicable to the unsteady motion of the strider’s driving leg. Bodies moving at steady and unsteady speeds $u < c_{min} = 23$ cm/s can produce waves. Vanden-Broeck showed numerically that a body moving at steady speed $u < c_{min}$ can produce a solitary wave packet with decaying tails (Vanden-Broeck & Dias 1992, Dias et al. 1996). An object floating on a free surface and bobbing up and down with a vertical speed $U \cos \omega t$ with $U < c_m$ may create a wave field (Taneda 1991). The most relevant example is that of infant water striders, that are observed in our study to generate both waves and vortices even with driving leg speeds $u < c_m$.

Assumption 3 is also incorrect. Our experiments from Chapter 3 indicate that infant water striders’ driving leg tip speeds are comparable to 23 cm/s (with peak leg tip speeds for infants observed up to 28 cm/s).

While simply and elegantly stated, Denny’s paradox does not stand up to careful scrutiny. Water-walking insects need only call upon curvature or hydrodynamic forces other than wave drag in order to move. One may thus readily resolve Denny’s Paradox without elucidating how water-walkers propel themselves along the surface. Questions suggested by Denny’s Paradox are ‘how do water striders move’ or ‘what is the dominant hydrodynamic force acting on their driving leg?’ In Chapter 4 we have found that the motion of water striders are characterized by low Weber, high Reynolds and low Bond number: they move by generating curvature forces with their driving leg using the free surface much like a trampoline.
5.2 Statics

Figure 5-2: The relation between maximum curvature force $F_s = \sigma P$ and body weight $F_g = Mg$ for 342 species of water striders. $\sigma$ is the surface tension of either pond water (67 dynes/cm) or sea water (74 dynes/cm; White 1994) at 14°C and $P = 4(L_1 + L_2 + L_3)$ is the combined lengths of the tarsal segments (see insert). Anatomical measurements were compiled from existing data (Andersen 1982, Hungerford 1919, Henry & Froeschner 1998, Tseng & Rowe 1999, Cobben 1960). Open symbols denote striders observed in our laboratory. The solid line represents $Ba = 1$, the minimum requirement for static stability on the surface. Characteristic error bars are shown.

The force balance on a stationary water strider may be understood in terms of the statics of floating, non-wetting bodies which we examined in the context of water-walking insects in §2.3 (Keller 1998). The weight $W$ of a stationary water strider is supported by some combination of the buoyancy force, $F_b$, and the curvature force, $F_c$, associated with the surface tension $\sigma$: $W = F_b + F_c$ (written previously in Equation (2.10)). Keller (1998) demonstrated that the ratio of $F_b$ is $F_c$ is equal to that of the fluid volumes displaced inside and outside the contact line. For a long, thin body such as a water strider leg, this ratio is
thus $F_b/F_c \sim w/L_c$, where $w$ is the strider leg diameter, $L_c = (\frac{\sigma}{\rho g})^{1/2} \sim 2$ mm the capillary length, and $\rho$ the density of water. The appropriate value for $w \sim 80 \mu m$ (measured in Chapter 2) indicates that $F_b/F_c \ll 1$: the strider’s weight is supported almost exclusively by surface tension.

Figure 5-2 illustrates the dependence of the maximum surface tension force on body weight for 342 species of water striders. Here, $F_g = Mg$ where $g$ is the gravitational acceleration, $M = \rho_s V$ the body mass, $V$ the insect volume and $\rho_s = 1.2$ g/cc the insect density. The maximum curvature force is defined by $F_s = 2\sigma P$ where $\sigma$ is the surface tension of either pond water (67 dynes/cm) or sea water (White 1994; 74 dynes/cm) at $14^\circ C$ and $P = 2(L_1 + L_2 + L_3)$ is the combined lengths of the tarsal segments (see insert, Figure 5-2). The surface tension force is more than adequate to support the water strider’s weight; however, the margin of safety, given by the Baudoin number $Ba = F_g/F_s$ increases with increasing body size. If the proportions of the water strider were independent of its characteristic size $L$, one would expect $P \sim L$ and hence $F_s \sim L$, and $F_g \sim L^3$: isometry would thus suggest $F_s \sim F_g^{1/3}$, a relation indicated by the dash-dot line. The best fit to the data is given by $F_s = 48 F_g^{0.58}$ (dashed line). The observed dependence illustrates that as the striders increase in size, their legs become proportionately longer. It is only thus that the largest water strider (corresponding to the rightmost point in Figure 5-2, Gigantometra gigas (Tseng & Rowe 1999), whose length may exceed 20 cm, is a viable water-walker. The giant water strider, with a margin of safety $Ba = 0.5$, can just barely support the weight of another strider, and so mate on the free surface (Figure 5-3).

![Figure 5-3: Two water striders mating on the water surface. The larger female water supports the weight of the male.](image-url)
5.3 Dynamics and Momentum transfer

A series of laboratory experiments were conducted in order to elucidate the hydrodynamic propulsion mechanism of the water strider *Gerris remigis*. Water striders were collected from local freshwater ponds and maintained in aquaria. The striders reproduced every several weeks, providing the opportunity to study the first-instar nymph water striders in a laboratory setting. The striders were filmed using a high-speed video camera at 500 frames per second and the images were digitized and analyzed using Midas motion analysis software. Particle tracking was performed by seeding water with either 5% by volume Kalliroscope or Pliolite particles of characteristic size 50-200 µm. Dye studies were performed using food coloring and Thymol Blue. Images of the wave and vortex fields were obtained from both plan and side views. The surface signature of the capillary waves was measured with a technique adopted from Schooley (1958).

The Reynolds number characterizing the adult leg stroke is \( Re = \frac{UL_2}{\nu} \sim 10^3 \), where \( L_2 \sim 0.3 \text{ cm} \) is the length of the rowing leg’s tarsal segment in contact with the water (see Figure 5-2) and \( U \sim 100 \text{ cm/s} \) is the peak leg speed. For the 0.01 s duration of the stroke, the driving legs apply a total force \( F \sim 50 \text{ dynes} \), the magnitude of which was deduced independently by measuring the striders’ acceleration and their leaping height (§3.2.4). A substantially greater applied force would lead to the strider breaking through the free surface. The water strider is thus ideally tuned to life at the water surface: it applies as great a force as possible without jeopardizing its status as a water-walker.

![Figure 5-4: A schematic illustration of the flow structures generated by the driving stroke: capillary waves and subsurface hemispherical vortices.](image)

The propulsion of water striders is detailed in Chapter 3 and sketched schematically in Figure 5-4. Video sequences (Figure 3-6) show that water striders swings their legs, driving...
Figure 5-5: Flow visualization of the water strider’s rowing gait. **a**, Five strokes by the water strider generates a neat column of vortex pairs. **b**, The ambient texture results from Marangoni convection in the suspending fluid prompted by thymol blue on its surface. The starburst pattern results from the chunk of thymol blue evident at its centre reducing the local surface tension, thus driving surface divergence that sweeps away the dyed surface layer. The fluid is illuminated from below; consequently, the light-seeking water strider is drawn to the starbursts. Scale bars, 1 cm.
their feet along a circular arc through the fluid to generate a vortex. This vortex spins up a smaller partner vortex and the dipole translates backwards as the water strider lifts its legs from the water. Particle tracking (Figure 3-8) reveals that water striders transfers momentum to the fluid through dipolar vortices shed by its rowing legs. Dye studies also indicate the wake is marked by dipole pairs (Chapter 3; Figure 5-5) that translate backwards at a characteristic speed $V_v = 4 \text{ cm/s}$. A strider of mass $M \sim 0.01 \text{ g}$ achieves a characteristic speed $U \sim 100 \text{ cm/s}$ and so has a momentum $P = MU \sim 1 \text{ g cm/s}$. By integrating (2.57) with respect to time, the momentum of the water strider is equal to the momentum of the fluid in its wake.

$$MU = - \int V \rho u dV. \quad (5.2)$$

Note that this equation holds immediately after the stroke before viscous dissipative effects become important (i.e. before an elapsed time $\tau = L^2/\nu \approx 1 \text{ s}$ where $L = 1 \text{ mm}$). Our flow visualization shows that the momentum in the fluid is in the form of vortices and waves and so

$$MU = P_w + P_v \quad (5.3)$$

where $P_w$ is the momentum in the waves and $P_v$ is the momentum in the vortices. The characteristic radius of the roughly hemispherical vortices is 0.4 cm, and the total momentum in the pair of dipolar vortices of mass $M_v$ is thus $P_v = 2M_vV_v \sim 1 \text{ g cm/s}$, and so comparable to that of the strider. The contribution of the capillary wave packet to the momentum transfer may also be calculated. The time-averaged horizontal momentum associated with a single wavelength is shown in the Appendix A to be

$$P_{w'} = \pi k a^2 W/c \approx 0.02 \pm 0.01. \quad (5.4)$$

where the wavenumber $k$, wavespeed $c$, wave amplitude $a$, wave width $W$ were measured from our high speed video experiments in §3.2.2. Since the strider generates two packets of three wavelengths, the total wave momentum is $P_w = 6P_{w'} = 0.12 \text{ g cm/s}$. Therefore the waves generate a momentum an order of magnitude less that of the strider. The momentum transported by vortices in the wake of the water strider is comparable to that of the strider, and greatly in excess of that transported in the capillary wave field; moreover, the striders are capable of propeling themselves without generating discernible capillary waves. We thus
conclude that capillary waves do not play an essential role in the propulsion of _Gerridae_, and thereby circumvent Denny’s paradox.

### 5.4 The design and construction of a mechanical water strider

The water strider strikes the free surface with its central pair of legs in a rowing motion, thus deforming the free surface and so generating curvature forces that propel it forward (Andersen 1976; Figure 5-6a-c). The strider generally propels itself by either gliding along (Figure 5-6a) or leaping across (Figure 5-6b) the free surface. We here detail the design and fabrication of a self-contained device (Figure 5-7a) that uses the same propulsion mechanism as the water strider. We here enumerate the static and dynamic constraints that guided our design, and detail the manner in which we achieved dynamic similarity between the device and its natural counterpart.

![Figure 5-6: The motion of water striders (a infant, b adult, c adult, plan view), recorded on high speed film at 500 frames/second. a infant: time sequence [0 s 0.032 s, 0.064 s, 0.096 s], body length 1 mm. b adult, side view: time sequence [0 s, 0.04 s, 0.056 s, 0.082 s], body length 8 mm. c adult, plan view: time sequence [0 s, 0.01 s, 0.02 s, 0.03 s], body length 8 mm. d plan view of Robostrider rowing for five strokes: time sequence [0 s, 0.1 s, 0.2 s, 1.3 s], body length 9 cm.](image)
Robostrider was designed subject to constraints that render it analogous to its natural counterpart. First, in order for it to reside at rest on the surface, it had to be sufficiently light that its weight $Mg$ could be supported by curvature forces: $Ba = \frac{Mg}{\sigma P} < 1$, where $P$ is its contact perimeter and $\sigma$ the surface tension of water. We note that both Robostrider and the water strider are more dense than water; therefore, they cannot rely exclusively on buoyancy forces for weight support. The non-wetting character of the Robostrider’s driving legs was achieved by using stainless steel wire with a hydrophobic coating. Finally, we required that Robostrider have body proportions similar to that of its natural counterpart. Robostrider was built by Brian Chan, an undergraduate student from MIT (Chan 2002).

We also sought to achieve dynamic similarity between the Robostrider and water strider. We consider the driving leg as a cylinder of radius $w$ and length $L$ striking the free surface with a peak speed $U$ and rowing frequency $\omega$ (as considered in Figure 2-3). Buckingham’s Theorem (McMahon & Bonner 1985) indicates that the system is uniquely prescribed in terms of five dimensionless groups: the aspect ratio $\lambda = \frac{w}{L}$, the Reynolds number $Re = \frac{Uw}{\nu}$, the Bond number $Bo = \frac{\rho gw^2}{\sigma}$, the Weber number $We = \frac{\rho U^2 w}{\sigma}$, the Strouhal number $St = \frac{U}{(w\omega)}$, where $\nu$ and $\rho$ are the viscosity and density of water. Note that, if, instead of prescribing a speed $U$, we prescribe a force per unit length $F$ applied by the
driving leg, we would obtain the dimensionless group \( An = F/(2\sigma) \) which we shall refer to as the Andersen number. The maintenance of the meniscus adjoining the driving leg requires that \( We < 1 \) (Suter et al. 1997; Chapter 4): avoiding penetration of the surface requires that \( An < 1 \).

Figure 5-8: Schematics of the mechanical strider, top and side views. Insets detail top and side views of the pulley and elastic driving mechanism. All dimensions are in cm.

Robostrider is a self-contained device capable of being supported by the surface tension of water and rowing without breaking through the water surface (Figure 5-6c). The machine weighs 0.35 grams and measures 13 cm from leg tip to leg tip, making it comparable in size to the Giant Vietnamese water strider (Tseng & Rowe 1999). A design schematic is shown in Figure 5-8. Robostrider has an aluminum body frame and six legs made of hydrophobic 0.2-mm gauge stainless steel wire. Robostrider’s front and back legs support the device’s weight on the water surface and its middle legs are capable of rotating so that the leg tips strike the surface in a sculling motion. The middle legs are fit through the axis of a nylon pulley (radius \( R_1 = 0.09 \) cm), around which is wound a 9 cm elastic band (elastic modulus \( k = 3100 \) dynes per unit strain) anchored to the rear end of the body. The tension of the elastic band causes the pulley to unwind when released, driving the rowing leg tips in a circular motion of radius \( R_2 = 1 \) cm. The total force applied by Robostrider’s legs is 
\[
2F = F_e R_1/R_2
\]
where the force \( F_e \) provided by the elastic band is given by Hooke’s law, 
\[
F_e = k \Delta x/\Delta x_0
\]
where the maximum strain \( \Delta x/\Delta x_0 = 1.5 \). The maximum distance travelled with a fully wound pulley was 20 cm, or five leg strokes. High speed film shot at 500 frames per second (Figure 5-6c) indicate that Robostrider propelled itself with leg tips speeds of \( U = 20 \) cm/s without breaking the water surface. Flow visualization using thymol blue
Table 5.1: Physical parameters describing the geometry and dynamics of the adult water strider and Robostrider

<table>
<thead>
<tr>
<th></th>
<th>$w$ (cm)</th>
<th>$L$ (cm)</th>
<th>$W$ (dyn)</th>
<th>$U$ (cm/s)</th>
<th>$\omega$ (1/s)</th>
<th>$P$ (cm)</th>
<th>$F$ (dyn/cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water strider</td>
<td>0.012</td>
<td>0.58</td>
<td>4.5</td>
<td>27</td>
<td>100</td>
<td>2.2</td>
<td>60</td>
</tr>
<tr>
<td>Robostrider</td>
<td>0.018</td>
<td>4.3</td>
<td>350</td>
<td>18</td>
<td>60</td>
<td>56</td>
<td>49</td>
</tr>
</tbody>
</table>

Table 5.2: Dimensionless groups characterizing the statics and dynamics of Robostrider and its natural counterpart.

<table>
<thead>
<tr>
<th></th>
<th>$\lambda$</th>
<th>$Re$</th>
<th>$Bo$</th>
<th>$We$</th>
<th>$St$</th>
<th>$An$</th>
<th>$Ba$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water strider</td>
<td>0.02</td>
<td>$8 \cdot 10^2$</td>
<td>0.05</td>
<td>$2 \cdot 10^{-3}$</td>
<td>22</td>
<td>0.4</td>
<td>0.03</td>
</tr>
<tr>
<td>Robostrider</td>
<td>0.004</td>
<td>$4 \cdot 10^4$</td>
<td>0.04</td>
<td>$4 \cdot 10^{-5}$</td>
<td>55</td>
<td>0.4</td>
<td>0.8</td>
</tr>
</tbody>
</table>

showed that Robostrider generates a wake containing vortices, similar in form to that of water striders (Figure 5-6b).

The physical parameters and dimensionless groups characterizing the dynamics of the mechanical and natural water striders are summarized in Tables 5.4 and 5.4. The total force $2F$ applied by the adult water strider of mass $M$ was calculated from its acceleration $\frac{dU}{dT}$: $2F = M \frac{dU}{dT}$, and from its maximum leap height $H$: $2F = MgH/L$, where $L$ is the contact length of the middle leg.

The construction of scaled-up dynamically similar models has been used with success to study the motion of fish (Triantafyllou et al. 2000) and flies (Dickinson et al. 1999). We have presented the first design for a water-walking device that relies on surface tension for weight support, and successfully propels itself without penetrating the free surface. Its propulsion is shown to be dynamically similar to that of the natural water strider. We find that Robostrider demonstrates the feasibility of a water-walking machine and several improvements are readily envisaged. Parris Wellman, a graduate student in robotics at Harvard in 1996, built a mechanical water-runner mimicking the basilisk lizard from a Coke-can body and two cylindrical “feet” that rotate like paddle wheels. Actuation of the driving legs with shape memory alloys (e.g. ‘muscle wires’) that contract upon heating is one means of improving maneuverability. However, these actuators would require a lightweight battery as a power source rather than the current elastic storage mechanism. The next generation of water-walking machines, currently being built by Sitti (2005) and Brasso and coworkers.
will be relatively sophisticated devices equipped with a solar panel, remote control, micro-actuators, and non-wetting nanomaterials (Gao & Jiang 2004).

5.5 Discussion

Our experiments (Chapter 3) show that many water-walkers (e.g. spiders, Mesovelia, Hydrometra) generate both surface waves and vortices in their wake. As we saw in Equation (2.35) from Chapter 2, the type of momentum and energy transfer is highly dependent on the size of the creature. The type of momentum transfer is determined by the Weber number, which prescribes the relative magnitude of the inertia forces to curvature force. Creatures with high Weber number transfer energy into the kinetic energy of the fluid (Equation (2.51)). To them, surface tension is negligible; therefore at high Reynolds number (over time scales over which dissipation is negligible), the momentum of the fluid is equal to the momentum of the creatures.

Figure 5-9: The trajectory of vortices in the wake of the water strider. The solid line represents the trajectory predicted by a model by Afanasyev & Korabel (2004).

The propagation of vortex dipoles has been studied outside the context of water striders. Cantwell (1986) found using theory that 2/3 of the applied impulse ends up in the
momentum of the fluid; the remaining $1/3$ is removed by a pressure field acting at $\infty$. The partition of the momentum in vortices and waves is currently being considered numerically by Buhler (2006). Afanasyev & Korabel (2004) showed that an impulsive force generates dipolar vortices that travel \( L(t) \sim t^{1/4} \). Figure 5-9 shows the trajectory of vortices versus this theoretically predicted trajectory. We find the vortices do not propagate as the rate predicted. One reason for this discrepancy may be due to the differences in the physical picture. Afanasyev & Korabel (2004)’s theory describes the motion of a single dipolar vortex, which travels in a straight line. The vortices shed by water striders appear in pairs (Figure 3-6); their interaction causes them to propagate on a curved trajectory as shown in Figure 3-6. More work must be done to rationalize the motion of the vortices generated by water striders.

In this chapter we hope to have communicated the value of examining the momentum transfer to rationalize the propulsion of water-walkers. From our experiments in Chapter 2, we noted that vortical momentum transfer was observed in both acceleration and deceleration of spiders, striders, and insects that propel themselves using the alternating tripod gait. Future work should examine the momentum transfer for leaping and other gaits not considered in this study. For example, it remains unclear whether leaping striders shed downward-propagating vortices.

Figure 5-10: The vortical wakes of a water strider (a), visualized using thymol blue, and a rowboat (b).

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Chapter 6

Quasi-static propulsion

“Nature will bear the closest inspection. She invites us to lay our eye level with her smallest leaf, and take an insect view of its plain.”

- Henry David Thoreau, Journal, 22 October 1839

In the experiments reported in §3.2.5 and §3.2.6, we observed two distinct forms of quasi-static locomotion: meniscus-climbing and Marangoni propulsion. In §2.3, we found that in the limit of small Weber number and small Bond number, the hydrodynamic force on the body is dominated by the surface force, which may contain components due to curvature and Marangoni stresses,

\[ F_H = \int_S \sigma (\nabla \cdot \mathbf{n}) \mathbf{n} dS - \int_S \nabla \sigma dS \] (6.1)

where \( C \) is the contact line on the body and \( \mathbf{n} \) is the normal to the surface. In this chapter we rationalize in turn meniscus-climbing and Marangoni propulsion.

6.1 Meniscus climbing

In order to reach land, as is required to lay eggs and escape predators, a water-walking insect must first surmount the concave fluid menisci that border the water’s edge. The ability to climb menisci was a necessary adaptation for ancestral water-walkers as they evolved to live exclusively on the water surface (Andersen 1976). Fisher spiders and adult water striders can leap over menisci, but to insects smaller than the capillary length \( \ell_c \).
these menisci appear as frictionless mountains. Insects have evolved an ingenious technique to ascend the menisci: by locking into a static body posture and deforming the free surface, the insect generates a lateral capillary force that draws it up the mensicus. In Chapter 3 we observed that the insect’s wetting properties provide a natural distinction between meniscus climbers. Wetting climbers, such as the terrestrial *Pyrrhalta* and *Stenus*, are circumscribed by a contact line and deform the surface by arching their backs (Figure 3-21). Non-wetting climbers such as *Mesovelia* and *Hydrometra* possess retractable wetting claws that they use to deform the free surface (Figure 3-24). Before we proceed to a discussion of the propulsion of wetting and non-wetting climbers, we first review the literature on capillary forces between floating bodies.

Capillary forces have been studied extensively in the context of floating particles and are well understood. A comprehensive review is presented by Kralchevsky & Denkov (2001). Physically, floating particles attract because the sum of the surface and gravitational potential energies of the fluid and the particles decrease when the particles approach one another. These energies and the resulting attractive force can be written explicitly for floating points, rods and spheres. Nicolson (1949) was the first to analyze the interactions between floating particles and found an expression for the force between floating bubbles with small Bond number. Gifford & Scriven (1971) computed numerically the force between floating rods. Chan *et al.* (1981) extended the work of Nicolson to find approximate expressions for the attractive force between pairs of floating horizontal cylinders and spheres with small Bond number. Kralchevsky *et al.* (1992) determined the force between pairs of vertical cylinders and spheres; their work is summarized in Kralchevsky (2001). The importance of capillary forces in tessellation and self-assembly of floating bodies is described by Whitesides & Grzybowski (2002).

6.1.1 Wetting climbers

By considering energetics we can gain insight into the meniscus-climbing mechanism. By arching its back to match the curvature of the meniscus, the larva of *Pyrrhalta* may generate a lateral force that drives it up the meniscus. At high Reynolds number, low Weber and Bond number, the conservation of energy for the system is given by substituting $u = 0$ into
Figure 6-1: Schematic of the meniscus-climbing larva *Pyrrhalta*. By arching its back to match the curvature of the meniscus, the beetle will ascend the meniscus if the anomalous surface energy generated by the surface deformations 1 and 2 exceed the gravitational energy of the larva at the top of the slope.

(2.58) and integrating with respect to time,

\[ C = \frac{1}{2} MU^2 + \Delta Mgz + \sigma A \]  

where \( C \) is a constant given by the insect’s energy input to the system, i.e. from initial kinetic energy.

Consider an insect attempting to run and slide up the meniscus. Here the energy at the beginning is given by the kinetic energy of the creature at the bottom, \( \frac{1}{2} MU^2 \). The creature would need to achieve a speed so that its kinetic energy exceeds the required gravitational potential energy: the insect needs to exceed a capillary escape velocity \( \sqrt{2gH} \approx 27 \text{ cm/s} \). This speed is within reach of adult water striders and spiders which can row up or jump over menisci. However, smaller water-walking insects cannot attain that speed; instead they use a capillary propulsion technique to be described in what follows.

Consider that an insect at the bottom of the meniscus generates anomalous surface energy through deforming the interface. The corresponding energy of the system may be written

\[ E_1 = \sigma(\Delta A_1 + \Delta A_2) \]  

where \( \Delta A_1 \) and \( \Delta A_2 \) are the change in fluid surface area in back and front of the insect respectively (Figure 6-1). Since the creature arches its back to match the curvature of the meniscus, the system at its end state contains no anomalous surface energy. Consequently, the larva of mass \( M \) will be pulled forward if the anomalous surface energy it generates exceeds the insect’s gravitational potential energy \( MgH \) at the meniscus’ apex (Figure 6-1).
6.1.2 Non-wetting climbers

Non-wetting insects can also deform the free surface to climb, but since they have many legs, we must consider carefully the torque and force balances on the body. Here we derive the governing equations for a six-legged non-wetting insect climbing the meniscus.

Consider an insect with six legs that can apply forces normal to the free surface, as shown in Figure 6-2. Let the forces applied by the insect be $\vec{F} = [F_{1L} \ F_{2L} \ F_{3L} \ F_{1R} \ F_{2R} \ F_{3R}]$ where the subscript $ij$ denotes the $i$th leg ($i = 1, 2, 3$) on the $j$th side where $j = L$ for left and $R$ for right. We use the convention $F > 0$ to mean the insect pulls up; $F < 0$ means the insect pushes down on the free surface. Consider a frame of reference in which the insect’s center of mass is taken to be the origin and it is attempting to climb in the $x$-direction.

Let the $(x, y)$ coordinates of the leg tips be $(L_{ij,x} \ L_{ij,y})$. The motion of the insect has six degrees of freedom, translation in the $x, y, z$ directions and rotation (yaw, pitch, roll) around the $x, y, z$ axes. The translational and angular accelerations of the insect are specified by force and torque balances. The force balances are

\[
M \frac{d^2 x_0}{dt^2} = -B(F_{ij}, L_{ij}) \cot \theta \cos \psi(x_0)e^{-x_0/\ell_c} + Mg \sin \psi(x_0) 
\]

\[
M \frac{d^2 y_0}{dt^2} = 0 
\]

\[
M \frac{d^2 z_0}{dt^2} = \cos \psi(x_0) \sum_{i=1,2,3} F_{ij} - Mg 
\]

where the term

\[
B(F_i, L_i) = \sum_{i=1,2,3}^{j=L,R} F_{ij} e^{L_{ij}/\ell_c} 
\]
Figure 6-3: Schematic illustration of the meniscus-climbing *Mesovelia*: it pulls up with its wetting front and hind claws, and pushes down with its middle legs. \( \mathbf{n} \) denotes the normal to the undeformed meniscus, \( \eta(x) \), and \( x_0 \) the lateral position of the insect’s center of mass. 

represents the net capillary force. The torque balances around the \( x, y \) and \( z \) axes are

\[
\begin{align*}
I_{xx} \frac{d\omega_x}{dt} &= \sum_{i=1,2,3} \sum_{j=L,R} F_{ij} L_{ij,y} \\
I_{yy} \frac{d\omega_y}{dt} &= \sum_{i=1,2,3} \sum_{j=L,R} F_{ij} L_{ij,x} \\
I_{zz} \frac{d\omega_z}{dt} &= \sum_{i=1,2,3} \sum_{j=L,R} \cos \psi(x_0) \cot \theta F_{ij} e^{L_{ij,x}/\ell_c} L_{ij,y}
\end{align*}
\]  

(6.8)

(6.9)

(6.10)

where \( I_{ii} \) is the moment of inertia in the \( i \)th direction and \( \omega_i \) is the angular velocity in the \( i \)th direction. These six equations of motion govern the translation and rotation of an insect propelling itself by surface deformation in the vicinity of a meniscus. Note that these equations are only valid when the slope of the meniscus is small.

6.1.3 Application to the meniscus-climbing *Mesovelia*

In §3.2.6 we described the meniscus-climbing *Mesovelia*. *Mesovelia* assumes a posture that is symmetric across the \( xz \) plane (Figure 6-3); each of its front and rear tarsi pull up with forces \( F_1 \) and \( F_3 \) at horizontal positions \( x_0 - L_1 \) and \( x_0 + L_3 \), respectively; the middle tarsi push down with force \( F_2 \) at position \( x_0 + L_2 \). Substituting these values for the force and leg
position into equations (6.6) and (6.10), the normal force balance on the insect and torque balance about its middle leg are, respectively,

\[ 2F_2 = 2F_1 + 2F_3 + Mg \cos \psi(x_0) \]  \hspace{1cm} (6.11)  
\[ 2F_3L_3 = 2F_1L_1 - MgL_2 \cos \psi(x_0). \]  \hspace{1cm} (6.12)

The remaining torque balances (yaw and roll) are satisfied by symmetry of the forces applied. The acceleration of the insect is determined by the tangential force balance in (6.6), which may be written

\[ M \frac{d^2x_0}{dt^2} = -2B(F_i, L_i) \cot \theta \cos \psi(x_0)e^{-x_0/\ell_e} + Mg \sin \psi(x_0) \]  \hspace{1cm} (6.13)

where the second term represents the net capillary force and

\[ B(F_i, L_i) = F_1e^{L_1/\ell_e} - F_2e^{L_2/\ell_e} + F_3e^{-L_3/\ell_e}. \]  \hspace{1cm} (6.14)

For the insect to maximize \( B(F_i, L_i) \), it should extend pull up as hard it can with its front and legs, balance torques by pulling up in back and push down in the middle to support its weight. Since the leg positions are known from our experiments, we have four unknowns \((F_1, F_2, F_3, x_0)\) and three equations (two force balances and torque balance). We can solve for the position of the insect \(x_0\) using a single free parameter, \(F_1\), the force applied by the first leg. Note that we have neglected drag on the insect in our description of Mesovelia’s propulsion. Ultimately, one expects a balance to be acheived in which capillary thrust is balanced by hydrodynamic drag; however our experiments indicate that the insects are accelerating throughout the meniscus-climbing, which suggests that drag is indeed negligible.

Figure 6-4 shows the observed trajectories of a Mesovelia of length 2 mm and weight 0.2 dynes. Accompanying theoretical trajectories were obtained by numerically integrating equation (6.13). The insect’s position and leg configuration were recorded from high-speed video; the insect’s weight and the meniscus contact angle on plexiglass (40°) were measured using a scale and a still camera, respectively. Given the leg position and meniscus contact angle, there is a single unknown in the model, \(F_1\). For Mesovelia, \(F_1\) was inferred from the trajectory to be 3 dynes, a value consistent with the maximum force the front leg tip of diameter \(w \sim 0.02\) cm can apply to the free surface without breaking through, \(F_1 \sim \pi w \sigma\).
Figure 6-4: Observed evolution of insect speed during the ascent of menisci. Insects are *Mesovelia* (A, circles), *Hydrometra* (B, triangles; Andersen 1976) and the *Pyrrhalta* larva (C, squares). Circles around the insects’ feet indicate the sense of the surface deflection: white upwards and black downwards. Theoretical predictions based on (6.13) are presented as dashed lines. Inferred forces $F_1$ applied by the frontmost appendage are given in dynes. The sensitivity of the theoretical trajectories to $F_1$ are indicated for the beetle larva trajectory. For the *Hydrometra* data (Andersen 1976), the best-fit trajectory yielded the net capillary force, from which the individual $F_i$ values were calculated. We assumed the meniscus contact angle to be $40^\circ$, comparable to the contact angle of water on plexiglass, and then inferred the net capillary force by optimally fitting the observed trajectory. The individual forces $F_i$ applied by the insect were then calculated by consideration of the four governing equations (the normal force balance (6.6) and three torque balances, (6.10)) and the upper bounds on the forces applied by each leg. The error bars (shown for one point but applicable to every data point) reflect the uncertainty associated with measuring the body position.
The corresponding $F_2$ is comparable to the maximum force, $2\sigma L$, the insect leg can apply without breaking through with the tarsal segment, of length $L$, of its middle leg (inset A, Figure 6-4). The trajectory of the beetle larvae, of length 6 mm and weight 150 dynes, was similarly computed via (6.13), by setting $F_2 = 0$. Once again, the single unknown in modeling the beetle larva’s ascent is $F_1$, which is equal to $F_3$ by symmetry; the best fit is obtained with a force of 20 dynes that corresponds to the maximum surface tension force it can generate with its frontal perimeter of 3 mm. The sensitivity of the predicted trajectory to $F_1$ is shown in Figure 6-4.

The climbing trajectory for the tilting climber *Hydrometra*, a water-walker of length 1.14 cm and weight 1.8 dynes, reported by Andersen (1976) is also presented. An accompanying theoretical trajectory was computed from the reported leg positions and inferred values of $\theta$ and the net capillary force. We assumed the meniscus contact angle to be 40°, comparable to the contact angle of water on plexiglass, the material most likely used in Andersen’s experiments, and then inferred the net capillary force by optimally fitting the observed trajectory. The individual forces $F_i$ applied by the insect were then calculated by consideration of the four equations (the normal force balance in Equation (6.6) and three torque balances in Equation (6.10)) and the upper bounds for the forces applied by each leg. We infer applied forces comparable in magnitude to the insect’s weight.

### 6.2 Marangoni propulsion

In our experiments in §3.2.5 we observed *Microvelia* propelling itself by secreting surfactants. In this section we rationalize the peak speeds achieved. We begin by examining the evolution of the surfactant that generate the wakes of *Mesovelia* revealed by flow visualization. We proceed by examining the insect’s peak speed and the communication of Marangoni stresses across the insect’s hair layer.

#### 6.2.1 Evolution of surfactant

Increasing the concentration of surfactants on the surface of a fluid decreases the surface tension until the surfactant has saturated the surface. The generic relation between the concentration of an insoluble surfactant and the surface tension is given by Frumkin’s equa-
Figure 6-5: The Marangoni swimmer *Microvelia*. a, Side view. Inset shows the dense hair covering on its leg. b, The tongue-like structure protruding from the rostrum that releases surfactants on the free surface. c, A close-up of the tongue.

\[ \sigma_0 - \sigma = -C \log \left(1 - \frac{\Gamma_2}{\Gamma_m}\right), \]  

(6.15)

where \(\sigma_0\) is the surface tension of the clean interface and \(\Gamma_m\) and \(\Gamma_2\) are the surface concentration of the surfactant and the saturation concentration respectively. The constant \(C = 2.3RT\Gamma_m\) where \(R\) is the gas constant and \(T\) the temperature of the fluid. The evolution of the surfactant is prescribed by (Stone 1989)

\[ \frac{\partial \Gamma}{\partial t} + \nabla_s \cdot (\Gamma \mathbf{u}_s) + \Gamma (\nabla_s \cdot \mathbf{n})(\mathbf{u} \cdot \mathbf{n}) = D \nabla_s^2 \Gamma \]  

(6.16)

where \(\nabla_s = (I - \mathbf{n} \mathbf{n}) \cdot \nabla\) is the surface gradient operator, \(\mathbf{u}_s = (I - \mathbf{n} \mathbf{n}) \cdot \mathbf{u}\) is the velocity along the surface, and \(D\) is the diffusion coefficient. Equation (6.16) accounts for the transport of surfactant in terms of diffusion and convection in directions tangential and normal to the surface. Experiments conducted by Schildknecht (1976) and verified by ourselves (§3.2.5) indicate that the surfactant ejected by *Microvelia* is insoluble or weakly insoluble in water. Over the time scale of the propulsion, diffusion of \(\Gamma\) may thus be neglected.

### 6.2.2 Dynamics

*Microvelia* is covered with a dense mat of hairs and rests atop the surface on six hairy legs. The leg can be considered as a two-dimensional array of cylindrical hairs vertically penetrating the water surface (Figure 3-16a). Each hair has a radius \(R\) and a contact angle \(\theta\) with the fluid. The surface tension force on a single cylindrical hair centered at the origin
Figure 6-6: A schematic illustration of the array of hairs on a water-walking insect leg. a) Top view of array of vertical hairs. There is a gradient of surface tension in the x-direction. b) Side view of a single hair from the array in a) resting on the surface. The hair has a contact line C and contact angle $\theta$.

(Figure 3-16b) is

$$ F_{s,\text{hair}} = \int_C \sigma(x, y) \ t \ d\ell $$  \hspace{1cm} (6.17)

If the insect is being propelled in the $x$ direction, we can reasonably assume that on the lengthscale of a single hair, the surface tension varies slowly in the $x$-direction. Therefore we approximate $\sigma$ with a Taylor’s expansion at $x=0$, $\sigma(x) = \sigma_0 + \frac{d\sigma}{dx}|_0 x + O(x^2)$. Using cylindrical coordinates $(r, \phi, z)$ in which $d\ell = Rd\phi$, the tangent $t = \cos \theta \hat{r} + \sin \theta \hat{z}$, the radial unit vector $\hat{r} = \cos \phi \hat{x} + \sin \phi \hat{y}$ and $x = R \cos \phi$ we find that the resultant surface tension force on the hair is

$$ F_{s,\text{hair}} = 2\pi R \sigma_0 \sin \theta \hat{z} + \pi R^2 \frac{d\sigma}{dx}|_0 \cos \theta \hat{x}, $$  \hspace{1cm} (6.18)

with a lateral component

$$ F_{s,\text{hair}} \cdot \hat{x} = \pi R^2 \frac{d\sigma}{dx}|_0 \cos \theta, $$  \hspace{1cm} (6.19)

The above equation states that the net Marangoni force is proportional to the gradient in surface tension and the area of the hair. The Marangoni force on an array of hairs is thus proportional to the area fraction of the hairs in contact with the surface. The Marangoni force on a Marangoni swimmers can be written

$$ F_s \cdot \hat{x} = f A \frac{d\sigma}{dx}|_0 \cos \theta, $$  \hspace{1cm} (6.20)
where $f$ is the area fraction consisting of the hairs in contact with the surface and $A$ is the area of the insect’s legs.

The propulsive force on a Marangoni swimmer thus scales as $F_s \sim f \Delta \sigma / LA$ where $L$ is the body size, $A$ is the leg contact area and $\Delta \sigma$ is the maximum change in surface tension by the surfactant. A Microvelia with $L = 1 \text{mm}$, $A = 0.1 \text{mm}^2$ and a mass of $M = 10^{-3} \text{g}$ has an acceleration of 150 cm/s$^2$, found using high speed video. Using measurements of $\Delta \sigma = 20 \text{dynes/cm}$ (Schildknecht 1976) and the area fraction $f = 0.03$ (Gao & Jiang 2004), we obtain $F_s \approx 0.1 \text{dynes}$ and $M \dot{U} \approx 0.2 \text{dynes}$ and therefore the insect motion satisfies Newton’s law, $F = M \dot{U}$. This result suggests that accounting for the Marangoni force on the insect requires consideration of the details of its hair covering.
Chapter 7

Concluding Remarks

“There who dwell, as scientists or laymen, among the beauties and mysteries of the earth are never alone or weary of life.”

–Rachel Carson, author of Silent Spring (1965)

7.1 Conclusions

We have reported the results of a combined experimental and theoretical study of water-walking arthropods. In Chapter 2, we conducted a formal fluid mechanical treatment of locomotion on the water surface that provided the foundations from which we developed our understanding of water-walking insects. We derived relations for the transfer of force, momentum and energy between the insect and its environment. These equations were nondimensionalized, so that the relative magnitudes of their various components could be assessed.

In Chapter 3, we presented the results of an experimental study of water-walking arthropods. Here we collected a large volume of dynamical data not previously found in the literature that characterize the five main types of motion: surface-slapping, rowing, galloping, meniscus-climbing and Marangoni propulsion. Each of these modes of propulsion use different components of the hydrodynamic force, that are enumerated in Table 7-1. Large surface-slapping creatures are propelled by a combination of buoyancy, added mass and form drag on their driving leg. Insects and spiders move by an alternating tripod gait, rowing or galloping; in each, the dominant hydrodynamic force is from some combination of curvature
Figure 7-1: The dynamic classification of water-walkers. Large water-walkers, such as the basilisk lizard (a), rely on a combination of form drag, added mass and gravitational forces generated by vigorous slapping of the free surface for both weight support and propulsion. Water-walking insects and spiders rely on surface tension for weight support. Propulsive forces for most insects, such as the water strider (b), are generated by some combination of form drag and curvature forces. Others may propel themselves using capillary forces (e.g. (c) the beetle larvae) or Marangoni stresses (e.g. (d) Mesovelia). Figure (a) courtesy of Hsieh (2004).
forces and form drag on the driving leg. Meniscus-climbing is performed by the creature holding a static posture in which it deforms the free surface in the presence of another meniscus; the capillary forces drive the creature forward. A creature uses Marangoni propulsion by secreting surfactants that propel the creature by gradients in surface tension. The first flow visualization studies of water-walking arthropods were conducted, demonstrating that many water-walking insects generate coherent vortices that transport momentum in their wake.

In Chapter 4, we rationalized the different modes of propulsion by determining the relative magnitudes of the components of the hydrodynamic force in each. Water-walkers were found to be predominantly high Reynolds number and so to rely on inertial rather than viscous forces. We found that most water-walking arthropods rely on a combination of surface tension-induced curvature forces and dynamic pressure, $\rho U^2$ for propulsion. The relative magnitudes of the form drag and curvature force in resisting the leg is prescribed by the Weber number. The smallest water-walking insects propel themselves predominantly using surface tension forces. The larger water-walking insects generate thrust using both surface tension and dynamic pressure. Our study also demonstrates that water-walkers satisfy Froude's law of equivalence of Velocities, $U \sim L^{1/2}$, a dependence known to be satisfied by birds and fish but whose validity for water-walkers had not previously been demonstrated.

In Chapter 5, we provided a new physical picture for the motion of water striders: striders propel themselves by transferring momentum in the form of vortices. We thus conclude that capillary waves do not play an essential role in the propulsion of water striders, and thereby circumvent Denny’s paradox. The water strider generates thrust by rowing, using its legs as oars and its menisci as blades. As in the case of row boats, while waves are an inevitable consequence of the rowing action, they do not play a significant role in the momentum transfer necessary for propulsion. Our experimental study suggests that this new physical picture of rowing with menisci is relevant to many other water-walking insects. Finally we also describe the design of a mechanical water strider that is roughly analogous to its natural counterpart.

In Chapter 6, we rationalized two quasi-static propulsion mechanisms: meniscus-climbing and Marangoni propulsion. Meniscus climbing is a novel means of propulsion in that the insect propels itself in a quasi-static configuration, without moving its appendages. Using
energetics, we derived equations of motion for wetting and non-wetting meniscus-climbers and predict trajectories consistent with those observed. Biolocomotion is generally characterized by the transfer of muscular strain energy to the kinetic and gravitational potential energy of the creature, and the kinetic energy of the suspending fluid (Dickinson et al. 2000). We note that the energy pathway for meniscus-climbing is unique: through deforming the free surface, the insect converts muscular strain to the surface energy that powers its ascent. We also examined Marangoni propulsion, in which insects discharge surfactant in order to move. We rationalized the speeds observed in Marangoni propulsion by considering the precise manner in which Marangoni forces are communicated across the insect’s hair layer.

7.2 Discussion

Paradoxes in biolocomotion are of the general form “X cannot move as observed” and are useful because they clearly demarcate the limits of our understanding of locomotion. Nearly all past paradoxes (e.g. concerning bees, pigeons, dolphins and water striders) were based on the calculations of the steady force on the body; unsteady thrust mechanisms are now known to be ubiquitous in locomotion in all media (Dickinson et al. 2000). The Bumblebee Paradox (1930), the result of an anonymous engineer’s back of the envelope scaling argument, states that the bee’s wings are too small to generate sufficient power to fly (Rayner 1990). The initial calculation was performed using steady-state conditions, but recent work has identified unsteady flow mechanisms that account for the necessary lift (Ellington 1990, Dickinson et al. 1999). Gray’s Paradox (1936) was the finding that a dolphin requires only 1/7 the power to propel a rigid model of its body at the same speed (Gray 1936). It is now known that Gray’s calculation was in error for two reasons. First, Gray underestimated the power output of dolphins. Second, dolphin skin is thought to have a drag-reducing property (Bechert et al. 2000, Bushnell & Moore 1991).

One method of resolving such paradoxes has been through examination of the momentum transfer in the creature’s wake, which provides an alternative means by which to rationalize its propulsion. The Momentum Wake Paradox (of pigeons) stated that pigeons do not transfer sufficient momentum to be able to fly. It was based on the assumptions that pigeons transferred momentum in large ring vortices (Spedding et al. 1984). Spedding et al. (2003) resolved the paradox by repeating his momentum calculations and including the dif-
fuse patches of vorticity over the entire wake. Similarly, Denny’s paradox was based on the assumption that water striders transferred momentum exclusively in surface waves (Denny 1993, 2004); we resolved the paradox in Chapter 5 by demonstrating that, conversely, water striders transfer momentum principally in vortices.

Our investigation has been confined to a discussion of various modes of propulsion at the interface. Consideration of the broader role of capillary effects in surface-dwelling insects raises countless new questions. For example, both waves and Marangoni effects are used for communication at the free surface. While generally an inevitable consequence of their motion at the surface, a number of creatures use waves more creatively. The whirligig beetle is preceded by a field of capillary waves that enable it to locate prey via echolocation (Tucker 1969). The male water strider generates surface wave signals with frequency 80-90 Hz in order to identify its sex to prospective partners, thus eliminating the need for visual contact (Wilcox 1979). The fisher spider can detect its prey by way of the waves generated as it struggles to free itself from the interface (Bleckmann 1985). Perhaps more remarkable still is the snail that swims inverted on the free surface (Figure 7-2c; Brocher 1910). By using its cilia to shake the free surface at a particular frequency, the apple snail generates waves that focus the surface nutrients into a line that sinks in a concentrated plume-like form more readily collected (Estebenet 1995). The flatworm also propels itself using cilia on solid and free surfaces.

![Figure 7-2: A freshwater snail propelling itself inverted beneath the water surface.](image)

Surfactant has been shown to play a role in sexual attraction for certain water-walking arthropods. The male fisher spider finds females by following the pheromone-rich trail left in their wake (Roland & Rovner 1983). Andersen & Cheng (2004) have demonstrated that certain male water-walking insects eject a small volume of lipids containing pheromones that spreads at a characteristic rate of 10cm/s, and serves to attract females. The use of similar chemical signaling in the sea-faring water strider has been examined by Tsoukatou et al. (2001), and proposed as a means by which adults find one another to mate in the open.
ocean. Subsequent work by Petrakis et al. (2003) has been directed towards determining the precise chemistry of the ejecta. The possibility that the surfactant might serve to suppress the waves (Christensen 2005) resulting from their coupling and so stabilize mating has not been discussed.

The crucial role of the water-walking insect’s hair layer in the dynamics is just now being considered. We have seen that some non-wetting insects are able to survive dunkings by virtue of the plastron that accompanies them when they are submerged. In §2.1 we noted that maintenance of the plastron by the hair layer is necessary for the insect to remain non-wetting. Thorpe & Crisp (1947) showed that the plastron may be ruptured by hydrostatic pressure if the insect dives below a critical depth. In §2.1, we demonstrate that the plastron is maintained during the driving stroke by showing that the surface Weber number based on the hair density remains less than unity. Moreover, we found that faster water-walkers have a relatively fine hair layer as is required to resist wetting the presence of high dynamic pressures.

The hair layer may also play a role in the communication of forces between the water-walker and the fluid. In §6.2 we have shown that propulsive Marangoni stresses are transferred to the creature only through the contact of the hair with the fluid. Since the hair layer of the leg consists of mostly air pockets (93% by area, according to Gao & Jiang 2004), the resultant Marangoni stress on the creature is reduced accordingly. Further consideration of the dynamics of the hair will require consideration of its elastic properties and the configuration of hairs, the latter already having been measured using scanning electron micrographs by Andersen (1976). Addressing the role of the hair layer in the transfer of skin friction stresses would also be a useful undertaking, whose result might find industrial applications.

What role do the wetting properties have in their stability? Some water-walking insects have variable wetting properties that contribute critically to their stability on the surface (e.g. Anurida), or enable them to ascend menisci, or leap vertically off the free surface. While much work has been done on the static stability of floating bodies (e.g. Erdos et al. 1992), it would be valuable to consider the influence of variable wetting properties on the static and dynamic stability of floating bodies small relative to the capillary length.

Several constraints on the size of water-walker have been posed. We saw that one constraint on the maximum size of water-walking insects is the insect’s static support on
the water surface. Baudoin (1955) stated that the minimum size of a water-walking insect is determined by the requirement that the creature be able to manipulate the free surface (§1.1). Denny (2004) suggested that an additional constraint on the minimum size of water striders is given by consideration of their momentum transfer through vortices. Specifically, in order to generate vortices, the strider’s driving leg must have an associated Reynolds number of at least $UL/\nu = 100$ and therefore a minimum leg length $L$ and leg speed $U$ prescribed by $UL \geq 100\nu$. Using the infant water strider’s leg speed $U = 23$ cm/s we require that the smallest water strider have a leg length $L \geq 0.5$ mm, that is roughly consistent with the infant strider’s leg length of 1 mm. However, the result cannot be applied to water-walking insects in general. As we saw in our experiments in §3.2.1, water-walking insects need not transfer vortices in order to move (e.g. Microvelia). Novotny & Wilson (1997) state a constraint on the minimum size of insects based on their drinking through their probiscis. An insect can only eat using a proboscis if the sucking pressure the insect can generate exceeds the pressure drop through the proboscis, which is determined by the radius of the proboscis.

As engineers become ever more interested in the manufacture of micro- and nanoscale devices that operate at scales dominated by capillary effects, much may be learned from the natural world. It is noteworthy that the same physical mechanism employed by meniscus-climbing insects, specifically capillary attraction between floating bodies, has been used as a means of creating self-assembling structures on a micro- and nanoscale (Whitesides & Grzybowski 2002). Biomimetics, the development of machines based on living organisms, may now draw upon new lightweight materials and advances in robotics, and seems poised to move into the world of water-walkers. The first water-walking robots, designed to mimic the water strider (§5.4; Sitti 2005), have recently been constructed.

Suter et al. (1997) have presented the important physical picture of water-walking insects using their menisci as blades. While one expects the integrity of the meniscus to be maintained provided $We < 1$, it would be valuable to develop a theoretical rationale for the dependence of the hydrodynamic drag on $Re$ and $We$ reported by Suter et al. (1997). While we have here attempted to assess the relative magnitudes of the force components acting on the driving legs of water-walkers via simple scaling arguments, the problem is a complex one that deserves more rigorous treatment. How precisely is momentum transferred across the interface, and how are vortices shed by water-walkers? It seems clear that the mech-
anism is quite different for creatures large and small, in the latter case being dominated by surface tension. Is the maneuverability of water-walkers influenced by the details of the vortex shedding, as is the case for fish (Triantafyllou et al. 2000)?

It is hoped that this investigation has raised a number of fundamental fluid mechanics problems arising through the consideration of water-walking creatures, to date left largely unexplored by fluid dynamicists. In this thesis, we have applied modern technology (specifically, digital photography) towards understanding mechanisms of surface propulsion that evolved millions of years ago. In the words of F.S. Fitzgerald (1922), “So we beat on, boats against the current, borne back ceaselessly into the past.”
Appendix A

Wave momentum

Figure A-1: Schematic of the waves generated by the water strider’s driving stroke. We consider the linear wave packet generated by a single leg stroke: $\zeta(x, t) = Ae^{-|x-c_gt/L_e|}e^{i(kx-\omega t)}$ propagating in the $x$-direction with a group speed $c_g = \frac{d\omega}{dk}$, lateral extent $W$, and amplitude that decays with $|x-c_gt|$ over a distance $L_e$ corresponding to the envelope length.

We shall apply the momentum flux theorem (Newman 1977) to calculate the time-averaged momentum flux of a surface wave propagating in a fluid of finite depth (Figure A-1). The control volume is considered two-dimensional and the bottom rigid. The volume $V$ is taken to be a fixed volume whose sides are vertical. Let $S$ be the free surface, $S^+$ and $S^-$ be the vertical sides, without loss of generality assume a unidirectional wave propagates in the $x$-direction and $S^-$ is at $x = 0$ and $S^+$ is at $x = L > 0$. There is no flux across the surface or the rigid bottom, and hence $u \cdot n = 0$ there. Assuming high Reynolds number, the momentum flux theorem states that the rate of change of horizontal momentum $L_x$ (per
unit distance in the y-direction) is

\[ \frac{dL_x}{dt} = -\int_{S^+} - (p \mathbf{n} \cdot \hat{x} + \rho (\mathbf{u} \cdot \hat{x}) (\mathbf{u} \cdot \mathbf{n})) \, dS + \int_S \sigma_{xx} (\mathbf{n} \cdot \hat{x}) \, dS \]

where for linear waves, \( \nabla \cdot \mathbf{n} \approx \zeta_{xx} \) has been used. On \( S^\pm \), \( \mathbf{n} = \pm \hat{x} \). On \( S \), \( \mathbf{n} \cdot \hat{x} = -\zeta_x \).

Thus

\[ \int_S \sigma_{xx} (\mathbf{n} \cdot \hat{x}) \, dS = -\int_0^L \sigma_{xx} \zeta_x dx = \frac{\sigma}{2} (\zeta_x^2 (0, t) - \zeta_x^2 (L, t)) \]

and

\[ \frac{dL_x}{dt} = \int_{-H}^{\zeta(0, t)} (p + \rho g z + \rho u^2)_{x=0} \, dz - \int_{-H}^{\zeta(L, t)} (p + \rho g z + \rho u^2)_{x=L} \, dz + \frac{\sigma}{2} (\zeta_x^2 (0, t) - \zeta_x^2 (L, t)) \]

From Bernoulli’s equation, \( p = -\rho (g z + \phi_t + \frac{1}{2} u^2 + \frac{1}{2} w^2) \), and hence

\[ \frac{dL_x}{dt} = \rho \int_{-H}^{\zeta(0, t)} (-g z - \phi_t - \frac{1}{2} w^2 + \frac{1}{2} u^2)_{x=0} \, dz - \rho \int_{-H}^{\zeta(L, t)} (-g z - \phi_t - \frac{1}{2} w^2 + \frac{1}{2} u^2)_{x=L} \, dz + \frac{\sigma}{2} (\zeta_x^2 (0, t) - \zeta_x^2 (L, t)) \]

Let the wave amplitude at \( x = 0 \) be \( A^+ \) and that at \( x = L \) be \( A^- \). We assume the waves have mild slope and only retain the leading order of \( A^\pm (O(A^2)) \). Denoting the time average over a wave period as horizontal bars, we note that since \( \phi \) is periodic, \( \bar{\phi}_t = 0 \).

Then the mean horizontal momentum flux is

\[ \bar{L}_x = \frac{\rho \int_{-H}^{0} (-g z - \phi_t - \frac{1}{2} w^2 + \frac{1}{2} u^2)_{x=0} \, dz - \rho \int_{-H}^{0} (-g z - \phi_t - \frac{1}{2} w^2 + \frac{1}{2} u^2)_{x=L} \, dz}{\rho \int_{-H}^{\zeta(0, t)} (g z + \phi_t)_{x=0} \, dz + \rho \int_{-H}^{\zeta(L, t)} (g z + \phi_t)_{x=L} \, dz + O(A^3)} \]

\[ = \frac{\rho}{2} \int_{-H}^{0} (-g z - w^2 + u^2)_{x=0} \, dz - \frac{\rho}{2} \int_{-H}^{0} (-g z - w^2 + u^2)_{x=L} \, dz \]

\[ - \frac{g}{2} \zeta_x^2 (0, t) + \rho \zeta (0, t) (\phi_t)_{x=0, z=0} + \frac{g}{2} \zeta_x^2 (L, t) + \rho \zeta (L, t) (\phi_t)_{x=L, z=0} \]

\[ + \frac{\sigma}{2} (\zeta_x^2 (0, t) - \zeta_x^2 (L, t)) + O(A^3) \quad (A.1) \]

At leading order, the velocity potential and surface elevation for surface waves in water
of finite depth $H$ is given by

$$\phi^{(0)} = \frac{gA \cosh k (z + H)}{\omega \cosh kH} \sin (kx - \omega t), \quad (A.2)$$

$$\eta^{(0)} = A \cos (kx - \omega t). \quad (A.3)$$

The depth $H$ and wavenumber $k$ are assumed constant (flat bottom) but the amplitude $A$ can vary over long distances and times (in a multiple scales setup). The horizontal and

vertical components of velocity are

$$u^{(0)} = \phi^{(0)}_x = \frac{gkA \cosh k (z + H)}{\omega \cosh kH} \cos (kx - \omega t), \quad (A.4)$$

$$w^{(0)} = \phi^{(0)}_z = \frac{gkA \sinh k (z + H)}{\omega \cosh kH} \sin (kx - \omega t) \quad (A.5)$$

From (A.4) and (A.5), we have

$$\frac{(u^{(0)})^2}{2} = \frac{1}{2} \left( \frac{gkA \cosh k (z + H)}{\omega \cosh kH} \right)^2$$

$$\frac{(w^{(0)})^2}{2} = \frac{1}{2} \left( \frac{gkA \sinh k (z + H)}{\omega \cosh kH} \right)^2$$

Since $\cosh^2 x - \sinh^2 x = 1$, we have

$$\frac{(u^{(0)})^2 - (w^{(0)})^2}{2} = \frac{1}{2} \left( \frac{gkA}{\omega \cosh kH} \right)^2 \left( \cosh^2 k(z + H) - \sinh^2 k(z + H) \right)$$

$$= \frac{1}{2} \left( \frac{gkA}{\omega \cosh kH} \right)^2 \left( (A^-)^2 - (A^+)^2 \right)$$

Let the wave amplitude at $x = 0$ be $A^-$ and that at $x = L$ be $A^+$. Then

$$\frac{\rho}{2} \int_{-H}^{0} \left( -gz - w^2 + u^2 \right)_{x=0} dz - \frac{\rho}{2} \int_{-H}^{0} \left( -gz - w^2 + u^2 \right)_{x=L} dz$$

$$= \frac{\rho H}{4} \left( \frac{gk}{\omega \cosh kH} \right)^2 \left( (A^-)^2 - (A^+)^2 \right)$$

$$= \frac{\rho gkH}{2 \sinh 2kH} \left( (A^-)^2 - (A^+)^2 \right) \quad (A.6)$$

since $\omega^2 = gk \tanh kH$. Note that in the deep water (short wave) case, $kH \to \infty$ and this
term vanishes. From (A.2) and (A.3), we have

\[(\phi_t)_{z=0} = -g\zeta, \quad \bar{\zeta}^2 = \frac{1}{2}A^2, \quad \bar{\zeta}_x^2 = \frac{1}{2}k^2A^2, \quad \overline{\zeta(\phi_t)_{z=0}} = -g\bar{\zeta}^2 = -\frac{g}{2}A^2 \quad (A.7)\]

Substituting (A.6) and (A.7) into (A.1) gives

\[
\mathcal{L}_x = \frac{\rho g k}{2 \sinh 2kH} \left( (A^-)^2 - (A^+)^2 \right) - \frac{g}{4} \left( (A^-)^2 - (A^+)^2 \right) + \frac{\rho g}{2} \left( (A^-)^2 - (A^+)^2 \right)
+ \frac{\sigma k^2}{4} \left( (A^-)^2 - (A^+)^2 \right) + O(A^3)
= \frac{1}{4} \left\{ \rho g \left( 1 + \frac{2kH}{\sinh 2kH} \right) + \sigma k^2 \right\} \left( (A^-)^2 - (A^+)^2 \right) + O(A^3)
\]

The classical gravity wave result is found by taking \(\sigma = 0\).

Consider a wave train propagating in the \(x\)-direction into quiescent water. Then \(A^- = A\), \(A^+ = 0\), and the mean \(x\)-directed momentum flux per unit distance in the \(y\)-direction is, at leading order,

\[
\mathcal{L}_x = \frac{1}{4} \left\{ \rho g \left( 1 + \frac{2kH}{\sinh 2kH} \right) + \sigma k^2 \right\} A^2
\]

If the water is deep, \(kH \gg 1\), this simplifies to

\[
\mathcal{L}_x = \frac{\rho g + \sigma k^2}{4} A^2
\]

The momentum of the waves is thus proportional to the square of the amplitude of the wave. Using our measurements of the wavenumber and amplitude from our high speed video experiments, we apply this result to calculate the momentum of the waves in the wake of the water strider (§5.2).
## Appendix B

### Technical details of the experimental equipment

Table B.1: Instruments used in this study.

<table>
<thead>
<tr>
<th>Item</th>
<th>Manufacturer</th>
<th>Technical name</th>
<th>Notes</th>
</tr>
</thead>
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<td>Sony</td>
<td>DSC-F707</td>
<td>Excellent value</td>
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<td>Digital still camera</td>
<td>Sony</td>
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<td>Excellent value</td>
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<td>Fiber Optic Illuminator</td>
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<td>Fiber-Lite Model 190</td>
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<tr>
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<td></td>
<td>Robostrider energy source</td>
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<tr>
<td>LightTracer</td>
<td>Artograph</td>
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<td>Vortex visualization</td>
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<tr>
<td>Digital light microscope</td>
<td>Boreal</td>
<td>SKope 3000100</td>
<td>Insect leg width</td>
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<td>Digital calipers</td>
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Table B.2: Chemicals used in this study.

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<td>AQ-1000</td>
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<td>Bacteriostatic Stabilizer</td>
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Table B.3: Software used in this study.

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Table B.4: Creatures and equipment for creatures used in this study.

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<td>flatworms</td>
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<td>Petco</td>
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<td>food for <em>Anurida</em></td>
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Appendix C

Flow visualization using tobacco mosaic virus

A flow visualization technique using dilute solutions of tobacco mosaic virus (TMV) is described. Rod-shaped TMV-particles align with the direction of shear stress, an effect that produces an interference pattern when the TMV solution is viewed between crossed polarizers. Attractive features of this technique are that it is both transparent to the naked eye and benign to fish; we use it here to visualize the evolution and decay of the flows that they produce. We also report that dilute solutions of Kalliroscope are birefringent and so may similarly be used for qualitative in situ flow visualizations.

C.1 Introduction

For many years, engineers have known that certain fluids and solids become temporarily birefringent (able to refract light in two different directions) when subjected to shear. This effect is best observed when the doubly refractive material is placed between crossed polarizers; the transmission of light then generates interference patterns in the regions of strongest shear stress. This so-called photoelastic technique has been used extensively for stress analysis in solids. An analogous technique to visualize fluid motion was developed by Maxwell (1873) and became the subject of intense study in the 1940’s. Reviews of these research efforts may be found in Prados & Peebles (1958) and Cerf & Scheraga (1952).

In 1915, Freundlich et al. used birefringence to ascertain the shape of particles in certain colloidal suspensions (Dieselhorst & Freundlich 1916; Freundlich 1926). Freundlich rational-
izes that anisotropic particles such as rod or disks will align with their long axis parallel to the direction of shear stress. A solution of such particles will be birefringent if the particle’s short axis is shorter than the wavelength of light and the particle’s refractive index differs from that of the surrounding solution. Moreover, rods are birefringent when the direction of incident light is perpendicular to the direction of the flow; disks are birefringent when the incident light is both parallel to the direction of the flow and parallel to the faces of the particles. Freundlich showed that birefringence may be achieved with several readily obtainable chemicals, including colloidal suspensions of vanadium pentoxide (Humphrey 1987), and aniline blue which provides rainbow-colored interference patterns.

Several investigators have extracted quantitative information from the interference patterns of birefringent solutions. Prados & Peebles (1958) develop a technique to determine the velocity distribution from the interference pattern in two-dimensional laminar flows around a cylinder. Binnie (1945) use birefringence as an indicator of turbulence in pipe flow; Alcock & Sadron (1935) use birefringence to determine the velocity distribution between two plates and between two rotating cylinders. Pindera & Krishnamurthy (1978) conducted a study using lasers and found that the intensity of the birefringence depends on the frequency of the transmitted light.

Birefringence was instrumental to Takahashi & Rawlins (1933), and later Bawden et al. (1936) in determining the structure of tobacco mosaic virus (TMV), the first virus to be identified as the agent of plant disease. Portrait photographers, Ramsey and Muspratt, used a suspension of TMV to visualize the boundary layer of a swimming goldfish (Bawden
et al. 1936). Fritz Goro, Time-Life science photographer from 1937-1978, also photographed a fish using TMV and published his pictures in 1941 (reprinted in Figure C-1 and Goreau et al. 1993), but did not report the details of his technique. We have redeveloped Goro’s unpublished experimental technique and describe it here so that it will be more widely accessible to workers in fluid mechanics and biolocomotion.

Current experimental techniques used to visualize the wakes of swimming creatures include dye methods, Schlieren, and digital particle image velocimetry (DPIV). The injection of dye such as fluorescein, thymol blue or ink (Merzkirch 1974) is an effective technique for visualizing the wake structure of creatures such as jellyfish (Dabiri et al. 2005) and squid (Bartol et al. 2001) that move by jetting, or such as water-walking insects that move by rowing on the free surface (Hu et al. 2003). Since fish are too uncooperative for the injection of dye streamers to be effective, McCutchen (1976) applied the Schleiren technique (reviewed by Fiedler & Nottmeyere 1985) to visualizing the structure of a fish’s wake. In the Schleiren technique, a fish swimming through a thermally stratified fluid disrupts the stratification; the corresponding changes in refractive index are revealed by shadowgraphic projection.

Quantitative measurements of a fluid’s velocity field generally require the use of DPIV technique, in which a fluid is seeded with micro-particles, a plane of which is illuminated by a laser light sheet. Particle-tracking algorithms applied to videos of the motion may provide three-dimensional flow trajectories. DPIV has been used to visualize the wake structure behind live creatures such as fish (Drucker and Lauder, 1999-2001), copepods (Stamhuis and Videler, 1995), jellyfish, birds and others. We here turn our attention to a relatively qualitative but simple flow technique.

C.2 Experiments

The experiments discussed here were conducted using the apparatus depicted in Figure C-2. The apparatus was used in a darkened room; lighting was provided by a 250-Watt tungsten-halogen lamp (Vision Research, Inc., North Star) directed at a white sheet of paper. The light was sent through a linearly polarizing film, 40 cm by 30 cm (Edmund Industrial Optics, Techspec). Top views of the fish motion were filmed in a petri dish (diameter 14 cm, depth 2 cm) filled with a dilute solution of TMV. A digital video recorder (Sony, DCR-TRV950) and digital still camera (Sony, DSC-F707), fitted with crossed polarizing filters (Crystal

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Figure C-2: The experimental apparatus. A dilute suspension of TMV is illuminated with polarized light, and viewed through a crossed polarizer. In setup (a), the TMV solution is viewed from the side; in setup (b), the TMV solution is viewed from above.

Vision, 58 mm and 37 mm) recorded the motion of the fish. Side views used a similar apparatus, but in a glass tank (length 30 cm, span 1.5 cm, water depth 10 cm) rather than a petri dish. Bubbles were visualized in a thin glass tank (length 30 cm, span 0.3 cm, water depth 10 cm).

A concentrated TMV solution was diluted to 0.4 ± 0.05 mg/mL using tap water. The TMV was obtained from Deutsche Sammlung von Mikroorganismen und Zellkulturen (DSMZ), where the TMV was filtered from the juices of tobacco plants infected with the virus. The solution was refrigerated at 5°C but warmed before experiments to the fish’s body temperature of 27°C. We note that the dilutions of TMV used were optimal for flow visualization: more dilute solutions did not effectively visualize flow, while larger concentrations substantially increased the fluid viscosity and so altered the dynamics. Between experiments, the TMV solutions was strained of debris using filter paper.

In Figure C-3a, the fish maintains a steady position in the fluid by flicking its fins, generating a luminous wake of vortices. The intake of fluid through the fish’s mouth is evident as a glowing white region. Figure C-3b shows the fish’s triangular turbulent wake, the size, shape, and orientation of flow within its vortices are made evident by the TMV. We note that the turbulent wake structure is reminiscent of that created by a point source of momentum; here, the momentum is provided unsteadily by the fish’s driving strokes. To
Figure C-3: Black neon tetra fish, body length 3.2 cm, in TMV solution. (a) Side view. The vortical motions generated by its motion and fluid intake at its mouth are evident. (b) Top view. Its roughly conical turbulent wake is evident. To decelerate, the fish extends its pectoral fins and blows a stopping vortex from its mouth. In (c), the vortical wake results from a relatively leisurely swim from left to right.

Figure C-4: Video sequence of fish in TMV solution. Frames are 0.15 second apart. Note the luminescent boundary layer adjoining the fish, which indicates the intense local shear.
Figure C-5: Bubbles rising in a solution of TMV, leaving a vortical wake corresponding to a classical Karman vortex street.

Figure C-6: Top view of fish in a dilute Kalliroscope solution between crossed polarizers. Its turbulent wake is again evident.
decelerate, the fish extends its pectoral fins and blows out a puff of fluid thus producing a vortex ring (at right in Figure 3b), a behavior first reported by McCutchen (1977). The TMV enables the elucidation of the evolution and decay of vortices generated during normal swimming as well as during starting and stopping. Figure C-3c shows the wake resulting from a relatively leisurely swim. Figure C-4 shows a video sequence of the fish flicking its caudal fin producing a vortical wake suggestive of the reverse Karman vortex street (e.g. Videler et al. 2004). We note that the fish’s shear boundary layer is evident in the form of a light strip adjoining its body surface. Finally, this method works equally well to reveal the Karman vortex street behind rising bubbles (Figure C-5).

We note that flow structure may alternatively be visualized using a sufficiently low dilution ($10^{-4}$ mg/mL) of Kalliroscope (a.k.a. Pearlescence) that they may be tolerated by fish (Figure C-6). Such low concentrations of Kalliroscope are invisible to the naked eye, but observations using crossed polarizers again reveal the fish’s vortical wake.

C.3 Discussion

Notwithstanding the value of DPIV, there remains a need for simple qualitative techniques that can safely visualize the flow around living creatures. DPIV does not directly visualize the flow. Instead, positional differences between large numbers of particles must be measured and their vectors computed to reveal the flow patterns. It is expensive computationally and the sensitivity is limited by the minimum amount of motion that can be detected, which is a function of the illumination, brightness of the particle reflection, and speed of the camera. As it is a differential rather than continuous method, it cannot always provide sufficient resolution in areas of extremely rapid, small scale, or spatially variable flow, for example in visualizing the capture of food by copepod zooplankton (J. R. Strickler, pers. comm.) or the flagellar swimming of dinoflagellates. The use of polarized light and TMV provides a qualitative alternative that can be filmed to reveal the flow directly and continuously without the need for computation. A number of questions concerning the motion of live fish are relatively difficult to answer using DPIV, but readily addressed with TMV. For instance, is the flow near the skin of a fish laminar or turbulent? TMV provides a way to visualize the flow very close to boundaries, where the use of relatively large suspended particles may be limited.
TMV flow visualization techniques, lost for 64 years, have the potential to provide a wealth of new imagery revealing subtle details of fluid flow patterns heretofore invisible or poorly visualized, which may shed valuable light on many biological problems including mechanisms of swimming, changes in modes of swimming, prey tracking, chemotaxis, prey capture, feeding in both motile and sessile marine organisms, and interactions between schooling organisms. A recent paper used DPIV on fluid flow around models of swift wings in a flume at different Reynolds numbers and angles of attack to reveal that lift, drag, and mobility were related to whether leading edge vortices were attached or separated (Videler et al. 2004). These could be directly imaged with TMV flow visualizations, as parameters are continuously altered to identify transition thresholds. High speed cinematography could be used to study the evolution and decay of short-lived vortices and their effects on propulsion, prey tracking, and prey capture.
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